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Cranial variation in Columbian white-tailed deer populations: implications for taxonomy and restoration

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Abstract.—We examined variation in 18 cranial dimensions among three disjunct populations of white-tailed deer (*Odocoileus virginianus*) in the Pacific Northwest to test the hypothesis that they represent a single taxon. Previous allozyme analyses indicated considerable variation among the three populations, but genetic divergences were less than conventional benchmarks used to distinguish subspecies. We observed substantial variation in cranial dimensions among the three populations that graphically sorted into three distinct morphological groups and corresponded with east-west and north-south geographical gradients. Specimens of the northwestern white-tailed deer (*O. v. ochrourus*) from northern Idaho had longer and broader skulls than did Columbian white-tailed deer (*O. v. leucurus*) from the lower Columbia River or southwestern Oregon; specimens from southwestern Oregon had shorter rostra and narrower crania than those from the lower Columbia River. Even after controlling for differences in size related to age or sex, specimens from southwestern Oregon were relatively smaller animals with shorter faces and narrower posterior portions of the skulls than specimens in the other populations. These results do not support the hypothesis that the three groups represent a single taxon, nor do the results support the current taxonomy. Sample sizes were insufficient to fully evaluate if designating the three populations as distinct subspecies is warranted. Still, the three populations show considerable morphological and genetic variation, remain disjunct and isolated from each other, and likely are evolving along different trajectories because of geographical variation in habitat.

The Columbian white-tailed deer (*Odocoileus virginianus leucurus* [Douglas, 1829]) is one of three currently recognized subspecies of *Odocoileus virginianus* (Zimmermann 1780) indigenous to the western United States (Smith 1991). Historically, Columbian white-tailed deer (CWTD) occurred throughout most of western Oregon and southwestern Washington lowlands, associated with riparian vegetation of broad river valleys (Douglas 1829, Smith 1985). Extensive development of western Oregon following European settlement led to extirpation of CWTD from most of its historic range, including the Willamette Valley of west-central Oregon (Smith 1985). Jewett (1914) and Bailey (1936) concluded that CWTD survived in the Willamette Valley until late in the 19th century. Today, its distribution is limited to two isolated popula-

Fig. 1. Historic (stippled areas) and current (open circles and cross-hatching) distributions of Columbian white-tailed deer, *Odocoileus virginianus leucurus* Douglas (Smith 1985, 1987), and current distribution of Northwestern white-tailed deer, *O. v. ochrourus* Bailey, in Oregon and Washington (Johnson and Cassidy 1997, Washington Department of Fish and Wildlife 2000, Oregon Department of Fish and Wildlife, unpubl. data). Note that the Umpqua River branches into the North and South Umpqua rivers.

tions: one along the lower Columbia River composed of several subpopulations that occur on several islands upriver from a Washington mainland subpopulation; and a second in the interior valleys of the Umpqua River in Douglas Co., Oregon (Fig. 1). The CWTD remains allopatric with the other two western subspecies; the nearest, northwestern white-tailed deer (*O. v. ochrourus* Bailey 1932), is about 300 km east of the current range of *O. v. leucurus* (see Smith 1985, 1991).

The limited distribution of CWTD and imminent threat to remaining habitat prompted the U.S. Department of the Interior, Fish and Wildlife Service (FWS) to list *O. v. leucurus* as endangered in 1967 in the Federal Register (32 FR 4001). The Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR) was established in 1972 and the Douglas Co. population was included in the listing in 1978 (Smith 1985). Since then, much effort has been expended toward recovery of the endangered populations, but the process has been slow and arduous (Doremus and Pagel 2001). The FWS developed a recovery plan with specific goals and measurable objectives, including information needs, to help the CWTDNWR and Douglas Co. populations recover (Columbian White-tailed Deer Recovery Team 1983). Numerous studies documented the status and provide information on the population ecology of CWTD (Gavin 1979, Suring & Vohs 1979, Dublin 1980, Gavin et al. 1984, Smith 1985, 1987; Ricca 2000, Whitney 2001), but little attention was given to the taxonomy or genetic integrity of CWTD populations (Gavin & May 1988).

The original taxonomic description of CWTD was based on specimens collected from near the mouth of the Columbia River and from the lower Willamette River [=falls at present-day Oregon City, Clackamas Co., OR] (Douglas 1829). Douglas (1914) reported CWTD throughout the central river bottomlands of western Oregon, perhaps as far south as the Umpqua River valleys (in what is now Douglas Co.). Crews (1939) extended the range south to Grants Pass, Josephine Co., Oregon. To our knowledge, however, the relationship between deer from Douglas Co. and deer from the region of the type locality was never rigorously examined. When Bailey (1932) described the northwestern white-tailed deer (*O. v. ochrourus*), he compared the type specimen to white-tailed deer collected by Jewett (1914) from Douglas Co. rather than to deer collected near the type locality of *O. v. leucurus*. Clearly, data supporting the original descriptions of these two taxa were limited.

Gavin & May (1988) evaluated the taxonomic status of CWTD by comparing allozymes from 35 loci among multiple populations of white-tailed deer representing three subspecies, including *O. v. ochrourus*. They concluded that genetic distance between the two CWTD populations and between each of the CWTD populations and populations of *O. v. ochrourus* in Washington and Oregon was less than the difference of two putative subspecies of widely separated geographic regions. Gavin & May (1988) did not observe a consistent pattern of differentiation at several loci; rather, their conclusions were based on variation at a single locus. Moreover, they recommended that an examination of additional evidence should occur before assigning subspecific status to any putative populations of CWTD. The purpose of this paper is to evaluate the taxonomy of *O. v. leucurus* by use of morphometric data. Our objectives were: 1) to quantitatively characterize crania of white-tailed deer from Douglas Co., Oregon, the CWTDNWR, and the historic range of northwestern white-tailed deer; 2) to determine if significant variation in cranial features exists among the three groups; 3) to compare findings of this morphological investigation to earlier findings based on genetic distance among the populations (Gavin & May 1988); and 4) to use the results of this study to test the working hypothesis that white-tailed deer in the three populations belong to a single taxon.

Materials and Methods

We examined crania of adult white-tailed deer from northern Idaho (n = 6 females, 12 males), the Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR; Gavin & May 1988) in Washington and Oregon (n = 65 females, 52 males), and from Douglas Co., Oregon (n = 80 females, 49 males; Smith 1982). Samples from northern Idaho are museum specimens; age was determined by toothwear (Severinghaus 1949, Larson & Tabor 1980, Gee et al. 2002). Tom Gavin collected samples from the CWTDNWR (Gavin & May 1988); age was determined by number of tooth cementum annuli (Scheffer 1950). Samples from Douglas Co., Oregon, were collected by Winston Smith (1982); age was determined by either number of tooth cementum annuli or by toothwear (Larson & Taber 1980:154, Gee et al. 2002). Eighteen measurements (Fig. 2, Table 1) were recorded for complete crania. Many specimens were recovered dead along roads, and had damaged crania because of collisions with vehicles, which resulted in incomplete datasets for these animals. Gavin recorded all measurements. Because growth in deer does not become asymptotic until about 4 and 6 years-of-age for females and males, respectively, missing measurements were not estimated. We used data only from complete crania in statistical analyses.

Females were sorted into three age classes for each collection area: age class 1 contained 2–2.9 year olds, 2 contained 3–3.9

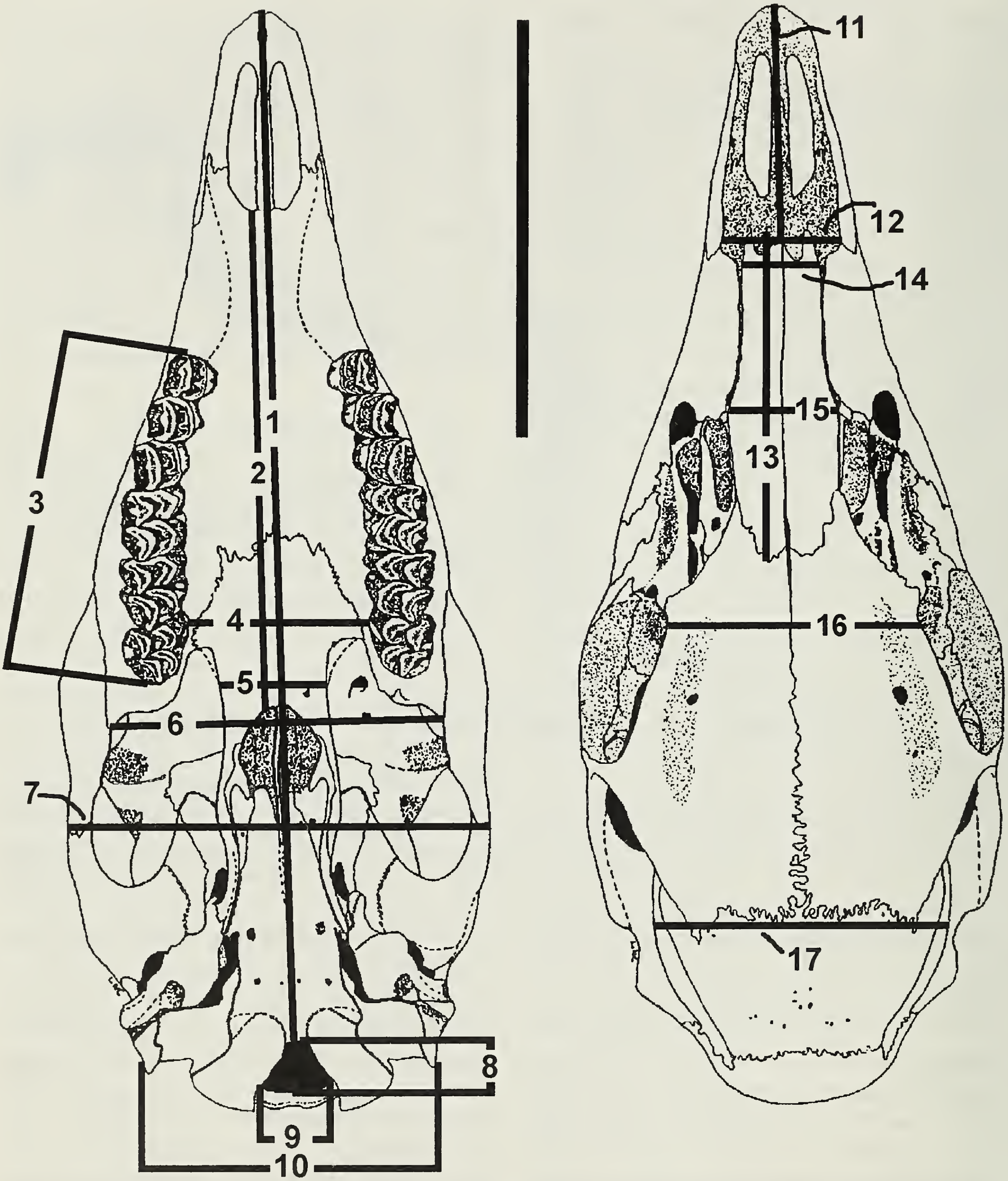

Fig. 2. Cranium of female white-tailed deer (*Odocoileus virginianus*; OSUFW [Oregon State University, Department of Fisheries and Wildlife mammal collection] 1140) illustrating dimensions recorded. 1, basilar length, 2, palatilar length, 3, length of upper molar series at alveolus, 4, breadth between M3s, 5, postpalatal breadth, 6, maxillary breadth, 7, zygomatic breadth, 8, height of foramen magnum, 9, width of foramen magnum, 10, mastoid breadth, 11, length of external nares, 12, breadth of external nares, 13, nasal length, 14, least nasal breadth, 15, greatest nasal breadth, 16, least interorbital breadth, and 17, breadth of braincase. The last dimension recorded was 18, depth of rostrum (not illustrated), which was measured with the cranium resting on a flat surface. It is the distance from the dorsal side of the premaxillae to the flat surface. Scale bar equals 10 cm.

year olds, and 3 contained ≥4 year olds. Males were sorted into four age classes for each collection area: age class 1 contained 2–2.9 year olds, 2 contained 3–3.9 year olds, 3 contained 4–5.9 year olds, and 4 contained ≥6 year olds.

Data were analyzed in SPSS 10.0.7 for Windows by use of the General Linear Model within a Multivariate Multiple Analysis of Variance (GLM MANOVA) and Canonical Discriminant Function Analysis (CDFA) with jackknife classification of specimens (Hair et al. 1987, McLachlan 1992). Age classes were designated as covariates because age was not a primary factor in acquiring specimens (Hair et al. 1987). Sample location ($n = 3$) and sex ($n = 2$) were treated as factors. Significance level was $P < 0.05$.

Initially, a GLM MANOVA was performed only with specimens having complete datasets (4 females and 2 males from Idaho, 14 females and 15 males from CWTDNWR, and 29 females and 10 males from Douglas Co., Oregon). The GLM MANOVA was repeated after data for each specimen were standardized by dividing each measurement by the area of its foramen magnum ($A = 0.25\pi \cdot \text{width} \cdot \text{height}$) to remove effects of size (Radinsky 1967) and to examine differences in shape of crania among collection areas. A CDFA was performed on standardized data present for the 11 dimensions deemed significant in the second GLM MANOVA for distinguishing specimens among the samples (6 females and 3 males from Idaho, 20 females and 22 males from CWTDNWR, and 38 females and 11 males from Douglas Co., Oregon) to present a pictorial representation of separation for specimens from the 3 localities.

Results

There was substantial variation among populations in cranial dimensions (Table 1). The initial GLM MANOVA of the original data indicated that significant differences ($F = 3.673–123.501$, $df = 2$) among specimens from the 3 sample areas occurred for all variables (Fig. 3A). When the interaction of collection area and sex was considered, however, only basilar length, least interorbital breadth, zygomatic breadth, and mastoid breadth were significantly different ($f = 3.256–9.487$, $df = 2$). The second GLM MANOVA of the standardized data set indicated significant differences ($F = 3.772–13.911$, $df = 2$) in the shape of the skulls for specimens among the three samples involving the following variables: basilar length, nasal length, breadth of the braincase, greatest width of nasals, least width of nasals, mastoid breadth, length of upper molar row, maxillary length, palatilar length, depth of rostrum, and width of external nares (Fig. 3B, Table 2). Values for these 11 standardized variables for specimens from the three samples were analyzed in CDFA (Fig. 4). The axis for Function 1 accounted for 71.4% of the variation in specimens among the areas and was related to skull shape. The axis for Function 2 incorporated the remaining variation (28.6%) in cranial dimensions, which was associated with overall skull size. All specimens from area 1, 85.7% of specimens from area 2, and 93.9% of specimens from area 3 were correctly classified into their *a priori* groups. Furthermore, in the plot of axes 1 and 2, with the exception of four individuals, three distinct groups were formed (Fig. 4). Even after controlling for differences in size related to sex and age, specimens from area 3 are distinguishable in the first axis from those in areas 1 and 2 by a combination of shorter basilar and nasal lengths, and narrower braincase and least width of the nasals (Table 1). On the second axis, specimens from area 1 are distinguishable from those in areas 2 and 3 by having longer basilar lengths and broader braincases. They also have narrower faces (as indicated by the narrower least width of the nasals) than specimens from area 2. Thus, it is apparent that even with size based on age and sex accounted for, specimens from area 3 (Douglas Co., Oregon) are still rel-

Table 1.—Means ± *SE*, ranges (in parentheses), and *CV*s followed by *n* of measurements of skull dimensions for female and male *Odocoileus virginanus* from northern Idaho, the Columbian White-tailed Deer National Wildlife Refuge (CWTDNWR) in Washington and Oregon, and Douglas Co., Oregon. Dimensions are shown in Fig. 2.

	Northern Idaho		CWTDNWR		Douglas Co., Oregon	
Dimensions	Males	Females	Males	Females	Males	Females
Basilar length	278.25 ± 3.010 (273–286) 0.220, 4	251.17 ± 2.227 (244–260) 0.022, 6	262.18 ± 1.490 (244–276) 0.033, 33	244.57 ± 1.025 (231–256) 0.025, 37	235.96 ± 1.592 (225–257) 0.034, 25	223.74 ± 0.913 (210–244) 0.034, 68
Palatilar length	135.62 ± 1.491 (130.8–139.6) 0.027, 6	125.78 ± 1.991 (120.2–131.6) 0.039, 6	125.74 ± 0.845 (114.3–140.0) 0.045, 45	118.75 ± 0.591 (109.3–127.5) 0.037, 54	113.69 ± 0.628 (104.8–122.4) 0.045, 41	109.30 ± 0.620 (97.9–123.1) 0.047, 68
Length of upper molar series	76.59 ± 1.167 (73.3–83.6) 0.046, 9	74.53 ± 1.195 (70.5–79.1) 0.039, 6	76.47 ± 0.359 (71.6–81.8) 0.032, 47	73.89 ± 0.461 (67.2–80.8) 0.044, 50	72.23 ± 0.465 (66.3–77.3) 0.036, 31	70.09 ± 0.470 (57.3–78.6) 0.052, 59
Breadth between M3s	49.61 ± 0.527 (47.4–53.5) 0.035, 11	46.87 ± 0.685 (45.1–49.1) 0.036, 6	46.99 ± 0.386 (42.7–54.9) 0.054, 44	43.49 ± 0.279 (39.7–49.3) 0.050, 60	45.62 ± 0.359 (39.7–52.8) 0.052, 44	42.85 ± 0.284 (36.2–47.6) 0.055, 70
Postpalatal breadth	28.95 ± 0.384 (26.4–30.4) 0.042, 10	26.52 ± 0.694 (24.8–28.4) 0.059, 5	25.89 ± 0.158 (22.6–30.7) 0.060, 48	24.76 ± 0.218 (20.3–30.7) 0.065, 55	24.88 ± 0.242 (21.4–29.3) 0.062, 41	24.13 ± 0.223 (20.9–27.8) 0.073, 62
Maxillary breadth	86.54 ± 1.406 (79.7–93.2) 0.054, 11	82.38 ± 1.002 (78.5–85.5) 0.030, 6	82.89 ± 0.515 (75.8–91.2) 0.043, 47	78.46 ± 0.362 (72.7–87.6) 0.037, 64	81.91 ± 0.492 (73.9–88.0) 0.040, 44	79.13 ± 0.377 (70.3–86.4) 0.042, 77
Zygomatic breadth	116.69 ± 1.152 (113.0–124.5) 0.033, 11	108.28 ± 1.274 (104.9–113.0) 0.029, 6	108.73 ± 0.788 (96.5–120.0) 0.049, 45	101.37 ± 0.358 (95.9–107.3) 0.028, 62	105.67 ± 0.460 (99.9–111.4) 0.029, 43	100.87 ± 0.514 (90.40–116.4) 0.044, 74
Height of foramen magnum	20.67 ± 0.439 (18.0–23.2) 0.074, 12	21.83 ± 0.381 (20.7–23.1) 0.043, 6	18.96 ± 0.180 (14.4–21.8) 0.068, 51	19.97 ± 0.176 (16.9–23.6) 0.071, 64	19.56 ± 0.197 (16.7–22.7) 0.071, 49	20.19 ± 0.022 (17.4–23.9) 0.065, 77
Width of foramen magnum	20.36 ± 0.539 (16.2–22.0) 0.092, 12	20.83 ± 0.305 (19.9–22.1) 0.036, 6	19.29 ± 0.182 (16.5–22.4) 0.067, 50	19.49 ± 0.134 (17.1–22.2) 0.055, 64	19.67 ± 0.196 (17.0–22.2) 0.070, 49	18.94 ± 0.136 (16.3–22.5) 0.063, 77
Mastoid breadth	86.63 ± 1.154 (82.3–96.5) 0.046, 12	73.03 ± 1.403 (68.3–76.9) 0.047, 6	75.19 ± 0.744 (64.5–90.6) 0.070, 50	65.46 ± 0.311 (59.7–71.5) 0.038, 64	69.28 ± 0.531 (62.3–79.7) 0.054, 49	62.47 ± 0.376 (54.4–69.0) 0.053, 78
Length of external nares	78.28 ± 1.372 (74.3–80.6) 0.035, 4	70.70 ± 1.343 (67.6–76.7) 0.047, 6	73.44 ± 0.658 (62.3–80.3) 0.052, 33	69.81 ± 0.560 (63.8–77.6) 0.047, 35	70.76 ± 0.841 (63.4–80.0) 0.059, 25	67.01 ± 0.492 (53.6–76.5) 0.061, 69

Table 1.—Continued.

Dimensions	Northern Idaho		CWTDNWR		Douglas Co., Oregon	
	Males	Females	Males	Females	Males	Females
Breadth of external nares	33.88 ± 0.892	29.67 ± 0.966	31.87 ± 0.390	30.58 ± 0.426	28.59 ± 0.406	27.73 ± 0.291
	(31.8–35.6)	(26.5–33.2)	(27.4–34.9)	(23.7–34.5)	(23.9–33.1)	(22.7–34.4)
	0.053, 4	0.080, 6	0.064, 27	0.080, 33	0.063, 20	0.086, 67
Nasal length	89.60 ± 2.486	83.12 ± 0.908	83.18 ± 0.788	76.35 ± 0.717	69.15 ± 0.917	65.80 ± 0.578
	(81.6–100.4)	(80.9–86.8)	(70.4–95.0)	(62.7–88.9)	(52.6–79.1)	(50.5–79.3)
	0.073, 7	0.027, 6	0.062, 43	0.066, 50	0.088, 44	0.078, 78
Least nasal breadth	20.05 ± 0.757	17.25 ± 0.575	21.41 ± 0.339	19.00 ± 0.212	18.85 ± 0.222	17.34 ± 0.205
	(17.4–23.9)	(15.6–19.3)	(16.8–25.9)	(16.0–22.9)	(16.8–22.5)	(13.5–20.8)
	0.107, 8	0.082, 6	0.103, 42	0.077, 48	0.073, 38	0.098, 68
Greatest nasal breadth	30.32 ± 0.934	24.95 ± 0.768	29.23 ± 0.395	26.53 ± 0.325	26.14 ± 0.125	24.38 ± 0.285
	(24.5–33.1)	(22.3–27.5)	(24.6–37.0)	(23.2–32.7)	(22.4–31.0)	(18.7–33.2)
	0.092, 9	0.075, 6	0.087, 42	0.085, 48	0.083, 38	0.098, 70
Least interorbital breadth	71.58 ± 0.754	61.53 ± 0.580	63.07 ± 0.499	58.10 ± 0.308	60.65 ± 0.395	56.21 ± 0.313
	(68.0–77.2)	(60.1–63.3)	(54.9–73.8)	(50.9–63.6)	(55.8–67.3)	(50.5–62.5)
	0.037, 12	0.023, 6	0.056, 50	0.043, 65	0.046, 49	0.050, 80
Breadth of braincase	79.20 ± 1.268	71.33 ± 0.516	74.00 ± 0.480	71.23 ± 0.304	72.39 ± 0.357	69.35 ± 0.250
	(71.2–85.1)	(69.0–72.7)	(61.5–80.6)	(66.7–76.8)	(67.4–76.8)	(36.2–47.6)
	0.055, 12	0.018, 6	0.047, 52	0.034, 65	0.034, 48	0.055, 70
Elevation of rostrum	32.53 ± 2.199	31.27 ± 1.619	38.98 ± 0.991	38.83 ± 0.929	36.21 ± 1.236	33.89 ± 0.732
	(27.3–37.8)	(25.7–35.0)	(25.6–46.4)	(24.9–49.5)	(27.0–51.2)	(17.2–47.0)
	0.135, 4	0.127, 6	0.134, 28	0.142, 35	0.164, 23	0.171, 63

Table 2.—Covariate and factors affecting 16 standardized response variables recorded from skulls of *Odocoileus virginianus* from the CWTDNWR, Washington and Oregon, Douglas Co., Oregon, and northern Idaho. We standardized data for response variables by dividing each measurement by the area of the foramen magnum ($A = 0.25\pi WH$) for that individual (Radinsky 1967). The General Linear Model is presented for each statistically significant response variable as SS, MS with f and *p* below except for the Error column. The covariate Age class had 3 classes for females and 4 for males. The factors were sex (female, male) and collection locality.

Response variables and multivariate test	Age class *d.f.* = 1	Sex *d.f.* = 1	Collection locality *d.f.* = 2	Collection locality + Sex *d.f.* = 2	Corrected model *d.f.* = 6	Error *d.f.* = 67
Basilar length		0.053, 0.053 7.64, 0.007	0.079, 0.039 5.66, 0.005		0.244, 0.041 5.84, 0.0001	0.467, 0.007
Nasal length		0.005, 0.005 4.68, 0.034	0.025, 0.012 12.56, 0.0001		0.0440, 0.007 7.45, 0.0001	0.066, 0.001
Greatest nasal breadth		0.001, 0.001 7.00, 0.010	0.002, 0.001 4.21, 0.019		0.005, 0.0001 4.54, 0.001	0.013, 0.0001
Least nasal breadth	0.0003, 0.0003 4.34, 0.041	0.001, 0.001 9.70, 0.003	0.001, 0.001 6.26, 0.003		0.003, 0.0001 7.20, 0.0001	0.005, 0.00001
Least interorbital breadth		0.007, 0.007 12.74, 0.001			0.014, 0.002 4.40, 0.001	0.034, 0.0001
Zygomatic breadth		0.009, 0.009 6.68, 0.012			0.026, 0.004 3.09, 0.010	0.095, 0.001
Breadth of braincase		0.003, 0.003 4.17, 0.045	0.005, 0.002 3.67, 0.031		0.015, 0.002 3.80, 0.003	0.043, 0.001
Mastoid breadth		0.017, 0.017 34.61, 0.0001	0.003, 0.002 3.14, 0.050	0.005, 0.003 5.10, 0.009	0.039, 0.006 13.32, 0.0001	0.032, 0.001
Length of upper molar series at alveolus			0.008, 0.004 6.01, 0.004		0.013, 0.002 3.29, 0.007	0.044, 0.001
Maxillary breadth					0.013, 0.002 2.49, 0.031	0.058, 0.001
Breadth between M3s					0.005, 0.001 2.57, 0.027	0.022, 0.001
Palatilar length		0.009, 0.009 4.84, 0.031	0.018, 0.009 4.91, 0.010		0.051, 0.008 4.72, 0.0001	0.121, 0.002
Postpalatal breadth		0.0001, 0.0001 4.04, 0.049			0.001, 0.0002 2.17, 0.057	0.007, 0.0001
Elevation of rostrum			0.006, 0.003 5.69, 0.005		0.010, 0.002 3.31, 0.006	0.035, 0.001
Length of external nares		0.003, 0.003 6.01, 0.017			0.012, 0.002 3.65, 0.003	0.038, 0.001

Table 2.—Continued.

Response variables and multivariate test	Age class *d.f.* = 1	Sex *d.f.* = 1	Collection locality *d.f.* = 2	Collection locality + Sex *d.f.* = 2	Corrected model *d.f.* = 6	Error *d.f.* = 67
Breadth of external nares			0.001, 0.001 5.16, 0.008		0.003, 0.001 3.71, 0.003	0.009, 0.001
Wilkes' Lambda	Value = 0.550 $f = 2.65$ *d.f.* = 16, $p = 0.004$	Value = 0.269 $f = 8.82$ *d.f.* = 16, $p = 0.0001$	Value = 0.088 $f = 7.74$ *d.f.* = 32, $p = 0.0001$	Value = 0.449 $f = 1.60$ *d.f.* = 32, $p = 0.040$		

atively smaller animals with shorter faces and narrower skulls than those specimens from either area 1 (northern Idaho) or area 2 (CWTDNWR).

Discussion

Assumptions and limitations of analyses.—Although we collected a reasonably large number of skulls from each of the localities, incomplete data from many specimens substantially reduced our sample sizes for statistical analysis, especially specimens assigned to *O. v. ochrourus.* Small sample size can be problematic, especially for MANOVA where statistical power is easily compromised (Johnson & Wichern 1998). In addition, departure from normality, an important assumption of MANOVA, occurs more frequently with small sample sizes. Fortunately, MANOVA is relatively robust to violations of assumptions in many circumstances (Johnson & Wichern 1998). Also, because of the large effect size (differences among means of treatments) among populations with many cranial dimensions, statistical power probably was not an issue in our analyses. Comparisonwise error rates ranged from 0.013 to 0.0001 (Table 2).

Small sample size also contributes to classification bias in CDFA, a consequence of which is an overestimate of divergence among taxa (Lance et al. 2000). In this study, we used the results of CDFA strictly for illustrative rather than analytical purposes. Still, we used a less biased jackknife technique for subsequent classification of specimens (Hair et al. 1987, McLachlan 1992, Johnson & Wichern 1998, Lance et al. 2000).

Cranial variation and taxonomy.—The taxonomy of white-tailed deer, like that of most of the North American mammal fauna, predates development of genetic techniques and consequently early descriptions of taxa were based on variation of morphological attributes, especially cranial characteristics (e.g., *Ovis canadensis,* Cowan

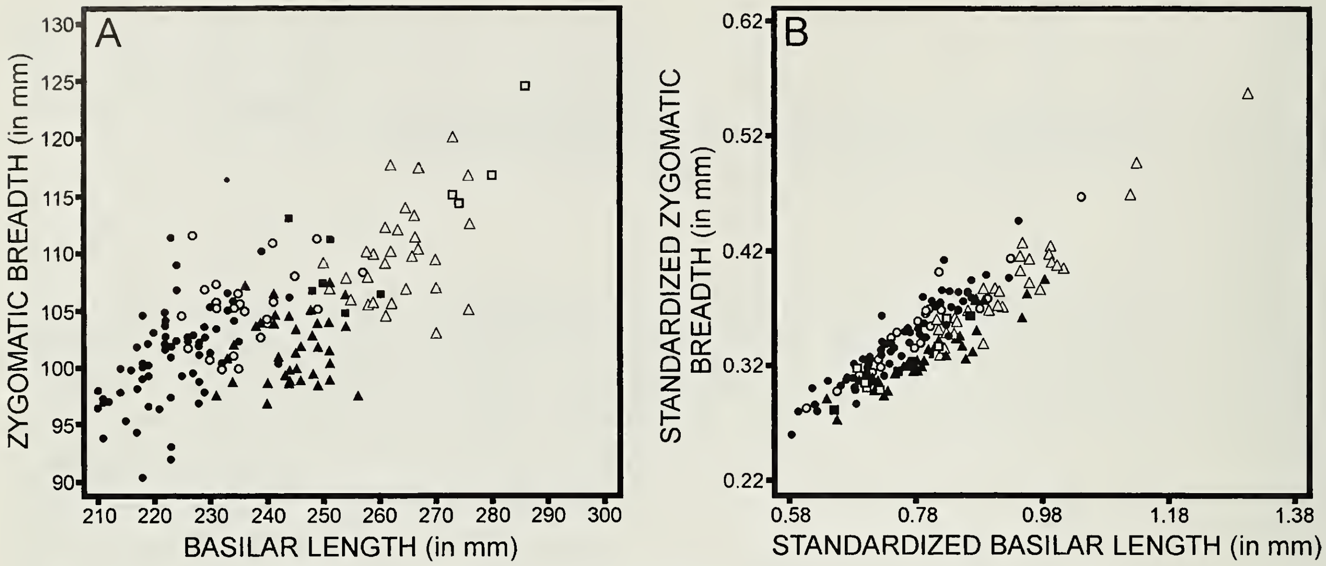

Fig. 3. A. Plot of basilar length and zygomatic breadth illustrating a decrease in size of female and male white-tailed deer (*Odocoileus virginianus*) from northern Idaho (females ■, males ☐), the Columbian White-tailed Deer National Wildlife Refuge in Washington and Oregon (females ▲, males △), to Douglas Co., Oregon (females ●, males ○). B. Plot of standardized basilar length and standardized zygomatic breadth illustrating the same relative sizes for female and male white-tailed deer (*Odocoileus virginianus*) from the same collection areas.

1940). Much of the historical taxonomy of species and subspecies lacks an adequate quantitative basis and reflects a typological view inconsistent with an evolutionary perspective (Ball & Avise 1992, Wehausen & Ramey 2000). Recent developments in molecular biology (e.g., Cook et al. 2001) and statistical analyses (e.g., Steppan & Sullivan 2000) have changed the way mammalogists do systematics, which in many instances has resulted in revisions of existing taxonomy (Steppan & Sullivan 2000, Wehausen & Ramey 2000, Cook et al. 2001). Still, morphometry can be a useful tool in elucidating evolutionary and taxonomic relationships (Wehausen & Ramey 1993, Genov 1999, Molina & Molinari 1999), especially when used in conjunction with genetic data (e.g., Wehausen & Ramey 2000).

We used variation in cranial morphology to test the hypothesis that deer in the three populations belong to a single taxon. This hypothesis was proposed on the basis of allozyme variation among three white-tailed deer populations (Gavin & May 1988). The results of our analyses indicate significant variation among the three populations for several cranial dimensions (Table 2). Thus, our results do not support the current taxonomy, which implies that white-tailed deer from the lower Columbia River and Douglas Co. (*O. v. leucurus*) are similar, yet distinguishable from white-tailed deer in eastern Oregon, eastern Washington, and Idaho (*O. v. ochrourus*). Rather, our results clearly delineate three distinct morphological populations (Fig. 4, Table 2) rather than a single unified taxon.

Similar geographical variation in cranial dimensions has been reported for bighorn sheep, *Ovis canadensis* Shaw (Wehausen & Ramey 1993, 2000), wild boar, *Sus scrofa* Linnaeus (Genov 1999), black bear, *Ursus americanus* Pallas (Kennedy et al. 2002), and other white-tailed deer (Molina & Molinari 1999). The key issue in interpreting cranial variation in the context of subspecific taxonomy is whether the morphological variation is indicative of corresponding genetic divergences; or, whether it is largely ecophenotypic variation that resulted from regional differences in habitat or other environmental differences (Wehausen & Ramey 2000, Kennedy et al. 2002). Some taxa (e.g., black bear) show clinal variation, i.e., significant correlations between skull mor-

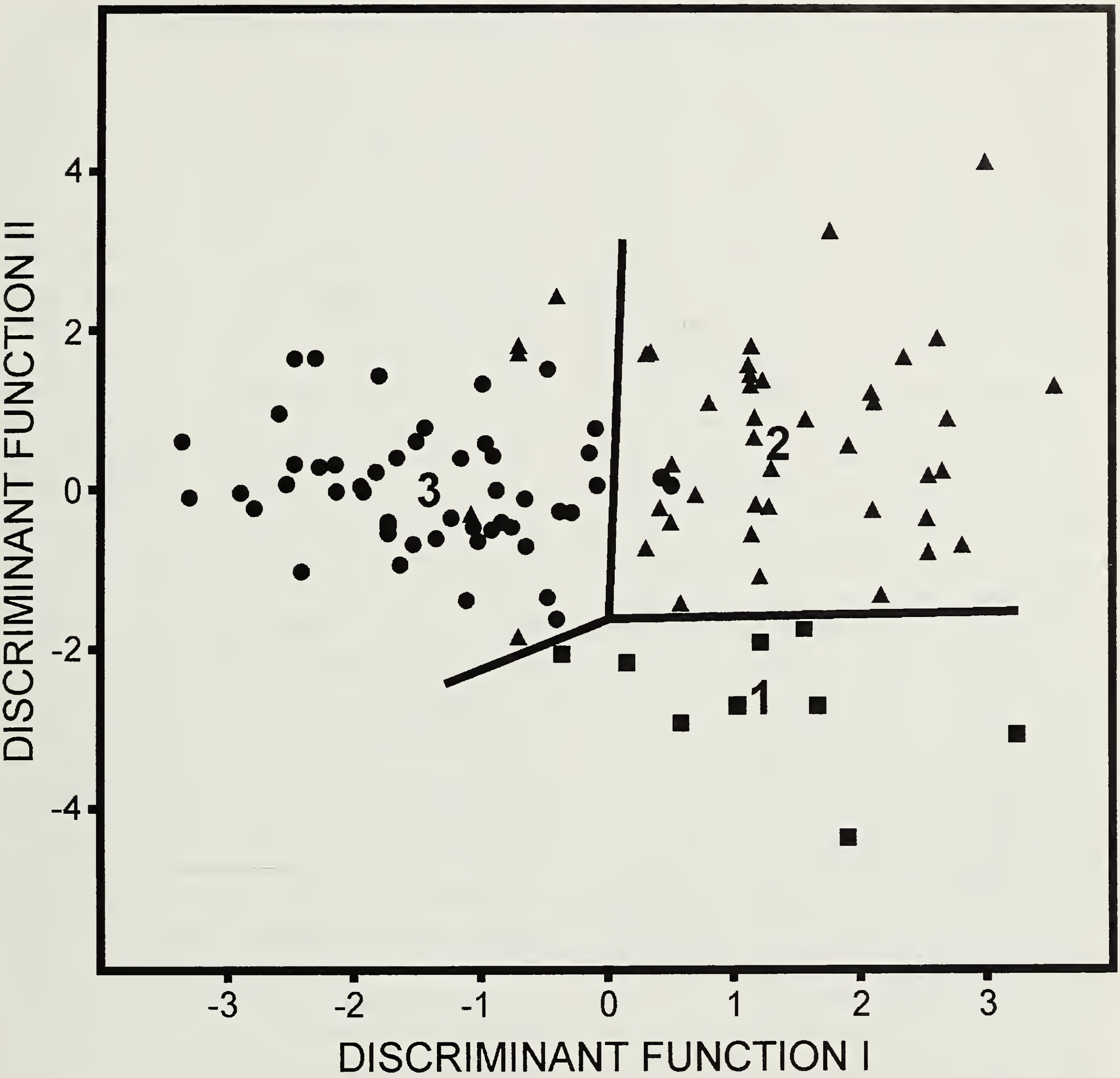

Fig. 4. Canonical-variates plot of specimens from 1 (■), northern Idaho, 2 (▲), the Columbian White-tailed Deer National Wildlife Refuge in Washington and Oregon, and 3 (●), Douglas Co., Oregon. Function 1 accounted for 71.4% and Function 2 28.6% of the variation among the areas. Group centroids are indicated by numbers. Specimens from the three areas sorted into three distinct morphological groups; straight lines, drawn by eye, within the graph delineate the groups. Differences in shape of the cranium are characterized as follows: specimens from area 3 have overall shorter and narrower skulls than those from areas 1 and 2; and specimens from area 1 have a longer rostrum (as indicated by significantly longer nasals) and narrower cranium than those from area 2.

phology and climatic or other environmental gradients (Kennedy et al. 2002), and display substantial genetic dissimilarity among regional populations (Miller 1995). In our study, the pattern of cranial variation was somewhat similar to that reported for black bears (Kennedy et al. 2002) with skull size varying along a west to east gradient and decreasing from north to south. The lower Columbia River population had features intermediate between those of the Idaho and Douglas Co. populations. Unlike black bears (Miller 1995), however, there was no clear evidence of corresponding genetic divergences at one locus among the disjunct regional populations (Gavin & May 1988).

Gavin & May (1988) reported that white-tailed deer populations from the Pacific Northwest showed relatively low genetic divergence. In a large number of possible pair-wise comparisons Gavin & May (1988) found Nei's (1971) genetic distances between *O. v. borealis* from New York and white-tailed deer populations from the Pacific Northwest (0.037) were an order of magnitude greater than genetic differences among white-tailed deer populations of Oregon and Washington. Moreover, white-tailed deer from Idaho showed less divergence from the Douglas Co. population than from the lower Columbia River population. Genetic distances (Nei 1971) between *O. v. ochrourus* from Oregon and Washington and *O. v. leucurus* in southwestern Oregon, and between *O. v. ochrourus* and white-tailed deer from the lower Columbia River were 0.003 and 0.010, respectively. Also, they found that genetic divergence between *O. v. leucurus* populations on the Oregon and Washington sides of the lower Columbia River (0.007) was greater than between sampled *O. v. ochrourus* populations in Oregon and Washington (Fig. 1), or between *O. v. leucurus* populations in southwestern Oregon and *O. v. ochrourus* populations (0.002).

Genetic and morphological data commonly suggest different conclusions regarding taxonomy of mammals. Recent examples include *Ovis canadensis* (Wehausen & Ramey 1993, 2000) and *Sus scrofa* (Genov 1999), where separation of subspecies based solely on morphology (Cowan 1940, Genov 1999) was not supported by more rigorous analysis in conjunction with genetic data (Wehausen & Ramey 2000). The tendency has been to rely on molecular data, which presumably provides less ambiguous evidence. Ball & Avise (1992) proposed that subspecies are major subdivisions of the gene pool diversity of species where such subunits can be corroborated by independent, genetically based traits. According to this view, subspecies should have distinguishing attributes that have an evolutionary basis (Wehausen & Ramey 2000).

We found white-tailed deer populations of Oregon and Washington distinguishable by cranial dimensions, but Gavin & May (1988) found no compelling evidence from an evolutionary basis for this variation. The putative historical ranges of *O. virginianus* populations in the Pacific Northwest (Bailey 1932, Grinnell 1933, Smith 1985, Williams 1986, Gavin & May 1988) suggest that populations interbred freely. Before European settlement, white-tailed deer occupied most of the riparian floodplains and other deciduous lowlands in western, central, and northeastern Oregon. The range of *O. v. ochrourus* extended from northeastern California (Grinnell 1933) north to west-central British Columbia and east to north-central Wyoming (Hall 1981, Smith 1991). In Oregon, *O. v. ochrourus* occurred in the Klamath Basin (Walsingham 1873), which is only about 100 km east of the southernmost range of *O. v. leucurus* in southwestern Oregon (Smith 1985). Throughout east-central Oregon, *O. v. ochrourus* occupied floodplain and riparian communities, frequenting deciduous woodlands and woody thickets associated with streams and marshes (Walsingham 1873, Cowan 1936). Similarly, *O. v. leucurus* occurred throughout the river valleys and other deciduous woodlands of western Oregon (Smith 1985). The Cascade Range likely represented a barrier for free movement of white-tailed deer between central and western Oregon; however, opportunities for gene flow before European settlement presumably existed along the Columbia River and in south-central Oregon where river valleys cut through the Cascade Range at relatively low elevations. Without geographic isolation or strong selective pressures associated with markedly different environmental conditions (e.g., Wehausen & Ramey 1993, 2000), there is little reason to believe that historic populations of white-tailed deer in Oregon (and the Pacific Northwest) were not a single, contiguous breeding population.

Today, circumstances are very different; the populations clearly are isolated from one another (Fig. 1). White-tailed deer in northeastern Oregon apparently have extended their range westward and southward in recent years (Oregon Department of Fish and Wildlife, unpubl. data). Still, land use and natural barriers throughout central Oregon represent significant impediments to dispersal and natural expansion. Efforts to translocate deer may establish isolated local populations, but much of the native habitat in central Oregon has been modified (Verts & Carraway 1998). Moreover, availability and connectivity of habitat in western Oregon and along the Columbia River is such that future opportunities for natural or facilitated expansion are unlikely. This, combined with the potential competition from black-tailed deer *Odocoileus hemionus* (Smith 1985), renders the likelihood of *O. v. leucurus* reoccupying significant portions of its historic range extremely low.

We believe it is prudent to consider the question of taxonomy in the context of current circumstances rather than belabor what might have been. Neither earlier genetic research nor our morphological study provides compelling evidence to warrant an unambiguous resolution of this question. Consequently, the current taxonomy, although not directly supported by either line of evidence, cannot be refuted with certainty. Nonetheless, the three populations are morphologically distinct, geographically isolated, occupy different habitats (Gavin 1979, Smith 1985, Verts & Carraway 1998), and likely represent unique gene-pool subdivisions of *O. virginianus* (Ball & Avise 1992, Wehausen & Ramey 2000). With these populations isolated and gene flow interrupted, genetic divergence may become significant in time (Avise 1994).

Implications for recovery and conservation.—Nomenclature shapes the view of how nature is organized (Avise 1994) and taxonomic units have become the foundation of conservation efforts (Cook & MacDonald 2001). Current taxonomy views white-tailed deer populations of the lower Columbia River and Douglas Co. as *O. v. leucurus,* which may allow translocation of individuals from either location for the purpose of restoring populations in portions of its historic range. Our results do not support current taxonomy, but indicate that deer from the lower Columbia River and Douglas Co. are morphologically distinct. Because of geographic isolation and differences in habitat, we believe that in time the two populations will become sufficiently genetically divergent to warrant separation into two taxa. For that reason, we think it is prudent to choose a conservative approach to restoring white-tailed deer in western Oregon and refrain from translocating deer from Douglas Co. (or eastern Oregon) to supplement populations along the lower Columbia River or establish populations in the Willamette River valley.

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Literature Cited

Avise, J. 1994. Molecular markers, natural history, and evolution. Chapman and Hall, New York, 511 pp.

Bailey, V. 1932. The northwestern white-tail deer.—

Proceedings of the Biological Society of Washington 45:43–44.

———. 1936. The mammals and life zones of Oregon.—North American Fauna 55:1–416.

Ball, M. R., & J. C. Avise. 1992. Mitochondrial DNA phylogeographic differentiation among avian populations and the significance of subspecies.—The Auk 109:626–636.

Columbian White-tailed Deer Recovery Team. 1983. Revised Columbian white-tailed deer recovery plan. U.S. Fish and Wildlife Service, Portland, Oregon, 75 pp.

Cook, J. A., & S. O. MacDonald. 2001. Should endemism be a focus of conservation efforts along the north Pacific coast of North America?—Biological Conservation 97:207–213.

———, A. L. Bidlack, C. J. Conroy, J. R. Demboski, M. A. Fleming, A. M. Runck, K. D. Stone, & S. O. MacDonald. 2001. A phylogeographic perspective on endemism in the Alexander Archipelago of southeast Alaska.—Biological Conservation 97:215–227.

Cowan, I. M. 1936. Distribution and variation in deer (*Odocoileus*) of the Pacific Coastal Region of North America.—California Fish and Game 22: 155–246.

———. 1940. Distribution and variation in the native sheep of North America.—The American Midland Naturalist 24:505–580.

Crews, A. K. 1939. A study of the Oregon white-tailed deer, *Odocoileus virginianus leucurus* (Douglas). M.S. thesis, Oregon State University, Corvallis, 45 pp.

Doremus, H., & J. E. Pagel. 2001. Why listing may be forever: perspectives on delisting under the U.S. Endangered Species Act.—Conservation Biology 15:1258–1268.

Douglas, D. 1829. Observations on two undescribed species of North American mammals (*Cervus leucurus* et *Ovis californicus*).—Zoological Journal 4:330–332.

———. 1914. Journal kept by David Douglas during his travels in North America 1823–1827. W. Wesley and Son, London, U.K., 364 pp.

Dublin, H. T. 1980. Relating deer diets to forage quality and quantity—the Columbian white-tailed deer. M.S. thesis, University of Washington, Seattle, 135 pp.

Gavin, T. A. 1979. Population ecology of the Columbian white-tailed deer. Ph.D. dissertation, Oregon State University, Corvallis, 149 pp.

———, & B. May. 1988. Taxonomic status and genetic purity of Columbian white-tailed deer.—The Journal of Wildlife Management 52:1–10.

———, L. H. Suring, P. A. Vohs, Jr., & E. C. Meslow. 1984. Population characteristics, spatial organization, and natural mortality in the Columbian white-tailed deer.—Wildlife Monographs 91:1–41.

Gee, K. L., J. H. Holman, M. K. Causey, A. N. Rossi, & J. B. Armstrong. 2002. Aging white-tailed deer by tooth replacement and wear: a critical evaluation of a time-honored technique.—Wildlife Society Bulletin 30:387–393.

Genov, P. V. 1999. A review of the cranial characteristics of the wild boar (*Sus scrofa* Linnaeus 1758), with systematic conclusions.—Mammal Review 29:205–238.

Grinnell, J. 1933. Review of the Recent mammal fauna of California.—University of California Publications in Zoology 40:71–284.

Hair, J. F., Jr., R. E. Anderson, & R. L. Tatham. 1987. Multivariate data analysis with readings, 2nd edition. Macmillan Publishing Company, New York, 449 pp.

Hall, E. R. 1981. The mammals of North America. Wiley-Interscience, New York, 2:601–1181 + *90*.

Jewett, S. G. 1914. The white-tailed and other deer in Oregon.—The Oregon Sportsman 2:5–9.

Johnson, R. A., & D. W. Wichern. 1998. Applied multivariate statistical analysis, 4th edition. Prentice-Hall, Upper Saddle River, New Jersey, 816 pp.

Kennedy, M. L., P. K. Kennedy, M. A. Bogan, & J. L. Waits. 2002. Geographic variation in the black bear (*Ursus americanus*) in the eastern United States and Canada.—Southwestern Naturalist 47:257–266.

Lance, R. E., M. L. Kennedy, & P. L. Leberg. 2000. Classification bias in discriminant function analysis used to evaluate putatively different taxa.—Journal of Mammalogy 81:245–249

Larson, J. S., & R. D. Taber. 1980. Criteria of sex and age. Pp. 143–202 *in* S. D. Schemnitz, ed., Wildlife management techniques manual, 4th edition, The Wildlife Society, Washington, D.C., 686 pp.

McLachlan, G. J. 1992. Discriminant analysis and statistical pattern recognition. John Wiley & Sons, Inc., New York, 526 pp.

Miller, D. A. 1995. Systematic classification of black bears in the southeastern United States. M.S. thesis, Virginia Tech University, Blacksburg, 102 pp.

Molina, M., & J. Molinari. 1999. Taxonomy of Venezuelan white-tailed deer (*Odocoileus*, Cervidae, Mammalia) based on cranial and mandibular traits.—Canadian Journal of Zoology 77: 632–645.

Nei, M. 1971. Identity of genes and genetic distance between populations.—Genetics 68(Supplement):47.

Radinsky, L. 1967. Relative brain size: a new measure.—Science 155:836–837.

Ricca, M. A. 2000. Movements, habitat associations, and survival of Columbian white-tailed deer in Western Oregon. M.S. thesis, Oregon State University, Corvallis, 170 pp.

Scheffer, V. B. 1950. Growth layers on the teeth of Pinnipedia as an indication of age.—Science 112:309–311.

Severinghaus, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer.—Journal of Wildlife Management 13:195–216.

Smith, W. P. 1982. Status and habitat use of Columbian white-tailed deer in Douglas County, Oregon. Ph.D. dissertation, Oregon State University, Corvallis, 273 pp.

———. 1985. Current geographic distribution and abundance of Columbian white-tailed deer, *Odocoileus virginianus leucurus* (Douglas).—Northwest Science 59:243–251.

———. 1987. Dispersion and habitat use by sympatric Columbian white-tailed deer and Columbian black-tailed deer.—Journal of Mammalogy 68: 337–347.

———. 1991. Odocoileus virginianus.—Mammalian Species 388:1–13.

Steppan, S. J., & J. Sullivan. 2000. The emerging statistical perspective in systematics: a comment on Mares and Braun.—Journal of Mammalogy 81:260–270.

Suring, L. H., & P. A. Vohs, Jr. 1979. Habitat use by Columbian white-tailed deer.—Journal of Wildlife Management 43:610–619.

Verts, B. J., & L. N. Carraway. 1998. Land mammals of Oregon. University of California Press, Berkeley, 668 pp.

Wehausen, J. D., & R. R. Ramey. 1993. A morphometric reevaluation of the Peninsular subspecies.—Desert Bighorn Council Transactions 37: 1–10.

———, & R. R. Ramey, II. 2000. Cranial morphometric and evolutionary relationships in the northern range of *Ovis canadensis.*—Journal of Mammalogy 81:145–161.

Walsingham, T. L. 1873. On the distribution of the different species of deer and other ruminants in northern California and Oregon.—Proceedings of the Zoological Society of London 1873:561–563.

Whitney, L. W. 2001. Ecological relationships between Columbian white-tailed and black-tailed deer in Southwest Oregon. M.S. thesis, Oregon State University, Corvallis, 106 pp.

Williams, D. F. 1986. Mammalian species of special concern in California. Wildlife Management Division Administrative Report 86-1, California Department of Fish and Game, Sacramento, 111 pp.

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New subgenus of leptarctine (Carnivora: Mustelidae) from the Late Miocene of Nebraska, U.S.A.

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Abstract.—A new subgenus, *Pseudoleptarctus,* is described on the basis of a mandible from the late Clarendonian (late Miocene). The new leptarctine differs from other species in having a rounded trigonid and a well-defined hypoconulid on m1 and an enlarged accessory cusp on p3. *Pseudoleptarctus genowaysi* has the largest dentition known for leptarctines. The morphological similarities to procyonids indicate their shared aspects of diet.

Mustelid carnivores occupy various habitats and their diet ranges from insects to vertebrates. Qiu & Schmidt-Kittler (1982) and Lim & Martin (2002) considered Leptarctinae to be a subfamily of mustelids including *Craterogale* (N. America, M. Miocene), *Trocharion* (Europe, M. Miocene), *Hypsoparia* (N. America, U. Miocene), and *Leptarctus* (N. America and Asia, L. to U. Miocene). *Leptarctus* is one of the least known fossil carnivores and it occurs in the middle and late Miocene of North America and the Miocene of the Tung Gur region, 13.5–13.8 MYA, Inner Mongolia, China (Lim 1997, Lim & Miao 2000, Lim et al. 2001, Lim & Martin 2002a, Zhai 1964). Leidy (1856) described a P4 from South Dakota (Fort Randall Formation, Barstovian) for *Leptarctus primus,* the type species. Wortman (1894) described a lower jaw with c1, p3, and p4 from Nebraska (Clarendonian) and referred the specimen to *L. primus.* However, Matthew (1924) erected a new species, *Leptarctus wortmani* Matthew, 1924 for the specimen (Runningwater Formation, E. Hemingfordian) previously described by Wortman (1894). Simpson (1930) described a P4 from Florida (Lower Bone Valley Formation, L. Barstovian-E. Clarendonian) as *Leptarctus progressus* and concluded that it shows some resemblance to *Nasua* in its greater width and larger protocone. Stock (1930) described a skull fragment with P4 and M1 from Oregon (Mascall Formation, E. Barstovian) as *L. oregonensis.* Olsen (1957) placed *Mephititaxus* (Thomas Farm Local Fauna, E. Hemingfordian) as *L. ancipidens.* In 1959, a skull, mandible, atlas, and axis were discovered from the Tung Gur region, Nei Mongol, China and described as *L. neimenguensis* (Zhai 1964). Lim & Miao (2000) described *L. martini* based on a well-preserved skull from Nebraska (Valentine Formation, L. Barstovian) and Lim & Martin (2001a) described *L. kansasensis* based on fragments of a skull fragment and maxillary bone with left P3 and P4 from Kansas (Blick Quarry, Clarendonian). Lim et al. (2001) described an incomplete skull with right M1 and left P4-M1 from Texas (Hemphill Beds, E. Hemphillian) for *L. supremus.* Lim & Martin (2001b) described an anterior portion of skull with left P2-M1 and right P3-M2 from Nebraska (Republican River Beds, E. Hemphillian) for *L. desuii.*

The mammalian diet is reflected in dental morphology, jaw shape, and masticatory muscles (Smith 1993). *Leptarctus* has dental characteristics indicative of diet different from those of other mustelids. The upper incisors of *Leptarctus* can be distinguished by the peg-like and greatly reduced first and second upper incisors (Lim 1999b). The reduced upper canines suggest a non-carnivorous diet. The lower canine is strongly curved and grooved on its lingual side (Lim 1999a). A survey of the lower canines in modern carnivorous mammals revealed that the coati, *Nasua,* has a similar groove. *Nasua* is an omnivorous procyonid and one of the most frugivorous members of the Carnivora.

The edge of the masseteric fossa of the mandible is an insertion site for the masseter muscle which elevates and deviates the mandible while chewing (Turnbull 1970). The deep masseteric fossa of *Leptarctus* indicates a large masseter and suggests that *Leptarctus* could deviate the lower jaw laterally more than other mustelids. Olsen (1958) considered *L. ancipidens* to be a badger-like mustelid. However, the lower dentition of *L. ancipidens* (UF 5655) shows it differs more from *Taxidea taxus* than from *Procyon lotor.* The talonid on the m1 of *L. ancipidens* is long relative to the trigonid, a condition similar to the m1 of *Procyon lotor.* The talonid and trigonid of m1 in *Taxidea taxus* are of similar length. The m1 of *Pseudoleptarctus genowaysi* also has a long talonid (Fig. 1). This increased length of the talonid in *Leptarctus* and *Procyon* indicates that the anterior part of M1 that occluded with the talonid of m1 has increased its surface area. This structure shows that these animals had similar diets and needed a strong chewing capacity.

One distinction between *Leptarctus* and other mustelids is the great height of the zygomatic arches in *Leptarctus* (Lim 1996). The ventral edge of the zygomatic arch is an origin for the masseter, elevating the mandible and slightly deviating the mandible from side to side. The heavy zygomatic arch indicates a large masseter and suggests that *Leptarctus* had stronger chewing muscles than other mustelids.

Abbreviations used are: AMNH—Department of Vertebrate Paleontology, American Museum of Natural History; F:AM—Frick American Mammals, American Museum of Natural History; UF—Division of Vertebrate Paleontology, Florida Museum of Natural History, Gainesville, University of Florida; KUVP—Division of Vertebrate Paleontology, Natural History Museum and Biodiversity Research Center, University of Kansas; UNSM—Division of Vertebrate Paleontology, University of Nebraska State Museum.

Systematics

Order Carnivora Bowdich, 1821
Family Mustelidae Fischer von Waldheim, 1817
Subfamily Leptarctinae Gazin, 1936
Genus *Leptarctus* Leidy, 1856
Pseudoleptarctus, new subgenus

Diagnosis.—Large leptarctine with carnassial trigonid sub-equal in size to talonid and rounded anteriorly. The m1 crown is dominated by cross-lophs. The m2 is elongated. The p4 with primary and secondary cusps sub-equal in size. Thick cingula on premolars and molars.

Pseudoleptarctus genowaysi, new species

Figs. 1–3

Holotype.—UNSM 25470, a right mandible with p3-m1.

Type locality.—Cr-111, 2¼ mi SW of Burge P.O. on west side of the Snake River, Cherry County, Nebraska.

Referred specimens.—F:AM 25176, right mandible with canine, p3–4; F:AM 25211, left m1; F:AM 25167, right m1; F:AM 49412, left mandible with canine, p2-m2; F:AM 49413, right mandible with p3-m2.

Chronology.—Ash Hollow Formation, Late Clarendonian, Miocene.

Age.—*Pseudoleptarctus* refers to similarity to *Leptarctus. Pseudo* means false. The trivial name honors professor Hugh H. Genoways, former director of the University of

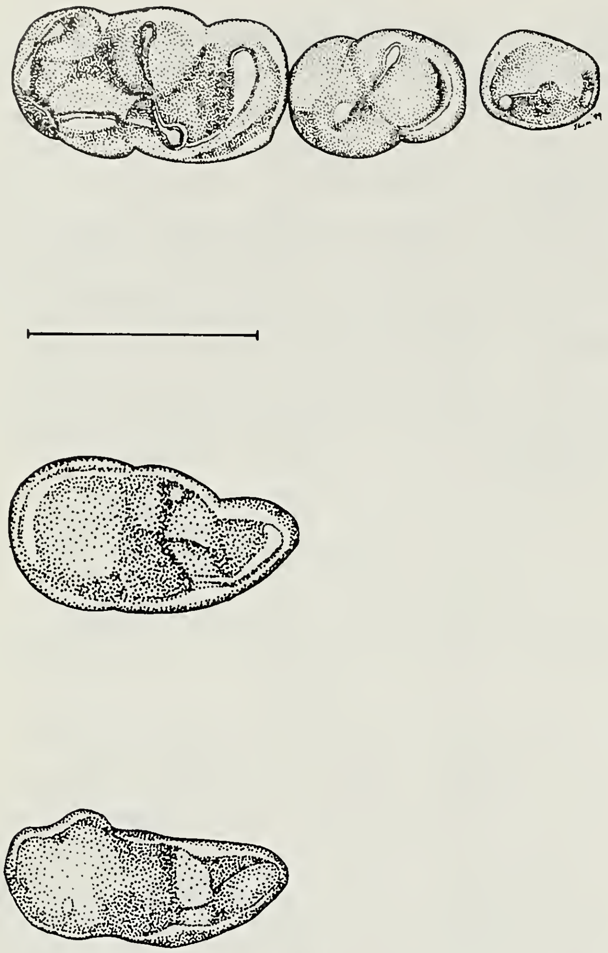

Fig. 1. Occlusal view (right p3-m1) of *P. genowaysi*, holotype, UNSM 25470, m1 of *L. wortmani* F:AM 25351 (middle) and m1 of *L. ancipidens* UF 5655 (bottom). Scale bar = 1 cm.

Nebraska State Museum, Lincoln, Nebraska.

Diagnosis.—Larger and more robust than *L. primus* and *L. wortmani.* The m1 has a labial cingulum, well-defined hypoconulid and the trigonid is rounded anteriorly. The m2 has a labial cingulum. Premolars and molar are more robust and rounded than in other *Leptarctus.* The second cusp of p4 enlarged and almost as big as the main cusp. The p3 has a small secondary cusp and a thick posterior cingulum.

Description.—The mandible is missing anterior parts of p3 and the ramus above the angular process. The dentition, p3–m1, is well-preserved. The teeth are more rounded and wider than in other *Leptarctus* (Fig. 1). The lower canines of F:AM 25176 and F:AM 49412 have a groove on the antero-labial side, characteristics of the leptarctines. The masseteric fossa is larger and deeper than in *L. primus* and *L. wortmani.*

In p3, a cingulum is located on the postero-lingual face of the tooth and a well-defined posterior accessory cusp is present postero-labially (Figs. 1–3).

The p4 has a round ridge on the anterior margin of the main cusp. The second cusp of p4 is well-developed and proportionately larger than in other *Leptarctus.*

The first molar has three large and high cusps on the trigonid. The metaconid is the highest cusp and a labial cingulum is present on the lateral surface of the connection between paraconid and protoconid. The talonid of m1 is expanded posteriorly by a median hypoconulid. The hypoconulid is connected to the hypoconid and the entoconid by a ridge. The second lower molar of F:AM 49412 has a labial cingulum, which differs from other species. The m2 is double-rooted and large and the mandibular foramen is deeper and more prominent compared to *L. primus* and *L. ancipidens.*

Discussion

The mandible (UNSM 25470) of *Pseudoleptarctus genowaysi* is the largest known leptarctine mandible. The presence of a distinctive cingulum in the labial side of m1 is unique among carnivores.

The lower canines of all leptarctines including *P. genowaysi* are curved and grooved on the lingual side. We know of no similar groove among modern carnivorous mammals with the exception of the coati, *Nasua* (Lim 1999a). *Nasua* is an omnivorous procyonid and one of the most frugivorous carnivores (Gompper & Decker 1998). The groove in both leptarctines and *Nasua* stops at the base of crown. *Solenodon,* a modern insectivore, has a deeper and broader groove on the antero-labial side of the lower canine as a conduit for toxic saliva, but the groove in *Solenodon* continues to the very edge of the lower jaw.

The p3 and p4 of *P. genowaysi* are very similar to those of *Nasua nasua* in having

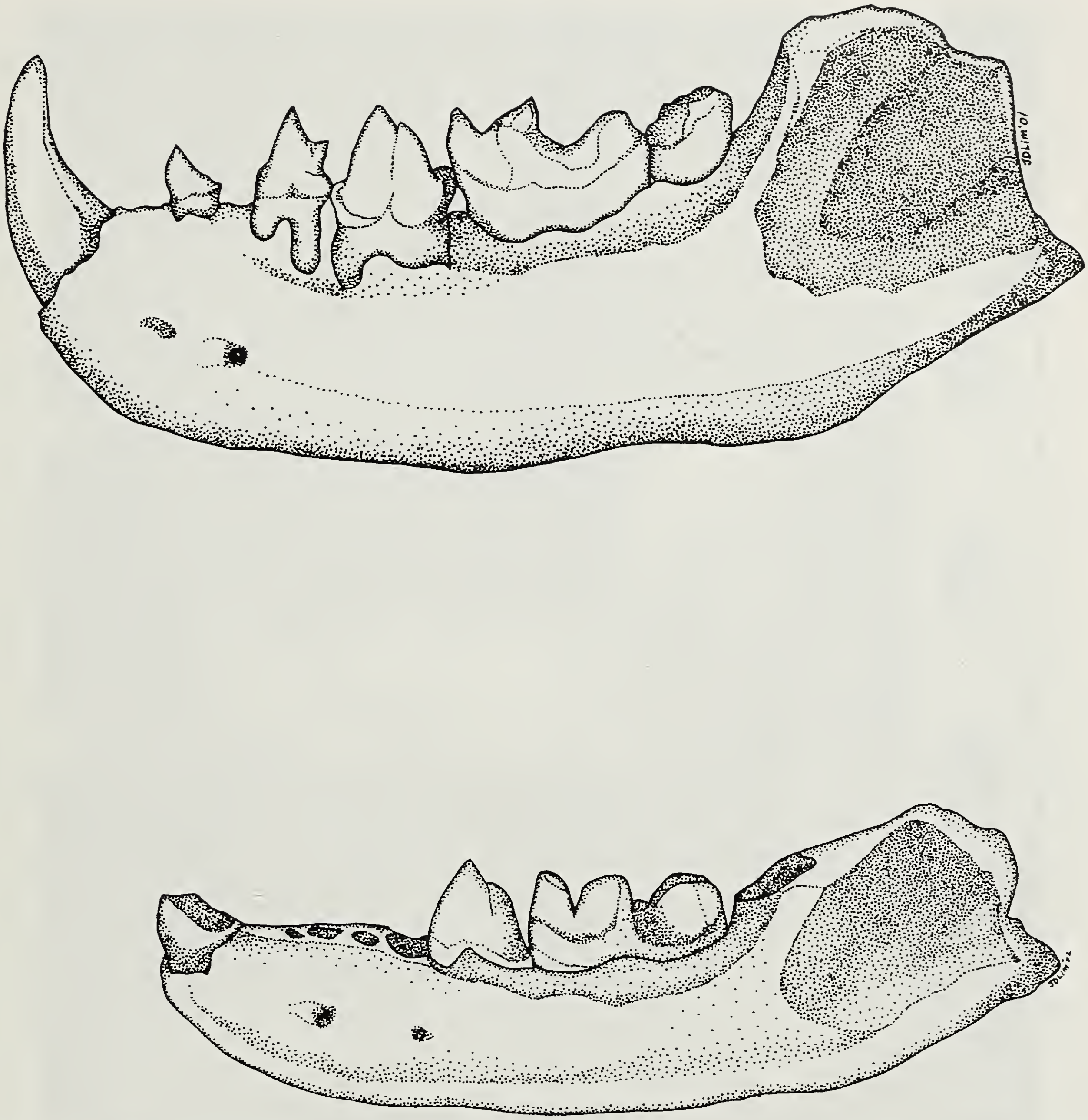

Fig. 2. Lateral views of mandibles of *P. genowaysi* (F:AM 49412, above) and *L. primus* (AMNH 18270, bottom), ×1.5.

a postero-lingual cingulum. The presence of an accessory cusp on the postero-external face on p3 is similar to that in *L. wortmani* while other leptarctines do not have the accessory cusp. The dentition and mandible of *Pseudoleptarctus genowaysi* are robust and bigger than those of *L. wortmani* (Fig. 3). The height of mandible (below m1) of *P. genowaysi* (UNSM 25470) is 45% greater than in *L. wortmani* (F:AM 25351). The p4 shows some similarities to procyonids. The secondary cusp on p4 is well-defined and similar in size to the first cusp as in *Procyon lotor* and *Nasua nasua.* Other leptarctines and living mustelids have a much smaller secondary cusp.

One of the most distinctive characters of the new species is the presence of a cingulum on the labial side of m1. The cingulum begins laterally at the paraconid and stops below the protoconid. The highest cusp of m1 is the metaconid while protoconids in *L. primus, L. wortmani,* and *L. ancipidens* are higher than the metaconid. The metaconids in *Procyon lotor* and *Nasua nasua* are also higher than the other

Fig. 3. Mandibles of leptarctines in lateral view. a, *P. genowaysi* UNSM 25470, holotype; b, *L. primus* KUVP 9153; *L. ancipidens* UF 5655; d, *L. wortmani* cast of F:AM 25351. Scale bar = 5 cm.

Table 1.—Measurements (mm) of lower teeth and mandibles of *P. genowaysi, L. primus, L. wortmani* and *L. ancipidens.*

	P. genowaysi (UNSM 25470)	*L. primus* (AMNH 18270)	*L. wortmani* (F:AM 25351)	*L. ancipidens* (UF 5655)
Height of mandible (below m1)	14.5	8.5	10	15.7
p3: Length	5.2		5.5	4.9
Width	4.0		3.5	3
p4: Length	8.3	5.4	7.1	6.5
Width	5.1	3.3	4.1	4.1
m1: Length	11.7	9.6	11.1	10.7
Width	6.7	4.2	5.6	4.9
Length between p3–m1	26.1		23.4	22.7

cusps on m1. The width of m1 in *P. genowaysi* is 1.6 times wider than in *L. primus* (Table 1). The talonid of m1 in *P. genowaysi* is enlarged with well-defined cusps (hypoconid, hypoconulid, and entoconid) as in *Procyon lotor.*

The carnassial is a critical tooth in carnivorous mammals and major changes in its structure usually indicate changes in dietary preference. In general, the more carnivorous the diet the greater the emphasis on antero-posterior lophing of the trigonid coupled with reduction of the talonid. Herbivory is usually signaled by reduction of the trigonid and enlargement of the talonid. *Leptarctus* follows this pattern. Cross-lophing is also characteristic of the teeth of herbivorous mammals. *Pseudoleptarctus* presents an unusual mixture of these features. The trigonid is not reduced being about the same length as the talonid, but its anterior margin is squared so that the tooth pattern is dominated by cross-lophs. This creates a tooth even more modified towards herbivory than that of the raccoon, *Procyon lotor,* and in some ways similar to that of the leaf-eating koala bear, *Phascolarctos cinereus.* We have previously pointed out other similarities between *Leptarctus* and koalas, and think that leaf-eating might have played a role in the leptarctine diet, especially in *Pseudoleptarctus* (Lim 1997, 1999). Examination of the muscle insertions indicates a greater capacity to deviate the mandible when chewing and this probably contributes to the rearrangement of cusps and the accentuation of cross-lophs. The lack of trigonid reduction (already present in *Leptarctus*) and the large double rooted m2 (as shown by the alveoli) are primitive character states as compared to *Leptarctus* and show that *Pseudoleptarctus* is not simply a late occurring and advanced species of *Leptarctus* but a separate line that split off early in leptarctine evolution. The widening of the trigonid occurs in parallel with widening of the p4 through enlargement of the secondary cusp and accentuation of the cingulum. Chewing force has shifted forward and this is reflected in a slight forward extension of the masseteric fossa as compared to *Leptarctus.* The reduced peg-like central incisors and the outward divergence of the canines in leptarctines suggests some specialized function and might have provided an exit for a long, slender, mobile tongue.

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Literature Cited

Gompper, M. E., & D. M. Decker. 1998. *Nasua nasua.*—Mammalian Species 580:1–9.

Leidy, J. 1856. Notices of extinct Vertebrata discovered by Dr. F. V. Hayden, during the expedition to the Sioux County under the command of Lieut G. K. Warren.—Proceeding of the Academy of Natural Sciences of Philadelphia 8:311–312.

Lim, J.-D. 1996. Dental evidence of *Leptarctus* as a frugivorous mustelid.—Journal of Vertebrate Paleontology 16(3):48A.

———. 1997. Functional morphology of *Leptarctus.*—Journal of Vertebrate Paleontology 17(3):60A.

———. 1999a. Systematics and functional morphology of Leptarctus (Mammalia: Mustelidae). Unpublished Ph.D. dissertation, University of Kansas, Lawrence, 151 pp.

———. 1999b. Evidence for *Leptarctus* as an arboreal frugivorous mustelid.—Journal of Vertebrate Paleontology 19(3):59A.

Lim, J.-D, & D. Miao. 2000. New species of *Leptarctus* (Carnivora: Mustelidae) From the Miocene of Nebraska, U.S.A.—Vertebra PalAsiatica 38(1):52–57.

Lim, J.-D, & L. D. Martin. 2001a. New evidence for plant-eating in a Miocene mustelid.—Current Science 81(3):314–317.

———. 2001b. A new species of *Leptarctus* (Mustelidae) from the Miocene of Kansas, USA.—Neues Jahrbuch für Geologie und Paläontologie Monatshefte 10:633–640.

Lim, J.-D, L. D. Martin, & R. W. Wilson. 2001. A new species of *Leptarctus* (Carnivora, Mustelidae) from the Late Miocene of Texas.—Journal of Paleontology 75:1043–1046.

Lim, J.-D, & L. D. Martin. 2002. A new fossil mustelid from the Miocene of South Dakota, USA.—Naturwissenschaften. DOI 10.1007/s00114-002-0315-1 (Published online: 20 March, 2002)

Matthew, W. D. 1924. Third Contribution of the Snake Creek Fauna.—Bulletin of American Museum of Natural History 50(2):59–210.

Olsen, S. J. 1957. Leptarctines from the Florida Miocene (Carnivora, Mustelidae).—American Museum Novitates 1861:1–7.

Olsen, S. J. 1958. The skull of *Leptarctus ancipidens* from the Florida Miocene.—Special Publication No. 2 Contribution to Florida Vertebrate Paleontology Paper 2:1–11.

Qiu, Z. & N. Schmidt-Kittler. 1982. On the phylogeny and zoogeography of the leptarctines (Carnivora, Mammalia).—Palaeontol Zeitschrift 56:131–145.

Simpson, G. G. 1930. Tertiary Land Mammal of Florida.—Bulletin of American Museum of Natural History 59(3):149–211.

Smith, K. K. 1993. The form of the feeding apparatus in terrestrial vertebrates: Studies of adaptation and constraint. Pp. 150–196 *in* J. Hanken & B. K. Hall, eds., The skull, vol. 3. University of Chicago Press, Chicago, 460 pp.

Stock, C. 1930. Carnivora New to the Mascal Miocene Fauna of Eastern Oregon.—Carnegie Institution of Washington Publication 404:43–48.

Turnbull, W. D. 1970. Mammalian masticatory apparatus.—Field Museum of Natural History (Fieldiana: Geology) 18:149–356.

Wortman, J. 1894. On the Affinities of *Leptarctus primus* of Leidy.—Bulletin of American Museum of Natural History 6:229–231.

Zhai, R. J. 1964. *Leptarctus* and other Carnivora from the Tung Gur Formation, Inner Mongolia.—Vertebrata PalAsiatica 8(1):27–32.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(1):23–28. 2003.

Species limits in the pygmy antwren (*Myrmotherula brachyura*) complex (Aves: Passeriformes: Thamnophilidae): 1. The taxonomic status of *Myrmotherula brachyura ignota*

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Abstract.—The taxonomic position of a trans-Andean avian population described as *Myrmotherula brachyura ignota* Griscom, 1929, has existed under a cloud of uncertainty for the past fifty years. Recent advances in the use of vocalizations in species-level taxonomy in suboscines, generally, and thamnophilids, specifically, provide a basis for a reexamination of the relationships of *M. b. ignota* to two closely related cis-Andean taxa, *M. brachyura* and *M. obscura.* Four independent vocal characters distinguish *M. b. ignota* from *M. brachyura,* whereas the vocalizations of *M. b. ignota* cannot be distinguished from those of *M. obscura. Myrmotherula b. ignota* and *M. obscura* also share plumage characters distinct from *M. brachyura. Myrmotherula ignota* is recognized as a distinct species, Moustached Antwren, of which *M. i. obscura* is a subspecies.

Smallest of the typical antbirds (Thamnophilidae), *Myrmotherula brachyura* was also one of the first in its family to be described (Hermann 1783). Unlike most thamnophilid species with widespread distributions for which a plethora of subspecies were described in the following almost 150 years, *M. brachyura* remained a monotypic species as late as 1924 (Cory and Hellmayr 1924) with a geographic range extending throughout Amazonia, the Guianas, and the region immediately northwest of the Andes. In 1929, the trans-Andean population in Panama and Colombia (now known to extend to northwestern Ecuador) was described as *M. b. ignota* (Griscom 1929) based on the briefest of descriptions: "Similar to typical *M. brachyura* of Cayenne and Amazonia, but the light streaking on pileum, wings, and back greatly reduced, resulting in more solidly blackish areas; female with much paler rufous crown stripes, and no fulvous on throat."

Zimmer (1932), after examining about 100 cis-Andean specimens of *M. brachyura,* noticed that some were "sharply distinguishable." He stated that if these specimens were found in allopatry with *M. brachyura,* he would have considered them conspecific, but because they occurred at the same locations as *M. brachyura,* he described them as a new species, *Myrmotherula obscura,* Short-billed Antwren. Zimmer's diagnosis and descriptions were much more complete than those of Griscom, but the salient points can be summarized as follows. Compared to *M. brachyura,* male upperparts and wings much darker (blacker), black mystacal stripe and black postocular stripe much broader, and length of bill reduced (ranges of measurements of exposed culmen abut but do not overlap); female with pale head markings narrower and more rufescent, back markings narrower and whiter, and mystacal streak, postocular area, and bill length differed like male. The geographic range of *M. obscura* has since been found to extend through southeastern Colombia, eastern Ecuador, northeastern Peru, and extreme west-central and southwest Amazonian Brazil.

In his description Zimmer (1932) did not compare specimens of *M. obscura* and *M. b. ignota,* apparently because he only had one male specimen of *M. b. ignota* at hand. *Myrmotherula b. ignota* is an uncommon bird in the field and in collections, and the paucity of specimens has hampered understanding of its taxonomic position. However, the similarity of plumage characters distinguishing *M. b. ignota* and *M. obscura* from *M. brachyura* is apparent from the descriptions. Subsequently, the similarity caused Bond (1950), who had obtained two additional female-plumaged specimens of *M. b. ignota,* to consult Hellmayr on the possibility that they could be more closely related to *M. obscura* than to *M. brachyura.* Their conclusions were inconclusive, confused by the finding that bill lengths of *M. b. ignota* fell into the range of those of *M. brachyura,* and Zimmer had emphasized bill length as an important character separating *M. brachyura* and *M. obscura.* Their considerations, however, led Meyer de Schauensee (1966) to write "It is possible that what is currently called *M. brachyura ignota* from Panama and northwest Colombia may prove to be specifically distinct from *M. brachyura* and conspecific with *M. obscura* . . ." Most recently, the seventh edition of the Check-list of North American Birds (American Ornithologists' Union 1998) noted the possibilities that *M. b. ignota* might be specifically distinct or more closely related to *M. obscura* than to *M. brachyura.*

Today, bolstered by the growing understanding that vocalizations in nearly all suboscines (including the Thamnophilidae) are innate, vocal characters are increasingly employed in examining species level questions in these families (Baptista & Kroodsma 2001). In an effort to provide a point of reference for considering species limits in the Thamnophilidae using vocal characters, Isler et al. (1998) compared characteristics of vocalizations of eight pairs of closely related but reproductively isolated, syntopic antbird species. Among these were *M. obscura* and *M. brachyura,* whose vocalizations in the region of sympatry were analyzed. Three independent vocal characters were found to distinguish loudsongs (sensu Willis 1967) of the two species, and in addition, each species included a call in its repertoire not known to be delivered by the other.

Given the diagnostic differences found between vocalizations of *M. obscura* and *M. brachyura,* an obvious question for empirical analysis is which of these species are the vocalizations of *M. b. ignota* most closely related? Earlier consideration of the question was hampered by the lack of vocal recordings of *M. b. ignota,* a situation similar to that facing earlier specimen comparisons. Ten years ago only one recording of *M. b. ignota,* a loudsong, was available. Its initial examination suggested that *M. b. ignota* was more closely related to *M. obscura* (M. & P. Isler, R. Ridgely in Ridgely & Tudor 1994), but the single example precluded analysis. Since then, a number of recordings of *M. b. ignota* have been obtained, and they allow us to address this fundamental question.

Methods

Because current species designations confuse rather than clarify the discussion, henceforth in this paper we refer to the three taxa simply as *brachyura, obscura,* and *ignota.*

Morphology.—Examination of specimens available at the National Museum of Natural History (USNM) indicated that descriptions of earlier authors (cited in the introduction) accurately reflected plumage coloration of the three taxa. Consequently, no additional plumage data were obtained. Because of the importance of bill measurements in the description of *obscura,* and because the differences in bill length between *ignota* and *obscura* deterred earlier workers from establishing a close relationship between the taxa, measurements of bill length were obtained, using MAX-CAL electronic digital calipers, from specimens of the Louisiana State University Museum of Natural Science, Baton Rouge, Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru, and USNM.

Vocalizations.—The sample of recordings of *brachyura* and *obscura* used and referenced in an earlier study of vocal differences (Isler et al. 1998) was employed in this analysis. The sample was obtained in the vicinity of the lower Río Napo in northern Peru. The reason for confining the sample to this area was to obviate the possibility of introducing geographic variation in the vocalizations of the wide-ranging *brachyura* into the comparison. Analysis of geographic variation in the vocalizations of *brachyura* was beyond the scope of this paper but will be addressed subsequently.

Seven recordings of *ignota* from Panama and three from Ecuador were employed. The recordings were not yet archived in an institutional collection. They were obtained at the following locations (listed as country, department, locality) which are followed by the name of recordist and number of individuals recorded. PANAMA: Colón: Canal Zone (R. Ridgely 1, B. Whitney 3). San Blas: Nusagandi (B. Whitney 1). Darién: Cerro Pirre (B. Whitney 1), Cana (B. Whitney 1). ECUADOR: Esmeraldas: 30 km E San Lorenzo (D. Lane 1). Pichincha: 20 km N Pedro Vicente Maldonaldo (D. Lane, 2).

Recordings were analyzed using "Canary 2.1.4" software (Charif et al. 1995). Procedures for analyzing vocalizations of *brachyura* and *obscura* were described in the earlier paper (Isler et al. 1998). Vocalizations of *ignota* were analyzed as follows. First, sound spectrograms were printed of each recording to identify vocalization types and to permit visual comparisons among recordings. In each recording, the first three measurable loudsongs were selected for measurement. Measurements were directed to vocal characteristics that had been found to differ diagnostically in the earlier comparisons of *brachyura* and *obscura.* Number of notes, duration, and pace (notes/sec) were obtained for the entire vocalization. Then, loudsongs were divided into five sections (Isler et al. 1998) to obtain the pace for each section and ratios of change of pace between sections. Measurements were also taken of the duration of the second, middle, and next-to-last notes and the spaces following them.

Finally, we determined whether vocal characters differed diagnostically between taxa, employing guidelines developed earlier (Isler et al. 1998, 1999). As described in more detail in the previous papers, such differences must be unambiguously distinct character states, or, in the case of continuous variables, ranges may not overlap and the means (x) and standard deviations (SD) of the population with the smaller set of measurements (a) and the population with the larger set of measurements (b) must meet the requirement:

$$x_a + t_a SD_a \leq x_b - t_b SD_b \qquad (1)$$

where t_i = the t-score at the 97.5 percentile of the t distribution for $n - 1$ degrees of freedom (except for ratios where this statistical test is inappropriate).

Results and Discussion

Morphology.—Principal plumage characters distinguishing the taxa are as follows. Males of *ignota* and *obscura* are similar to *brachyura* except mystacal streak is broader and more distinct, black postocular streak more prominent, and black of crown and upperparts more extensive. Male *obscura* differs from *ignota* in having fewer pale streaks and consequently more extensive black in the plumage, especially on upperparts. Female *ignota* and *obscura* similar to *brachyura* except malar and postocular streaks are more prominent (as in male) and light portions of head, throat, and breast are darker: tawny brown in *ignota,* and buff in *obscura* (distinguishing these two taxa) rather than white or white tinged buff as in *brachyura.*

Bill measurements were taken from a larger number of specimens of *ignota,* including the first specimens from Colombia, than were available to earlier authors. The mean of bill length (measured from the nares) for *ignota* in Panama is 8.4 ± *SD* of 0.2 mm (range 8.2 to 8.8, *n* = 8); in Colombia the mean was 7.9 ± *SD* of 0.2 mm (range 7.5 to 8.1, *n* = 7). Equivalent values for *obscura* in Peru are 7.5 ± *SD* of 0.3 mm (range 6.8 to 8.1, *n* = 16), and those for *brachyura* (various countries) are 8.7 ± *SD* of 0.3 mm (range 8.4 to 9.3, *n* = 8). These values confirm the difference in bill length between *ignota* in Panama and *obscura* found by earlier authors, but they also show that bill length of *ignota* in Colombia is intermediate, suggesting the possibility of clinal variation between populations of *ignota* in Panama and *obscura* in Amazonia.

Vocalizations.—The earlier study of vocal differences between *brachyura* and *obscura* (Isler et al. 1998) concluded that there are at least four independent vocal characters that distinguish the two taxa. These vocal differences, although primarily determined by measurements, are also evident in visual comparisons of sound spectrograms (Fig. 1). The examples shown in the figure are typical for each taxon, i.e., they represent a composite of the mean values of measurable vocal characters obtained for all spectrograms that were studied. No diagnostic differences have been found between vocalizations of *ignota* recorded in Panama and in Ecuador, and the example shown in Fig. 1 and the data that follow represent combined values for recordings obtained in both countries. The only recording available from near the type locality of *ignota,* that of a loudsong, conforms closely to the example shown.

Visual examination of the spectrograms (Fig. 1) shows that the vocalizations of *ignota* are similar to those of *obscura* and differ from those of *brachyura.* Visually apparent in comparisons, the loudsong of *brachyura* is faster in pace (notes/sec) than those of *obscura* and *ignota,* and the central notes of *brachyura* loudsongs are short and sharply downslurred sounding unmusical to the human ear, whereas those of *obscura* and *ignota* are longer and less steeply downslurred, having more of a musical quality. Less obvious visually, the pace of *brachyura* speeds up more than that of *obscura* and *ignota* (erroneously verbally described as the reverse in Isler et al. 1998 although the quantitative data were correct). In addition to the loudsong, *brachyura* and *obscura* deliver an abrupt note (Fig. 1B, G) that does not differ diagnosably between them (not yet recorded for *ignota*). However, a second type of call is clearly distinct. The second call of *brachyura* (*n* = 4) is a stereotyped trill (Fig. 1C), but those of *obscura* (*n* = 12) and *ignota* (*n* = 4) a downslurred note (Fig. 1E, H). The latter varies somewhat among individuals, as exemplified in Fig. 1, but is consistent in its essential characteristics.

Visual distinctions between loudsongs of *brachyura* (Fig. 1A) and those of *obscura* (Fig. 1D) and *ignota* (Fig. 1F) are supported by comparative analysis of measurements (data presented include the mean followed by the standard deviation and range). Comparing the entire loudsong, there was no overlap in ranges of the number of notes between *brachyura* loudsongs (28.3 ± 3.0, 23–33 notes; *n* = 11) and loudsongs of *ignota* (17.4 ± 1.8, 14–21; *n* = 11) and *obscura* (16.4 ± 3.2, 11–22; *n* = 19) although only the difference between *brachyura* and *ignota* meets our test of significance. On the other hand, *brachyura* loudsongs are significantly faster in pace than loudsongs of both *ignota* and *obscura*; (11.3 ± 0.7, 10.0–12.4 notes/sec) versus (6.6 ± 0.5, 6.0–7.5) and (6.1 ± 0.6, 5.0–7.0) respectively. Differences noted visually between the central notes of *brachyura* loudsongs and those of *ignota* and *obscura* are reflected in significant differences in the lengths of the middle notes; (28 ± 3, 21–32 msec) versus (62 ± 5, 54–71) and (62 ± 8, 45–77) respectively. Finally, change in pace in the initial half of the song is reflected in the

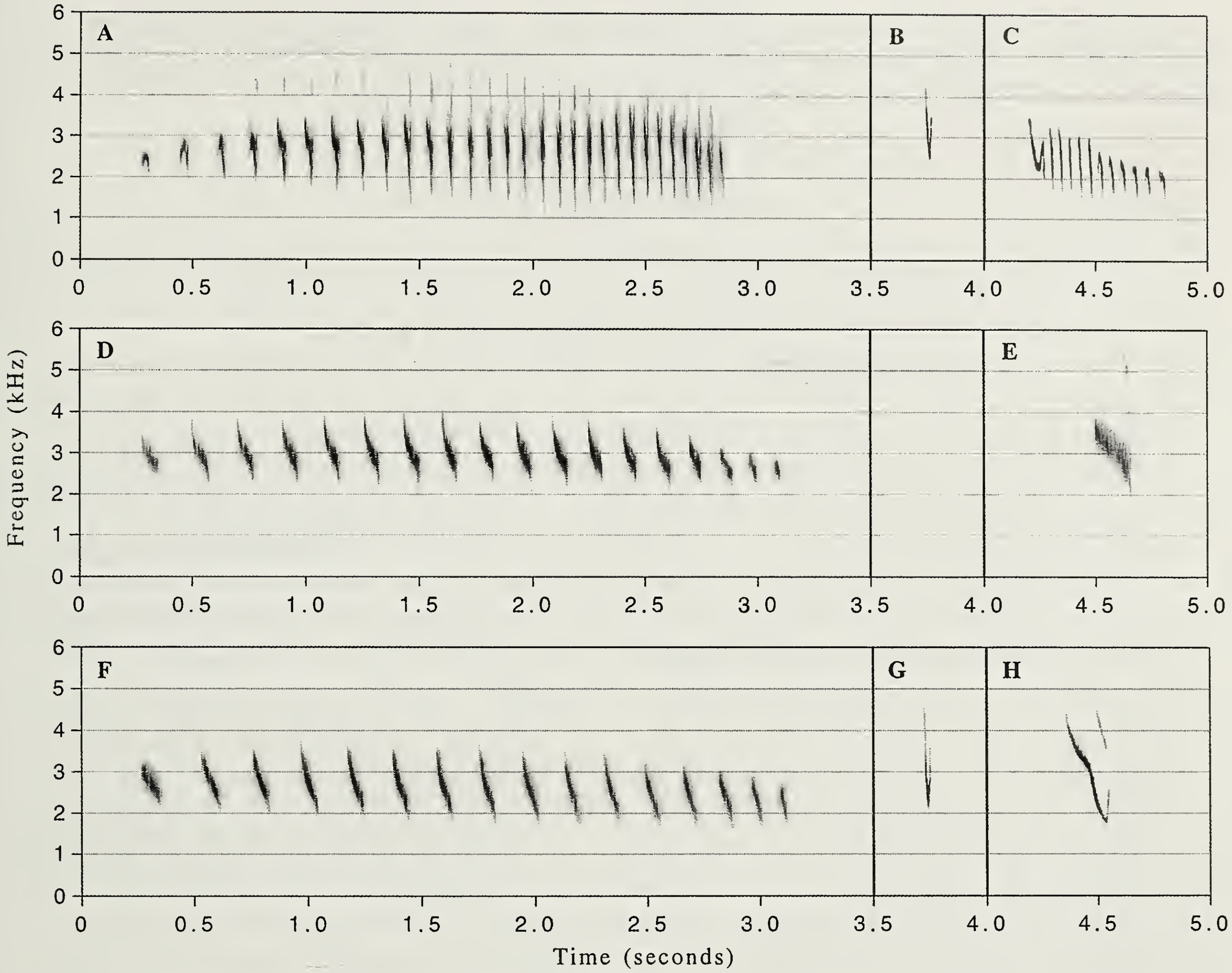

Fig. 1. Sound spectrograms of loudsongs and calls of taxa in the *Myrmotherula brachyura* complex. (A) loudsong of *brachyura* (Peru, Loreto, Quebrada Sucusari; ISL BMW.23:10; Whitney); (B) abrupt note of *brachyura* (Peru, Loreto, Quebrada Sucusari; ISL BMW.23:10; Whitney); (C) stereotyped trill of *brachyura* (Peru, Loreto, Quebrada Sucusari; ISL BMW.94:16; Whitney); (D) loudsong of *ignota* (Ecuador, Esmeraldas, 30 km SE of San Lorenzo; ISL DFL.5:01; Lane); (E) downslurred note of *ignota* (Ecuador, Esmeraldas, 30 km SE of San Lorenzo; ISL DFL.5:01; Lane); (F) loudsong of *obscura* (Peru, Loreto, Quebrada Sucusari; MLNS 30881; Parker); (G) abrupt note of *obscura* (Peru, Loreto, Quebrada Papaya; MLNS 29192; Parker); (H) downslurred note of *obscura* (Peru, Loreto, Quebrada Papaya; MLNS 29192; Parker). Identification data include location, archive number, and recordist. Acronyms for recording archives: MLNS = Macaulay Library of Natural Sounds, Cornell Laboratory of Ornithology, Ithaca, New York; ISL = recordings not yet archived in an institutional collection but copied into an inventory maintained by the authors.

ratio between the duration of the second note and space and that of the middle note and space, with the higher ratios expressing a greater reduction in duration and hence a more rapid acceleration in pace; values of this ratio are greater for *brachyura* (1.73 ± 0.11, 1.61–2.04) than for *ignota* (1.28 ± 0.10, 1.08–1.44) and *obscura* (1.29 ± 0.08, 1.18–1.47). In summary, four independent vocal characters differ diagnostically between *brachyura* and *ignota* and three between *brachyura* and *obscura*; vocal differences between *ignota* and *obscura* are insignificant.

Conclusions

Earlier studies have shown that *brachyura* and *obscura* are syntopic species that exhibit numerous diagnosable differences in vocalizations and morphology. Our comparison of *brachyura* and *ignota* demonstrates that these allopatric taxa differ to a similar extent vocally and morphologically as do the sympatric *brachyura* and *obscura*. We therefore conclude that *brachyura* and *ignota* are specifically distinct, and we recommend that *ignota* be raised to species level. However, *ignota* and *obscura* cannot be separated vocally, and given the minimal morphological distinctions between them and recognizing the principle of priority, we recommend that *obscura* be considered a subspecies of *Myrmotherula ignota* under the Biological Species Concept (Johnson et al. 1999). Additional data and analysis, including genetic studies, are needed to confirm whether differences between *M. i. ignota* and *M. i. obscura* warrant their maintenance as subspecies, or conversely, that they deserve recognition as distinct species.

We propose the English name Moustached Antwren for *M. ignota*. The name reflects the wide black mystacal stripe characteristic of both subspecies. The name Short-billed Antwren, previously given *obscura,* is no longer appropriate because bill lengths of the newly constituted species overlap the bill lengths of *brachyura*. Nor do we believe that Griscom's Antwren, proposed for *ignota* if it were to be considered a distinct species (Ridgely & Tudor 1994), is satisfactory. In our opinion, Zimmer's detective work in discovering *obscura* is much more worthy of recognition than Griscom's minimal description of *ignota,* and it seems best to use a plumage feature as a basis for the English name.

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Literature Cited

Baptista, L. F., & D. E. Kroodsma. 2001. Avian bioacoustics. Pp. 11–52 *in* J. del Hoyo, A. Elliot, & J. Sargatal, eds. Handbook of the birds of the world, vol. 6. Mousebirds to Hornbills. Lynx Edicions, Barcelona.

Bond, J. 1950. Notes on Peruvian Formicariidae.—Proceedings of Academy of Natural Sciences of Philadelphia 102:1–26.

Charif, R. A., S. Mitchell, & C. W. Clark. 1995. Canary 1.2 User's Manual. Cornell Laboratory of Ornithology, Ithaca, New York.

Cory, C. B., & C. E. Hellmayr. 1924. Catalogue of birds of the Americas. Pteroptochidae—Conopophagidae—Formicariidae.—Field Museum of Natural History (Zoological Series) 13, Pt. 3:1–369.

Griscom, L. 1929. A collection of birds from Cana, Darién.—Bulletin Museum of Comparative Zoology, Harvard University 69:149–190.

Hermann, J. 1783. Tabula affinitatum animalium olim academico specimine edita, nunc uberiore commentario illustratacum annotationaibus ad historiam naturalem animalium augendam facientibus. J. G. Treuttel, Strasbourg, 370 p.

Isler, M. L., P. R. Isler, & B. M. Whitney. 1998. Use of vocalizations to establish species limits in antbirds (Passeriformes; Thamnophilidae).—Auk 115:577–590.

———. 1999. Species limits in antbirds (Passeriformes; Thamnophilidae): the *Myrmotherula surinamensis* complex.—Auk 116:83–96.

Johnson, N. K., J. V. Remsen Jr., & C. Cicero. 1999. Resolution of the debate over species concepts in ornithology: a new comprehensive biological species concept. Pp. 1470–1482 *in* N. J. Adams and R. H. Slotow, eds., Proceedings 22nd International Ornithological Congress, Durban. BirdLife South Africa, Johannesburg.

Meyer de Schauensee, R. 1966. The species of birds of South America and their distribution. Livingston Publishing Company, Narbeth, Pennsylvania.

Ridgely, R. S., & G. Tudor. 1994. The birds of South America, vol. 2. The suboscine passerines. University of Texas Press, Austin.

Willis, E. O. 1967. The behavior of Bicolored Antbirds. University of California Publications in Zoology 79:1–132.

Zimmer, J. T. 1932. Studies of Peruvian birds. III. The genus *Myrmotherula* in Peru, with notes on extralimital forms, part 1.—American Museum Novitates 523:1–19.

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New fossil material with a redescription of the extinct Condor *Gymnogyps varonai* (Arredondo, 1971) from the Quaternary of Cuba (Aves: Vulturidae)

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Abstract.—New material of the Cuban Condor, originally described at *Antillovultur varonai* (Arredondo, 1971), indicates that it is definitely referable to the genus *Gymnogyps,* but possesses other unique features that support its status as an extinct endemic species. It is characterized by distinct cranial and premaxillary features that are associated with more powerful musculature for feeding. These features include dorso-ventral deepening of the skull, long and massive occipital processes, a large occipital condyle, and a more vaulted and broad rostrum compared with the living species *G. californianus.* Postcranial bones differ little from the living California Condor except in being larger and more robust. The Cuban Condor may have evolved relatively rapidly after a mainland population of *G. kofordi* or *G. californianus* reached the island and became specialized on the limited large prey available there during the Pleistocene.

Resumen.—Nuevo material del Cóndor Cubano, originalmente descrito como *Antillovultur varonai* (Arredondo, 1971), indica que éste es definitivamente referible al género *Gymnogyps,* pero posee caracteres únicos que sustentan su estado como especie endémica extinta. Se caracteriza por rasgos craneales y premaxilares distintivos, asociados a una musculatura potente, dado su modo de alimentación. El cráneo presenta una mayor profundidad dorsoventral, procesos occipitales largos y masivos, cóndilo occipital grande, y rostro más ancho y arqueado, en comparación con la especie viviente *G. californianus.* Los huesos postcraneales difieren poco del Cóndor de California, excepto por ser mayores y más robustos. El Cóndor Cubano pudo haber evolucionado relativamente rápido a partir de la colonización de la isla por una población continental de *G. kofordi* o *G. Californianus,* que se especializó en el consumo de las limitadas carroñas derivadas de la megafauna disponible en Cuba durante el Pleistoceno.

Condors are large members of the family Vulturidae (=Cathartidae auct.) that appear to have originated in North America and later colonized South America (Emslie 1988). The only condor known outside the continental mainland of the Americas is the Cuban Condor *Gymnogyps* ("*Antillovultur*") *varonai* (Arredondo 1971, 1976; Suárez 2000), providing evidence for the capability of these scavengers to cross large bodies of water (see Tambussi & Noriega 1999). The genus *Gymnogyps* Lesson was most diverse in the Pleistocene and only the California Condor (*G. californianus*) survives today (Emslie 1988). The earliest record of the genus is from late Pliocene (Blancan) deposits of Florida (Emslie 1988, 1998). In addition, the fossil species *Gym-*

nogyps kofordi is known from the early Pleistocene (middle Irvingtonian) of Florida (Emslie 1988). The only other fossil species in this genus are *G. howardae* from the late Pleistocene asphalt deposits of Talara Tar Seeps, Peru (Campbell 1979) and *G. varonai,* originally described as *Antillovultur varonai* (Arredondo, 1971) from Quaternary cave deposits of Cuba. The supposed species, *G. amplus,* from late Pleistocene asphalt deposits of Rancho La Brea (Rancholabrean) described by Miller (1911), is now considered to be a junior synonym of *G. californianus* and was a large, Pleistocene temporal subspecies (Emslie 1988).

Recently, Suárez (2000) reviewed newly recovered fossil material and the generic status of the Cuban Condor as well as its paleodistribution and possible origin. As a result of this review, the monotypic and endemic genus "*Antillovultur*", in which the species *varonai* was originally described, was considered congeneric with *Gymnogyps,* an assumption that had been made by other authors (Olson 1978, Emslie 1988).

Certain cranial and postcranial characters of *Gymnogyps varonai* were described by Suárez (2000), but were limited to only the generic, rather than the specific, position of the Cuban bird. Although some cranial features agreed with those described for fossil specimens of *G. californianus amplus* and *G. kofordi,* no direct comparisons were made with these taxa and the specific status of the Cuban bird has remained unclear since that time. Here we provide more detailed comparisons of the Cuban Condor with other fossil and living species.

Materials and Methods

Material examined.—The same specimens of the Cuban Condor, *Gymnogyps varonai,* listed with localities and depositories by Suárez (2000). Proximal end of a right radius, Instituto de Ecología y Sistemática, La Habana, Cuba (IZACC 400–813). Fossils from the paleontological collection of the Museo Nacional de Historia Natural, La Habana, Cuba (MNHNCu), recovered in asphalt deposits Las Breas de San Felipe (San Felipe II), 5.5 km west of Martí, Municipality of Martí, Matanzas Province, Cuba (for description and discussion of the chronology of this deposit see Iturralde-Vinent et al. 2000): fragmentary premaxillae (MNHNCu P4594, MNHNCu P4595), right coracoid (MNHNCu P4596), proximal right carpometacarpus (MNHNCu P4597) and distal left tarsometatarsus (MNHNCu P4598). Other fossil material examined is housed at: Museo Polivalente de Sagua la Grande, Villa Clara (MPSG), Collection of Oscar Arredondo, La Habana (OA), and Collection of William Suárez, La Habana (WS).

Comparative material of the living, post-Pleistocene subspecies of the California Condor, *Gymnogyps c. californianus* examined at the National Museum of Natural History, Smithsonian Institution (USNM), include the following skeletons: 13823, 17033, 17946–50, 345225, 346582, 489359, 489406, 489755, 492447. Comparisons with specimens of the fossil California Condor, *G. c. amplus* from Rancho la Brea, were made with the extensive collections of the George C. Page Museum, Los Angeles, California. Specimens of *G. kofordi* from Florida Museum of Natural History, Gainesville (UF) include the following paratypes: distal right ulna UF 63516; left femur UF 63513; distal left tarsometatarsus UF 31904. Casts of the holotypical right tarsometatarsus UF 63512, and paratypical fragmentary cranium UF 63517, also were used for comparison with this species. Osteological terminology herein follows that of Howard (1929), Fisher (1944), and Jollie (1976–1977). Measurements were taken with a vernier caliper to the nearest 0.1 mm, following the methods of Fisher (1944) and Emslie (1988) for the cranium. Measurements designated with a plus sign (+) are from specimens with wear and abrasion, and are approximate.

Systematic Paleontology

Class Aves
Order Ciconiiformes
Family Vulturidae (Illiger, 1811)
Genus *Gymnogyps* Lesson, 1842

Generic characters of *Gymnogyps* (Emslie 1988) found in the Cuban specimens (Suárez 2000) are: cranium in dorsal view with constriction at postorbital, supraorbital edge convex, postorbital pit deep, upper mandible short and robust with nasal bar near the horizontal position in lateral view, bony circle formed by medial septum. Carpometacarpus with large proximal symphysis (see Howard 1974); tarsometatarsus with concave surface of posterior shaft and with well-developed posterior protrusion on external cotyla.

Gymnogyps varonai (Arredondo, 1971)

Amended diagnosis.—*Gymnogyps varonai* differs from *G. californianus* Say, *G. kofordi* Emslie, and *G. howardae* Campbell (cranial material unknown in this species), in having: premaxillary short, broad and deeply vaulted, positioned near the level of the external nares (premaxillary larger and less vaulted in *G. californianus*; shorter, but less vaulted in *G. kofordi*), nasal bar very short, broad and flat (nasal bar relatively more slender, less broad and more rounded dorsally, not as flat in *G. californianus*; more slender, less broad, and constricted at the midpoint in *G. kofordi*), alinasal large, wide and flat, occupying more space in a shorter narial opening (alinasal small and less wide and flat, with narial opening larger in *G. californianus*; narial opening very large in *G. kofordi*); interpalatal space thin, maxilla wide, and maxillopalatines with a thin space between them so that they nearly touch at the mid line (interpalatal space wide in both *G. californianus* and *G. kofordi*); cranium high, with strong protrusion of the supraoccipital, large and massive occipital processes with lateral areas beside supraoccipital protrusion thin and high (supraoccipital less protruding, with lateral areas wide and not as high in *G. c. californianus*; supraoccipital protrusion similar in *G. c. amplus* and *G. kofordi,* but with lateral areas wide and not as high), space between both temporal fossae small and flat (space between both temporal fossae wide and less flattened in *G. c. californianus* and *G. kofordi*), nuchal crest rostrally placed causing the area between this crest and the postorbital process to be very short (larger in specimens of *G. c. amplus* and *G. kofordi*), interorbital space wide and flat (narrower and more rounded in *G. californianus* and *G. kofordi*), postorbital processes short with caudal orientation (postorbital processes larger with rostral orientation in *G. californianus*; larger with slightly more rostral position in *G. kofordi*); temporal fossa short antero-posteriorly, but deep and in general high and wide. Distal end of ulna flat in external-distal surface, external condyle short and wide, distal radial depression large and pneumatic, carpal tuberosity large (rounded external-distal surface, external condyle large with distal radial depression small, less pneumatic in *G. californianus*; large and pneumatic distal radial depression in *G. kofordi*). Tibiotarsus with internal and external cnemial crests weakly developed and projected with reduction of muscular insertions, anterior and posterior intercondylar sulcus very thin causing the external condyle in distal view to be shorter and more voluminous. Tasometatarsus relatively short and robust, distal foramen placed low on shaft though this feature is variable.

Comparative Description

The Cuban Condor is particularly distinct from from *G. californianus* and *G. kofordi* in having a deeper, more laterally-compressed cranium with exagerated occipital and opisthotic processes, and the more rostal placement of the nuchal crest (Fig. 1). The rostrum (Fig. 2) also is more robust and deeply vaulted, with the dorsal surface bulging slightly above the level of the nasal

Fig. 1. Partial skull (MPSG 21) of *Gymnogyps varonai* (middle) in comparison with the equivalent element in fossil (right) and living (left, USNM 492447) *G. californianus,* in dorsal (A) and lateral (B) views. Scale bar = 1 cm.

bar, more so than in *G. californianus* and *G. kofordi.* The mandible is similar to *Gymnogyps californianus* except in being generally more robust, with larger and blunter articular processes. This element is not known in *G. kofordi.*

Postcranial characters of the Cuban Condor that differ from *G. californianus* include coracoid with higher and more massive furcular facet and coraco-humeral surface, attachment for anterior articular ligament in distal humerus extends farther distal-externally on shaft, presence of small pneumatic foramen on proximal shaft of radius below capital tuberosity (similar to *G. kofordi*), distal ulna with prominent shelf on the carpal tuberosity with a large foramen located distal to the shelf (similar to *G. kofordi*) and external condyle that tapers and extends less proximally, tibiotarsus (Fig. 3) with relatively long fibular crest and distal end with narrow intercondylar fossa when viewed distally, and tarsometatarsus (Fig. 4) with long and narrow middle trochlea (similar to *G. kofordi*).

Measurements (mm).—Cranium (MPSG

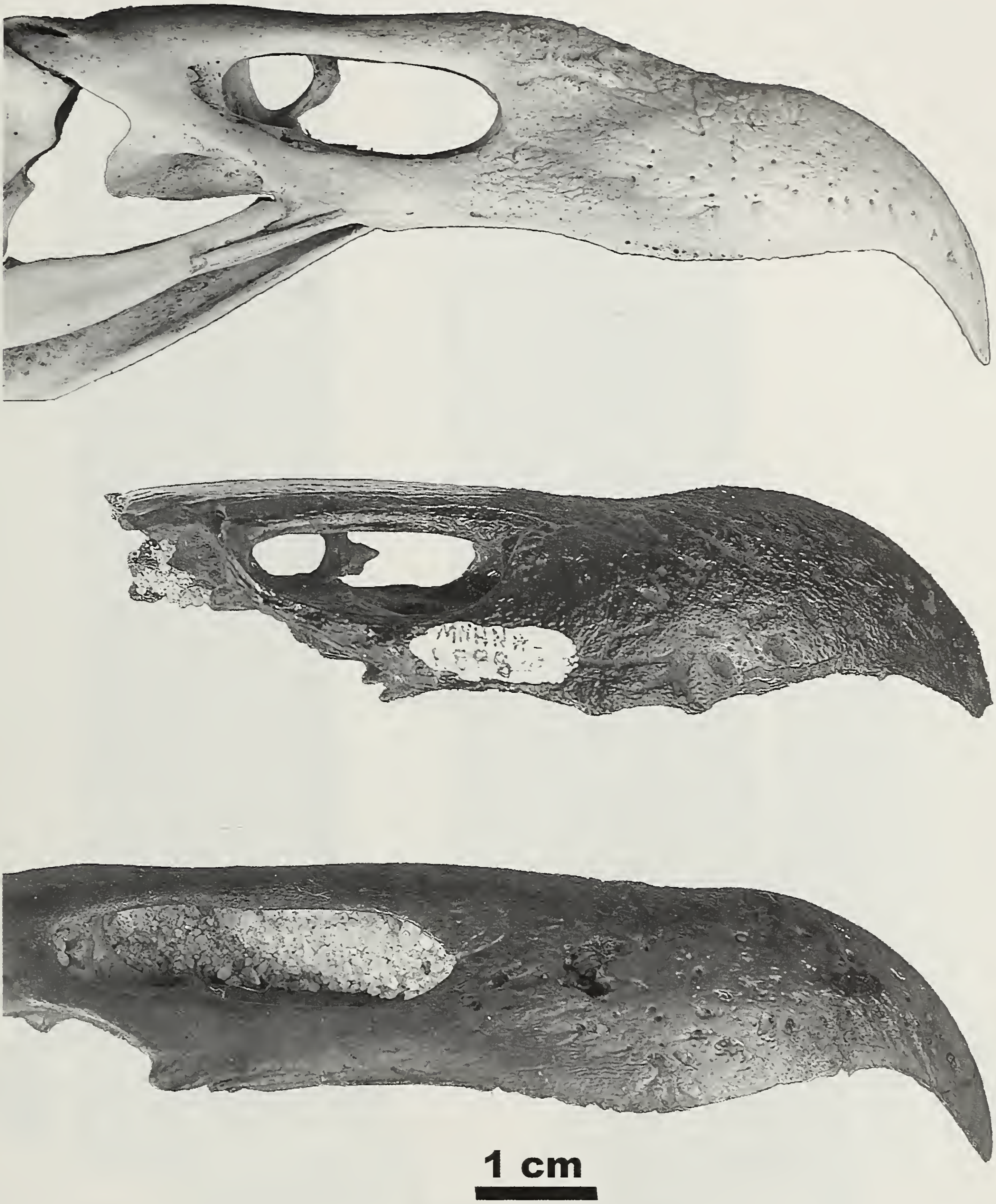

Fig. 2. Lateral view of the rostrum (upper mandible; MNHNCu P4613) of *Gymnogyps varonai* (middle) in comparison with the equivalent element in living (top, USNM 492447) and fossil (bottom) *G. californianus*. Scale bar = 1 cm.

21): temporal breadth, 43.2; cranial height, 38.8; postorbital position 51.9; postorbital breadth, 43.0; occipital breadth, 33.7. Premaxilla (MNHNCu P4613, formerly P588): breadth, 26.5; narial length, 21.9; narial breadth, 8.1; least breadth of nasal bar, 10.4; breadth of interpalatal space, 8.7; MNHNCu P4594: least breadth of nasal bar, 11.1.

Coracoid (MNHNCu P4596): total length, 98.9; least breadth at midpoint, 17.0; depth at level of midpoint of glenoid facet, 21.8. Humerus (MPSG 30 and 31): proximal breadth, 53.0 and 52.6, respec-

Fig. 3. Distal left tibiotarsus (MPSG 43) of *Gymnogyps varonai* (left) in comparison with the equivalent element in the living *G. californianus* (right, USNM 492447). Scale bar = 1 cm.

Fig. 4. Left (middle, WS 125) and right (right, WS 978) tarsometartarsi of *Gymnogyps varonai* in comparison with fossil *G. californianus* from Rancho la Brea (left). Scale bar = 1 cm.

tively; depth of head, 18.0 and 18.2; IZACC P80: least breadth and depth of shaft, 20.0 and 16.0; distal breadth and depth, 47.4 and 26.4; MPSG 32 and 33: distal breadth, 49.0 and 48.7, respectively; MPSG 33: distal depth, 25.1. Ulna (MPSG 34): distal breadth and depth, 22.9 and 23.3. Radius (MPSG 36 and 37, IZACC 400–813): greatest diameter at proximal end, 16.9, 15.7, and 15.8, respectively; MPSG 35: distal breadth, 23.6. Femur (OA 3202): total length, 141.0; proximal breadth, 37.3; depth of head, 17.0; least breadth shaft, 17.4; distal breadth, 35.6; MPSG 38: proximal breadth, 35.7; depth of head, 17.8. Tibiotarsus (MPSG 42): breadth of proximal end through articular surface, 28.3; MPSG 43: least breadth and depth of shaft, 14.2 and 11.6; depth of external condyle, 23.5; distal breadth, 26.2; MPSG 41: length of fibular crest, 53.2. Tarsometatarsus (WS 125): proximal breadth, 25.7+; least breadth and depth of shaft, 15.0 and 8.8; MPSG 45e: proximal depth, 22.4; least depth shaft, 7.1+; breadth and depth of trochlea for digit 4, 8.2 and 16.3+; WS 978: least breadth and depth of shaft, 14.7 and 8.8; distal breadth, 32.2+; breadth and depth of trochlea for digit 2, 9.6+ and 13.1+; breadth and depth of trochlea for digit 3, 11.4+ and 16.5; breadth and depth of trochlea for digit 4, 7.6 and 14.9+; MNHNCu P4598: distal breadth, 33.0; breadth and depth of trochlea for digit 2, 10.0 and 13.4; breadth and depth of trochlea for digit 3 depth, 11.7 and 16.6; breadth and depth of trochlea for digit 4, 8.3 and 13.4; OA 847: breadth and depth of trochlea for digit 4, 8.0 and 15.9.

Discussion

The Cuban Condor differs from other fossil and living *Gymnogyps* mainly in features of the skull. The long and massive occipital processes, the shape of the braincase, and the relatively large occipital condyle indicate that this species had large neck vertebrae and greater musculature in the head and neck associated with feeding. In addition, the relatively robust bill indicates that the Cuban Condor was more powerful and presumably could tear thick skin and sinew more easily than other condors of this genus. The more rostral placement of the nuchal crest in the Cuban Condor compared to other fossil and living *Gymnogyps* also is probably related to this more powerful feeding ability (see also Hertel 1995 for a description of cranial features related to scavenging). Postcranially, the Cuban species shows few differences in characters with other condors except for being relatively larger and more robust than *G. californianus californianus* or *G. kofordi,* and more similar to *G. c. amplus* (Suárez 2000).

The Cuban Condor may have descended from *Gymnogyps kofordi* or *G. californianus,* both of which occurred in Florida (Emslie 1998, Suárez 2000). We hypothesize that a population of one of these species reached Cuba in the early to late Pleistocene and quickly diverged into the endemic form. Although fossil evidence is lacking for the presence of condors in Cuba prior to the late Pleistocene, *G. varonai* shares more cranial and some postcranial similarities with *G. kofordi* than with *G. californianus,* although the rostrum is most similar to that of *G. californianus,* especially in the configuration of the nasal bar.

Once established in Cuba, rapid divergence from its Florida counterpart would be facilitated by its insular isolation. In addition, we speculate that limited large prey available at that time also might facilitate rapid morphological change in the cranial and bill regions. Large vertebrates known from the late Pleistocene of Cuba such as sloths [*Megalocnus, Parocnus* (=*Mesocnus*), *Acratocnus* (=*Miocnus*)], large rodents, and tortoises (*Geochelone*) were the main food sources for *Gymnogyps* (Suárez 2000). It is likely that the condors began to specialize on carcasses of these species and the thick hides of the sloths, and the hard carapaces of the turtles, selected for a more powerful feeding apparatus in Cuban Condors than in mainland species with more varied food sources.

Strong competitive interactions at carcasses with other scavenging birds identified in the fossil record of Cuba (Suárez 2001), including many raptorial species that were quite diverse in the Quaternary here, also may have increased the selective pressure for the robust cranial characters of *Gymnogyps varonai.* A more powerful bill for holding onto prey remains during interactions at a carcass may have made the Cuban Condor more competitive if food was limiting. Additional research on the functional morphology of the unique cranial characteristics of *G. varonai* with further studies of the extensive undescribed material of raptors from the Quaternary of Cuba are needed to further address this issue.

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Literature Cited

Arredondo, O. 1971. Nuevo género y especie de ave fósil (Accipitriformes: Vulturidae) del Pleistoceno de Cuba.—Memórias de la Sociedad de Ciencias Naturales La Salle 31(90):311–323.

———. 1976. The great predatory birds of the Pleistocene of Cuba. Pp. 169–187 *in* S. L. Olson, ed., Collected papers in avian paleontology honoring the 90th birthday of Alexander Wetmore.—Smithsonian Contributions to Paleobiology 27:1–211.

Campbell, K. E., Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru.—Life Sciences Contribution Royal Ontario Museum 118:1–203.

Emslie, S. D. 1988. The fossil history and phylogenetic relationships of condors (Ciconiiformes: Vulturidae) in the New World.—Journal of Vertebrate Paleontology 8:212–228.

———. 1998. Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida Peninsula.—Ornithological Monographs 50:1–113.

Fisher, H. I. 1944. The skulls of the cathartid vultures.—Condor 46:272–296.

Hertel, F. 1995. Ecomorphological indicators of feeding behavior in Recent and fossil raptors.—Auk 112:890–903.

Howard, H. 1929. The avifauna of Emeryville shellmound.—University of California Publications in Zoology 32:301–394.

———. 1974. Postcranial elements of the extinct condor, *Breagyps clarki* (Miller). Contributions in Sciences, Natural History Museum Los Angeles County 256:1–24.

Iturralde-Vinent, M., R. D. E. MacPhee, S. Díaz-Franco, R. Rojas-Consuegra, W. Suárez, & A. Lomba. 2000. Las Breas de San Felipe, a Quaternary asphalt seep near Martí (Matanzas Province, Cuba).—Caribbean Journal of Science 36(3–4): 300–313.

Jollie, M. 1976–1977. A contribution to the morphology and phylogeny of the Falconiformes.—Evolutionary Theory 1:285–298, 2:115–300, 3: 1–142.

Miller, L. 1911. Avifauna of the Pleistocene deposits of California.—University of California Publications, Bulletin, Department of Geology 6: 385–400.

Olson, S. L. 1978. A paleontological perspective of West Indian Birds and Mammals.—Academy of Natural Sciences of Philadelphia, Special Publication 13:99–117.

Suárez, W. 2000. Contribución al conocimiento del estatus genérico del cóndor extinto (Ciconiiformes: Vulturidae) del Cuaternario cubano.—Ornitología Neotropical 11:109–122.

———. 2001. A reevaluation of some fossils identified as vultures (Aves: Vulturidae) from Quaternary cave deposits of Cuba.—Caribbean Journal of Science 37(1–2):110–111.

Tambussi, P.C., & J. I. Noriega. 1999. The fossil record of condors (Ciconiiformes: Vulturidae) in Argentina. Pp. 177–184 *in* S. L. Olson, ed., Avian Paleontology at the close of the 20th Century: Proceedings of the 4th International meeting of the Society of Avian Paleontology and Evolution, Washington D.C., 4–7 June 1996.—Smithsonian Contributions to Paleobiology 89:1–344.

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A new gecko (Reptilia: Squamata: Genus *Lepidodactylus*) from Tuvalu, South-central Pacific

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Abstract.—A Group II *Lepidodactylus* was discovered during a recent biodiversity survey of Tuvalu. These geckos uniquely share a heavily pigmented oral cavity with the Rotuman *L. gardineri* and also are most similar to *L. gardineri* in scalation, size, and body proportions; however, differences in the pubic patch of enlarged scales and the thickness of the head support speciation of the Tuvaluan population. This population is described and characterized.

Two families of lizards are widespread and common colonizers of the islands of Oceania. The skinks (Scincidae) are diurnal and predominantly terrestrial lizards; the geckos are nocturnal and mainly arboreal ones. The origins and dates of these lizards' colonization of Oceania remain debatable, although recent man-assisted colonization seems unquestionably the mode of dispersal for a few species, e.g., moth skink (*Lipinia noctua*; Austin 1999) and house gecko (*Hemidactylus frenatus*; Case et al. 1994).

For other taxa, such as the geckos of the genus *Lepidodactylus,* dispersal throughout western Oceania likely occurred in the distant past and well before human colonization of this area, because several endemic species occur irregularly from Rotuma, Viti Levu, 'Eua and westward. These species (*L. gardineri, L. manni, L. euaensis,* respectively, and others) are morphologically well differentiated and largely forest residents, thereby suggesting long periods of isolation. The interrelationships of these three taxa to one another and to congeners of the more western island groups are unresolved. Phenetically, *Lepidodactylus* consists of three species groups (Brown & Parker 1977). Group III (*L. lugubris* and relatives) consists of bisexual and unisexual species and populations, and one or more Group III species occur on almost every island in Oceania. Group III members are considered to be the most derived taxa of *Lepidodactylus* (Ota et al. 1995), and their current distribution likely derives from natural and human-assisted dispersal. The other two phenetic groups, Group I (*L. pumilis* and allies) and Group II (*L. guppyi* and allies) are less specialized in morphology and are irregularly distributed among the islands west of and including the Tongan arc. *L. manni* (Fiji) and *L. euaensis* (Tonga) are members of Group I that is characterized by undivided digital lamellae, and *L. gardineri* (Rotuma) is a Group II species, characterized by a few subterminal divided lamellae.

It was, thus, surprising when a recent biotic survey in Tuvalu discovered another Group II *Lepidodactylus.* Individuals of this *Lepidodactylus* appear similar to *Lepidodactylus gardineri*; however, some subtle differences suggest that the Tuvaluan population represents a more ancient dispersal than a man-assisted one and that this population's isolation has resulted in speciation. We recommend that the Tuvulan population be known as:

Fig. 1. The holotype of *Lepidodactylus tepukapili,* USNM 531712.

Lepidodactylus tepukapili, new species
Fig. 1

Holotype.—USNM 531712, an adult male from Fuakea [Fuagea] (8°34′S, 179°04′E), Funafuti Atoll, Tuvalu, collected by Dick Watling on 4 September 1998.

Paratypes.—USNM 531713-16, a juvenile male, an adult female and two adult males, respectively, from Tepuka (8°28′S, 179°05′E), Funafuti Atoll, Tuvalu, collected by Dick Watling on 3 September 1998.

Diagnosis.—*Lepidodactylus tepukapili* is a Group II species with the division or deep notching of two or three of the subterminal digital lamellae of second through fifth digits of the fore- and hindfeet. It differs from other Group II members: by the possession of a continuous row of 36 or more femoral-precloacal pores in adult males, 35 or less in *L. novaeguineae, L. paurolepis, L. pulcher,* and *L. shebae*; by moderately dilated digital pads of fore- and hindfeet, only slightly dilated in *L. vanuatuensis*; by a bluish gray chin and throat, creamy white in *L. guppyi*; and by a larger pubic or precloacal patch of enlarged scales (median 18 vs. 13.5; Table 3) and a flatter head (median HeadL/SVL 103 vs. 123%: Table 2) in *L. gardineri.*

Etymology.—The specific name *tepukapili* derives from the Tuvaluan language and is used as a noun in apposition. Pili refers to any small lizard, (either gecko or skink), and Tepuka is the island on which the first specimens were discovered. Puka of tepuka is the root word for two culturally important trees on the island, i.e., pukavai, *Pisonia grandis,* and pukavaka, *Hernandia nymphaeifolia.*

Description of the holotype.—Snout–vent length 50.3 mm; head length 11.5; head width 7.6; head height 5.4; snout–eye length 4.6; naris-eye length 3.6; orbit diameter 3.2; eye-ear length 3.0; snout width 1.9; interorbital width 3.6; snout–forelimb length 17.0; trunk length 20.9; crus length 6.0; tail length 37 (regenerate). All measurement here and subsequently are in millimeters. Mensural and scalation characters defined in appendix.

Snout tapered, rounded at tip; rostral entering nares, width about 2.5 times height; nares bordered by five scales, three nasals, one rostral, and first supralabial; five scales touching rostral between left and right nares; 35 interorbital scales; ten left and nine right supralabials; eight left and nine right infralabials; mental scale distinct, its anterior width equals midline length; six postmental and seven chin scales.

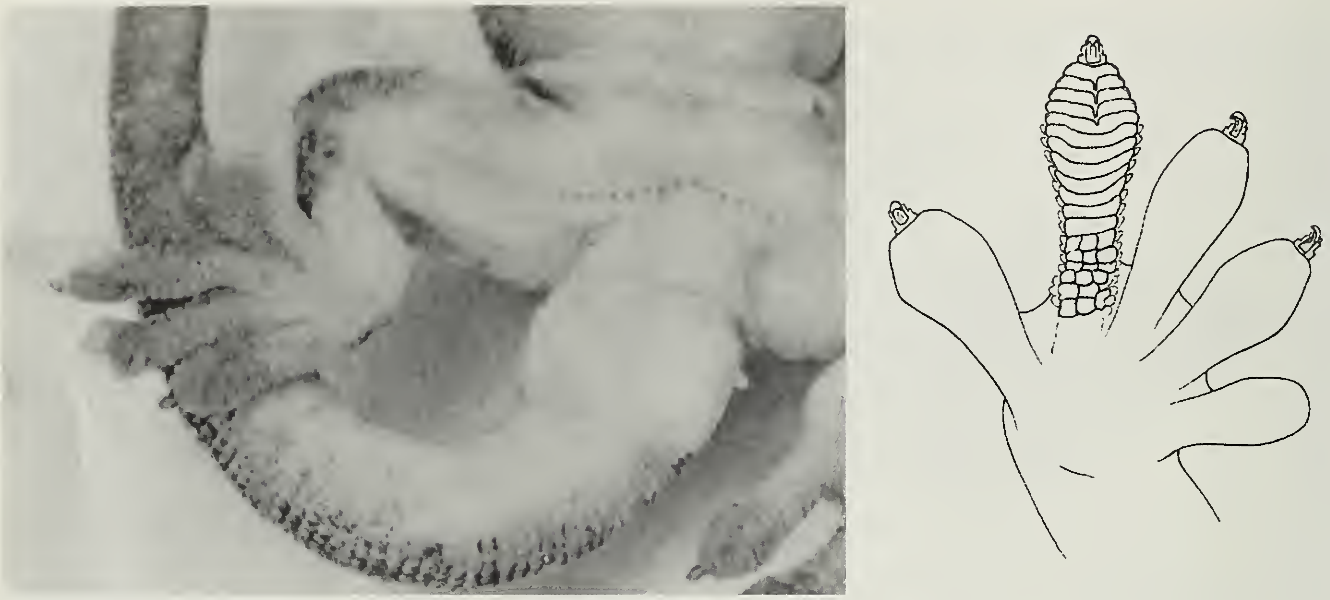

Fig. 2. Ventral view of the posterior trunk and limbs (left) and right hindfoot (right) of the holotype of *Lepidodactylus tepukapili*, USNM 531712.

Body slightly depressed; 118 rows of scales around midbody; dorsal and lateral scales granular, without enlarged tubercles, and in juxtaposition; ventral scales almost flat, cycloid, 2–3 times larger than dorsal scales; limbs well developed; subdigital lamellae 16/16 and 11/12 on left/right sides of on digits IV of fore- and hindfoot (Fig. 2), respectively; digital lamellae ventrally covering nearly all of forefoot digits and I–II digits of hindfoot, about ¾ of digits III–V of hindfoot; all digits of fore- and hindfoot clawed except the first; ultimate claw-bearing and penultimate phalanges of fore and hind digits raised above pad although only claw free and extending over distal edge of pad; fore- and hindfoot webbing modest (≤1/5 digit length); precloacal and femoral pore rows continuous with 38 excreting pores, reaching about ¾ length of thigh; scales adjacent to pore bearing ones enlarged, usually in two rows anterior to pore row and posteriorly forming pubic patch of enlarged scales (Fig. 2).

Posterior third of tail recently regenerate and likely regenerated from hemipenial sheath distally; tail subcylindrical throughout length, gradually tapering to a blunt tip; lateral margins without spines or skin flanges; scales on tail annulate, cycloid, larger ventrally than dorsally, and subcaudal scales about 1.5 times belly scales; base of tail distinctly swollen by hemipenes; single large, blunt cloacal spur on each side.

Color of holotype.—In preservation, dorsal ground color of head, body, limbs, and tail brown with faint and discontinuous mottling of darker brown; ventrally, chin to anterior throat dusky, thereafter white with slight ventrolateral dark flecking on belly, ventrally tail white except for dusky on recently regenerate portion. When first found, the gecko was a rich chocolate brown dorsally with lighter brown patches or mottling on the sides; the venter from chin onto tail was a bright dark yellow. Scales around eye and along upper lip were light, and interior of the mouth and tongue were black. The brighter coloration faded within an hour to a grayish brown dorsally and laterally, and a less intense yellow venter.

Variation.—The two adult male paratypes (USNM 531715–716) are distinctly smaller (43.5, 43.1 mm SVL, respectively) than the holotype but not greatly different from the adult female paratype (USNM 531714, 41.1 mm). There appear to be no proportional differences either between the smaller males and holotype or the female. The small sample size prevents any test of size dimorphism between adult females and males. The absence of dimorphism also appears to be the situation for most aspects of scalation. Comparing the scalation of the holotype with the four paratypes yield the following: Ros, width usually 2.5× height; RosC, absent in all; NaRos, no contact in all; NaInf, no contact in all; CircNa, invariant 3; SnS, 5 scales in holotype and either 4 or 5 in paratypes; IntorbS, 35 and 29–34; Suplab, 9 and 7–9; Inflab, 9 and 8–9; Men, width equals height in all; PosMen, 6 and 7–10; Chin, 7 and 8–14; Midb, 118 and 100–113; CloacS, 1 and 1–2; Subcaud, width 1.5× height and 1.0–2.0×; ForefL, 16 and 14–15; HindfL, 12 and 12–15; LamNF, invariant 2; LamNL, invariant 4th; PoreRS, 43 and 37–42; Web, invariant basal ¼th; PreclP, 17 and 12–18; for the males PreclPor, 38 and 39–40. These scalation traits show little variation within the Tuvalu sample.

Color notes for the individual *L. tepukapili* are not available and likely would display no greater variation among individuals than within an individual as an individual's coloration shifted owing to physiological and psychological state. In preservation, the paratypes share the dorsal ground color with the holotype, although the dark brown mottling is more extensive on all paratypes, and the mottling largely dominates the dorsal coloration of USNM 531714 and 531716. Similarly the paratypes share the holotype's ventral coloration with more ventrolateral flecking from the neck to the hindlimbs; their chins and throats are dusky but somewhat lighter than the holotype's.

Distribution.—*L. tepukapili* is known presently from two islands, Tepuka and Fuakea, in the Funafuti Atoll, Tuvalu. Limited searches on the main atoll island of Fongafale did not reveal any specimens.

Natural history.—McLean and Hosking (1992) described the habitats of Funafuti Atoll, and Tepuka's vegetation is almost entirely a 'Coconut and Broadleaf Woodland.' This mixed forest results from gardening and regeneration, which create a medium density coconut woodland harboring stands and scattered individuals of broadleaf trees, such as the wide ranging *Pisonia, Cordia, Calophyllum, Guettarda, Hernandia, Morinda, Hibiscus, Terminalia,* and *Thespesia.* Of these, *Pisonia* and *Hernandia* are the most common species. The understory includes *Ficus* and *Pipturus* scrub, and a groundcover of ferns, e.g., *Asplenium* and *Nephrolepis.* The smaller motu of Fuakea contains only a few coconuts in a similar mixture of broadleaf trees as on Tepuka.

L. tepukapili was found under loose bark and in crevices, at one and two metres from the ground on the trunks of living trees, specifically *Calophyllum inophyllum* and coconut. Search time was limited by other bioinventory task, and we believe that *L. tepukapili* probably occurs in a larger variety of microhabitats and tree types.

Comparison to Other Group II Members

As noted in the Introduction, the three species groups of *Lepidodactylus* are phenetically delimited. No study has tested the monophyly of these groups or, for that matter, tested the monophyly of the taxon *Lepidodactylus* (Kluge [1968] provided a set of diagnostic traits for this genus but did not address monophyly.). These two tasks are beyond the goals of our study; however, we wish to examine briefly the phylogenetic relationships of *L. tepukapili.*

Our assessment of relationships assumes the monophyly of the *guppyi* complex (=Group II *Lepidodactylus*). Tables 1 and 2 provide a summary of select mensural and scalation characteristics of this complex. Only three species (*gardineri, guppyi, vanuatuensis*) are represent by reasonable, yet statistically inadequate, samples of adult specimens. Sexual dimorphism is a common attribute among geckos. All members of the *guppyi* complex show this dimorphism in the presence of secreting precloacal-femoral pores in adult males and their absence in adult females. Otherwise there

Table 1.—Summary of selected mensural traits of adults of Group II *Lepidodactylus* species. Abbreviations are defined in section I of Appendix. Medians and ranges are presented for adults; SVL is in millimeters, proportions in percent; and sample size is in parentheses below specific name, females and males, respectively.

	SVL							
Taxon	Female	Male	Head/SVL	HeadW/SVL	OrbD/HeadL	Intorb/HeadL	TrunkL/SVL	CrusL/TrunkL
gardineri	49.7	49.7	23	11	30	32	44	27
(4, 5)	47.5–50.0	43.1–50.1	22–24	9–12	29–31	29–36	44–46	24–33
guppyi	45.6	40.5	24	10	30	36	48	24
(3, 4)	37.3–54.4	36.1–47.9	22–24	8–11	28–35	31–37	45–51	22–28
intermedius[1]	—	39.0	—	—	—	—	—	—
(2, 1)	?–42							
lombocensis[2]	38.0	37.5	—	—	—	—	—	—
(1, 1)								
novaeguineae	38.2	38.6	24	10	32	32	48	24
(5, 2)	35.8–39.0	38.3–38.9	23–25	8–12	30–33	29–36	44–51	21–24
paurolepis	—	37.7	23	9	29	31	46	25
(0, 3)		37.4–38.4	22–23	9–10	28–33	29–33	46–48	25–26
pulcher	—	39.0	25	11	33	29	45	27
(0, 1)								
shebae[3]	36.0	—	25	17	30	—	—	—
(1, 0)								
tepukapili	41.1	43.5	24	12	31	32	43	29
(1, 3)		43.1–50.3	23–25	11–12	28–33	30–33	42–49	26–29
vanuatuensis	44.2	35.3	24	10	30	31	47	24
(6, 4)	40.0–46.5	33.0–39.2	22–25	8–12	27–34	29–33	44–50	21–28

Data from literature: [1] Darevsky 1964; [2] Mertens 1929; [3] Brown & Tanner 1949.

is little commonality in the traits displaying statistically significant (Student's t test, $p < 0.05$) sexual dimorphism among these three samples. Only one other character, ForefL displays sexual dimorphism in *L. guppyi,* five characters (Suplab, CloacS, HeadL/SVL, HeadW/SVL, OrbD/HeadL) in *L. gardineri,* and seven characters (SVL, TrunkL, HeadW, EyeEar, SnW, Inflab, HeadL/SVL) in *L. vanuatuensis.* The sample sizes are simply too small to decide whether these dimorphic differences are real or a sampling bias. We provide body size differences for both males and females in Table 1, but otherwise the data are medians and ranges for all adult specimens (Tables 1, 2).

In overall size, *L. gardineri* averages larger than any other *guppyi* member (Table 1) and appears to have equal-sized females and males. *L. guppyi* and *L. tepukapili* are the next largest geckos of this group; females average larger in *L. guppyi* and possibly the reverse in *L. tepukapili,* but the small samples argue for caution for such an interpretation. Caution is re-enforced by the *L. vanuatuensis* sample with females nearly as large as female *L. guppyi* yet with males

Table 2.—Comparison of the relative head dimension of adult *Lepidodactylus gardineri* and *L. tepukapili.* Abbreviations are defined in section I of Appendix. Medians and ranges are presented for adults; proportions in percent; and sample sizes are same as in Table 1.

Taxon	HeadL/SVL	HeadH/SVL	HeadH/HeadL	EyeEar/HeadL	NeckL/HeadL
gardineri	23	103	45	34	157
	22–24	98–116	44–49	31–36	150–165
tepukapili	24	123	50	30	148
	22–25	107–126	47–53	26–35	138–154

Table 3.—Summary of selected scalation traits of adult Group II *Lepidodactylus*. Abbreviations are defined in section I of Appendix. Median and ranges of the traits are presented when known; all values are for females and males, except males only for CloacS and PoreRS; sample sizes are same as in Table 1.

Taxon	IntorbS	Suplab	Midbody	CloacS	PoreRS	PreclPore	PreclP	ForefL	HindfL	LamNL	Web
gardineri	33	9	111	3	39	38	18	15	12	4	1
	31–35	8–10	103–118	2–3	46–41	38–41	13–22	12–16	12–17	3–4	1–1
guppyi	35	9	115	2	42	41.5	14	13	10	3	2
	33–37	8–11	110–133	0–4	39–44	33–43	12–15	11–15	9–12	2–4	1–2
intermedius[1]	—	10–11	—	—	—	24	—	9–10	10–12	—	1
		(10)[3]	(121)[3]	(2)[3]					(8)[3]		
lombocensis[2,1]	—	9–10	—	—	—	20	—	10–11	12–14	—	—
		(11)[3]	(110–112)[3]	(1–2)[3]							(1)[3]
novaeguineae	35	9	118	2	18	16	16	12	11	2	2
	32–39	8–10	108–125	2–2	15–19	13–19	14–19	10–12	10–13	2–3	2–3
paurolepis	32	10	100	1	31	26	12	14	13	3	2
	31–32	10–11	99–110	1–2	30–33	25–29	11–13	11–14	12–16	3–3	1–1
pulcher	39	10	143	1	13	13	14	16	20	1	1
shebae[4]	—	10	—	—	—	—	—	—	11	2–3	2
						(30 or 32)[3]					
tepukapili	33	8.5	110	2	41.5	39	13.5	14.5	12	4	1
	29–35	7–9	105–118	1–2	37–45	38–40	12–17	14–16	12–13	4–4	1–1
vanuatuensis	33	9.5	100	1	40	26	13.5	12.5	11.5	3	1
	31–35	9–10	91–118	1–2	30–43	10–40	8–21	10–14	10–14	2–4	1–2

Data from literature: [1] Darevsky 1964; [2] Mertens 1929; [3] Ota et al. 2000; [4] Brown & Tanner 1949.

averaging smaller than all other *guppyi* group males or females (Table 1).

The standard head proportion traits (Table 1) of *Lepidodactylus* systematics show little difference among *guppyi* members; however, the shorter relative trunk length (TrunkL/SVL) and the longer relative crus length (CrusL/TrunkL) differentiate *L. gardineri* and *L. tepukapili* from the other *guppyi* members. Although these latter two species appear quite similar, several aspects of head shape (Table 2) are different. *L. tepukapili* has a thicker head relative to both body (HeadH/SVL) and head length (HeadH/HeadL) than does *L. gardineri*. This difference appears associated with a somewhat shorter head (EyeEar/HeadL, NeckL/HeadL; Table 2) in *L. tepukapili*. These proportional differences in head shape are not evident to the authors' eyes.

Discriminant function analyses (stepwise, backward entry) of male and female morphometric data show a strong differentiation of *L. gardineri* and *L. tepukapili* in multivariate space (Fig. 3). In the female analysis, none of the thirteen characters were eliminated in the final step, and classification attained 100% for the five taxa. For males, the final step retained six characters (SnEye, SnForel, SnW, NarEye, OrbD, CrusL) and attained 100% classification for all taxa except *L. guppyi* and *L. vanuatuensis* (75% each). Neither the relative positioning of the taxa clusters nor the classification accuracy should be weighed too heavily in interpretation of relationships owing to the small sample sizes of all taxa. We note only that these data offer confirmation to our interpretation of speciation of the Tuvalu population.

L. gardineri and *L. tepukapili* are similar in scalation (Table 3) with the exception of the pubic patch of enlarged scales, which is larger and has more scales in *L. gardineri*. In this trait, *L. gardineri* differs from all other Group II members; all other members are similar with the exception of *L. novaeguineae* and its intermediate-sized patch. Our impression is that *L. gardineri* and *L. tepukapili* are more similar to one another

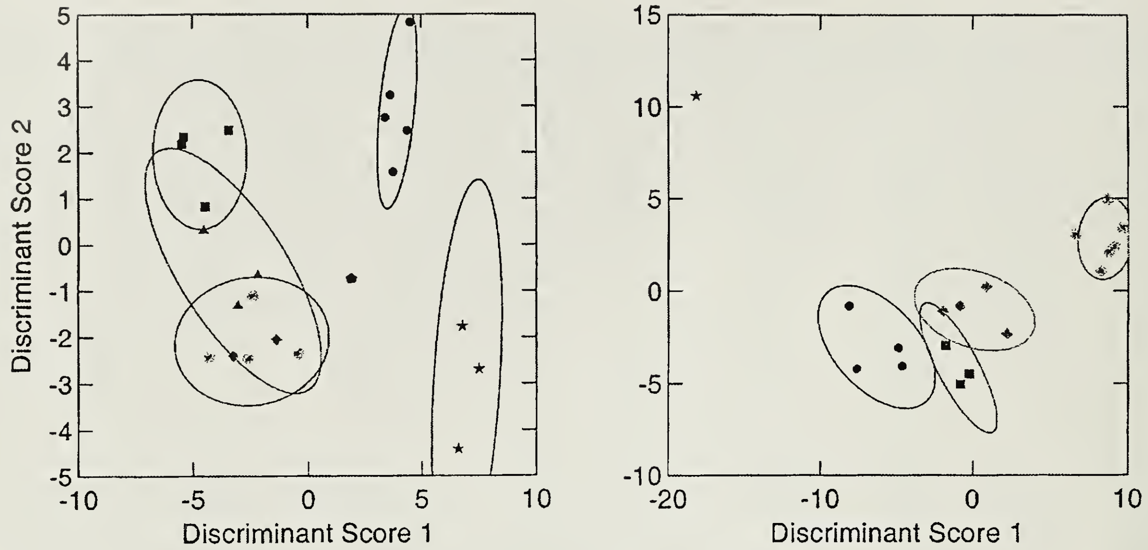

Fig. 3. Discriminant functional analyses of morphometric characters of Group II *Lepidodactylus,* males (left) and females (right). Each ellipse defines the 60% confidence limit. Species symbols are: *gardineri,* circle; *guppyi,* square; *novaeguineae,* diamond (no confidence ellipse shown for males); *paurolepis,* triangle; *pulcher,* pentagon (no confidence ellipse); *tepukapili,* star; *vanuatuensis,* star burst.

than either is to any other *guppyi* member. This similarity and the uniquely shared intense melanism of the oral cavity indicate that these two taxa share a common ancestor. They also presently represent the deepest penetration of Oceania by the Group II species. Their discovery in Tuvalu and the persistence of large tracts of forest in Samoa suggest that one of these taxa or a close relative probably occurs there also.

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Literature Cited

Austin, C. C. 1999. Lizards took express train to Polynesia.—Nature 397:113–114.

Brown, W. C., & F. Parker. 1977. Lizards of the genus *Lepidodactylus* (Gekkonidae) from the Indo-Australian Archipelago and the islands of the Pacific, with descriptions of new species.—Proceedings of the California Academy of Sciences, 4th ser. 41:253–265.

———, & V. M. Tanner. 1949. Discovery of the genus *Pseudogekko* with description of a new species from the Solomon Islands.—The Great Basin Naturalist 9:41–45.

Case, T. J., D. T. Bolger, & K. Petren. 1994. Invasions and competitive displacement among house geckos in the tropical Pacific.—Ecology 75: 464–477.

Darevsky, I. S. 1964. Two new species of gekkonid lizards from the Komodo island [sic] in Lesser Sundas Archipelago.—Zoologischer Anzeiger 173:169–174.

Kluge, A. G. 1967. Systematics, phylogeny, and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae).—Australian Journal of Zoology 15:1007–1108, plates 1–19.

———. 1968. Phylogenetic relationships of the gekkonid lizard genera *Lepidodactylus* Fitzinger, *Hemiphyllodactylus* Bleeker, and *Pseudogekko* Taylor.—Philippine Journal of Science [1966] 95:331–352.

———, & M. J. Eckardt. 1969. *Hemidactylus garnotii* Duméril and Bibron, a triploid all-female species of gekkonid lizard.—Copeia 1969(4):651–664.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985(3):802–832.

McLean, R. F., & P. L. Hosking. 1992. Tuvalu Land Resources Survey—Island Report No. 7 Funafuti. Prepared for the FAO/UNDP by the Dept. of Geography, Auckland University, New Zealand.

Mertens, R. 1929. Zwei neue Haftzeher aus dem Indo-Australischen Archipel (Rept.).—Senckenbergiana 11:237–241.

Ota, H, R. I. S. Darevsky, I. Ineich, & S. Yamashiro. 2000. Reevaluation of the taxonomic status of two *Lepidodactylus* species (Squamata: Gekkonidae) from the Lesser Sunda Archipelago, Indonesia.—Copeia 2002(4):1109–1113.

———, R. N. Fisher, I. Ineich, & T. J. Case. 1995. Geckos of the genus *Lepidodactylus* (Squamata: Reptilia) in Micronesia: description of a new species and reevaluation of the status of *Gecko moestus* Peters, 1867.—Copeia 1995:183–195.

———, & T. Hikida. 1988. A new species of *Lepidodactylus* (Sauria: Gekkonidae) from Sabah.—Copeia 1988:616–621.

Zug, G. R. 1998. Australian populations of the *Nactus pelagicus* complex (Reptilia: Gekkonidae).—Memoirs of the Queensland Museum 42: 613–626.

Appendix

I. Characters and analysis

Kluge (1967) defined a basic set of measurement and scale counts for geckos and subsequently (Kluge and Eckardt 1969) added additional characters and redefined some of the earlier ones. These characters and their definitions have been largely adopted by other herpetologists (e.g., Ota and Hikida 1989). We use a subset of these characters and their definitions. Each character and its abbreviation follow; we include a definition only where we record the character differently than the preceding researchers. Abbreviations follow Zug (1998) for ease of recognition. All characters reported for the right side.

Mensural characters.—Crus length: **CrusL**—Length of tibia from knee to heel. Eye-ear length: **EyeEar.** Head height: **HeadH**—Dorsoventral distance from the top of head to the underside of the jaw at the transverse plane intersecting the angle of jaws. Head length: **HeadL.** Head width: **HeadW**—Straight-line distance from left to right outer edge of jaw angles; this distance does not measure the jaw musculature broadening of the head. Interorbital width: **Interorb**—Transverse distance between the anterodorsal corners of left and right orbits. Nares-eye length: **NarEye.** Orbit diameter: **OrbD**—Eye diameter or length of other authors, although they measure anteroposterior axis length of orbit. Snout–eye length: **SnEye.** Snout–forelimb length: **SnForel.** Snout–vent length: **SVL.** Snout width: **SnW**—Internasal distance of other authors. Trunk length: **TrunkL**—Body length or axilla–groin length of others; distance between the posterior edge of the forelimb insertion (axilla) to the anterior edge of the hindlimb insertion (inguen).

Meristic characters.—Circumnasal scales: **CircNa**—Number of scales abutting naris, exclusive of rostral and first infralabial. Chin (secondary postmentals) scales: **Chin**—Number of scales transected by straight line from left to right 3rd-4th infralabial sutures. Cloacal spurs: **CloacS.** Femoral pores: **FemPor**—Number of pores perforating scales and secreting. Forefoot lamellae (scansors): **ForefL**—Number of 4th digit lamellae; lamella is wider than deep and contacts the marginal scales; fragmented proximal scales are excluded. Hindfoot lamellae (scansors): **HindfL**—As for ForefL. Infralabials: **Inflab.** Interorbital scales: **IntorbS.** Lamellar notching, first: **LamNF**—The number of the first lamella divided or deeply notched on 4th digit of hindfoot counting from terminal or ultimate lamella. Lamellar notching, last: **LamNL**—The last divided or notched lamellae, as in LamNF. Mental size: **Men**—Width to height proportion; scored as for Ros. Midbody scale rows: **Midb.** Naris-infralabial contact: **NaInf**—Naris abuts or separated from first infralabial. Naris-rostral contact: **NaRos**—Naris abuts or separated from rostral by scale. Precloacal and femoral pore-scales in contact: **PoreC**—Precloacal and femoral scales bearing pores, separate or continuous. Pore row scales: **PoreRS**—Number of enlarged scales in the precloacal-femoral pore-scale row, whether or not the scales contain pores. Postmental (primary) scales: **PosMen**—Number of scales touching mental and infralabials from left to right 3rd–4th infralabial sutures. Precloacal (preanal) pores: **PreclPor**—As for FemPor. Precloacal scale patch: **PreclP**—Number of scales as large or larger than the scales bearing precloacal pores and slightly larger than surrounding scales. Rostral size: **Ros**—Width to height proportion: 1, W = H; 1.5, W 1.5 times H; etc. in 0.5 intervals. Rostral cleft (crease): **RosC**—Absence or presence of midline cleft or crease. Snout scales: **SnS**—Number of scales between left and right nares and touching rostral. Subcaudal scales: **Subcaud**—Size of the median subcaudal scales relative to the dorsal caudal scales; score as for Ros. Supralabials: **Suplab.** Webbing: **Web**—Relative amount of webbing, four states: 0, none between the 2nd and 3rd digit of hindfoot; 1, slight, basal ¼ of 2nd digit's length; 2, moderate, ¼ to ⅓; 3, strong, more than ⅓.

Sex and maturity.—Examination of the gonads revealed sex and maturity. Females were considered mature when they possessed vitellogenic follicles, typically >1.5 mm diameter, oviducal eggs, or stretched oviducts; males when the testes and epididymides were enlarged, supplemented by the presence of secreting precloacal or femoral pores.

Comments on characters.—Several researchers have attempted to quantify digit shape and length, as well as other traits. Although we support quantification because it permits statistical analysis and presumably removes a degree of bias or subjectivity, many voucher specimens are not carefully prepared resulting in bent or folded specimens or parts thereof. Thus, we believe that quantification of some characters implies a degree of accuracy, which does not exist. Our selection of mensural characters emphasizes those possessing termini ending on bone and along axes that have rigorous bony struts reducing compression or bending. SnForel and TrunkL, for example, are two useful measurements but also two that can have significant variation resulting from poor preparation.

II. Specimens examined

Museum abbreviations follow Leviton et al. (1985).

Lepidodactylus gardineri Boulenger 1897 [type-locality: "Rotuma, north of the Fiji Islands"]. Rotuma: USNM 268142, 268145, 268147–48, 268151, 268153–54, 268156, 268161, 268169.

Lepidodactylus guppyi Boulenger 1884 ["Faro Island"]. Solomon Islands: CAS 139650, 156114; UMMZ 99966; USNM 120346, 120877–079, 313866.

Lepidodactylus novaeguineae Brown & Parker 1977 ["Lake Sentani area, West Irian"]. Papua New Guinea: CAS 11028–029, 12182, 89684; UMMZ 122450; USNM 112824–27, 119248.

Lepidodactylus paurolepis Ota, Fisher, Ineich & Case 1995 ["Ngerukewid Group (7°11′N, 134°16′E), Belau islands"]. Palau: USNM 284400, 284402–403.

Lepidodactylus pulcher Boulenger 1885 ["Admiralty Islands"]. Papua New Guinea: CAS 139832.

Lepidodactylus tepukapili new species. Tuvalu: USNM 531712–716.

Lepidodactylus vanuatuensis Ota, Fisher, Ineich, Case, Radtkey & Zug 1998 [". . . Espíritu Santo Island . . ."]. Vanuatu: USNM 323264–268, 334163, 334184–189.

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Ompok pinnatus, a new species of silurid catfish (Teleostei: Siluriformes: Siluridae) from mainland Southeast Asia

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Abstract.—A new species of silurid catfish, *Ompok pinnatus,* is described from the Chao Phraya and Mekong River drainages in mainland Southeast Asia (Indochina). It belongs to the *O. eugeneiatus* species group and closely resembles *O. eugeneiatus.* Together with *O. eugeneiatus,* it can be distinguished from all other congeners in having an extremely long dorsal fin (about one-fifth SL vs. about one-tenth SL), and from all except *O. eugeneiatus* in having the maxillary and mandibular barbels reaching beyond the base of the caudal fin vs. not reaching that point. It can be distinguished from *O. eugeneiatus* in having a longer dorsal fin, deeper caudal peduncle, shorter mandibular barbels and fewer anal-fin rays.

The family Siluridae is one of the most species-rich of Asian catfishes (Bornbusch, 1995), and yet little is understood of the phylogenetic relationships within the family. One such problematic group demonstrated to be paraphyletic by Bornbusch (1995) is *Ompok* Lacépède, which are medium-sized silurids usually found in lakes and large rivers throughout South and Southeast Asia. According to Bornbusch (1995), there are four distinct clades within *Ompok,* viz. *O. bimaculatus* group, *O. leiacanthus* group, *O. hypophthalmus* group, and *O. eugeneiatus* group.

The *O. eugeneiatus* group currently includes two nominal species: *Ompok eugeneiatus* (Vaillant, 1902) (described from western Borneo) and *O. sabanus* Inger & Chin, 1959 (described from northeastern Borneo). While examining material identified as *O. eugeneiatus* from mainland Southeast Asia (Indochina), differences were observed between them and supposedly conspecific material from Sumatra and Borneo. These differences were found to be significant enough to warrant the recognition of a separate Indochinese species, which is described herein.

Materials and Methods

Measurements were made with a dial caliper and data recorded to 0.1 mm. Counts and measurements were made on the left side of the specimens when possible. In tables and text, subunits of the head are presented as proportions of head length (HL). Head length and measurements of body parts are given as proportions of standard length (SL).

The measurements and terminologies follow largely those of Bornbusch (1991), with the following exceptions: pelvic-fin length is measured from the base to the tip of the second (usually the longest) ray. Caudal-fin length is the length of the first principal (usually the longest) ray of the upper lobe measured from the posterior margin of the hypural complex. Head width is measured at the opercle (across its widest point) but discounting any lateral projection of the branchiostegal membranes. Head depth is measured at the base of the occipital process. Interorbital distance is determined at the dorsalmost point (the narrowest distance) between the orbital margins. Institutional acronyms follow Leviton et al.

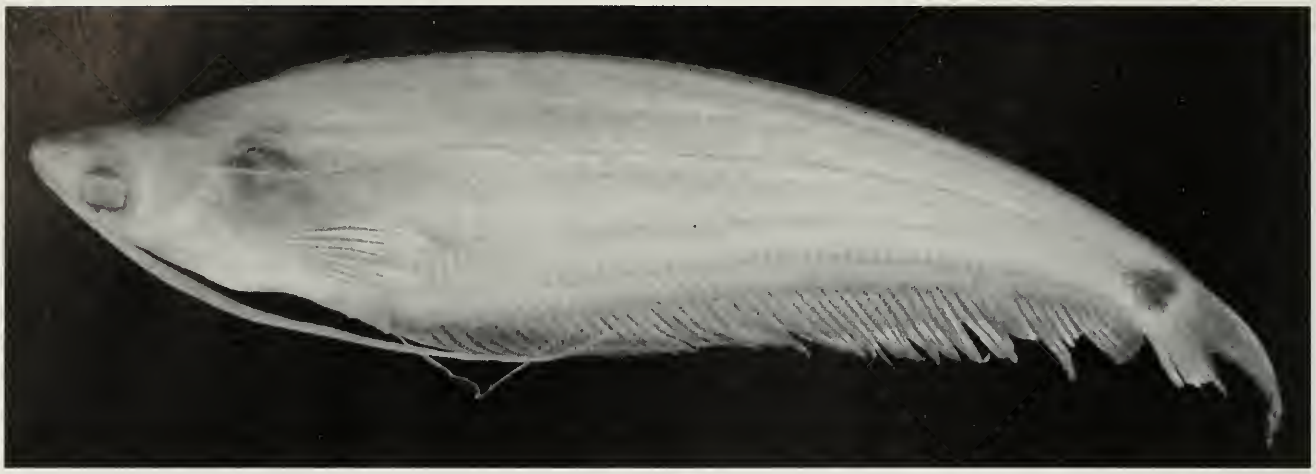

Fig. 1. *Ompok pinnatus,* holotype, UMMZ 232679,80.5 mm SL, Cambodia: Tonle Sap at Kompong Chhnang.

(1985) with the addition of CMK (collection of Maurice Kottelat, Cornol, Switzerland).

Comparative material.—*Ompok eugeneiatus:* CMK 16344, 1 ex., 72.5 mm SL; Borneo (Indonesia): Kalimantan Barat, Kapuas River drainage, Sungai Letang near Kampung Kandung Suli. UMMZ 209881, 1 ex., 91.3 mm SL; Borneo (Indonesia): Kalimantan Barat, Danau Piam near Ketungau, 38 km NNE of Sintang. ZMA 113.097, 1 ex., 104.8 mm SL; Sumatra: Taluk. ZMA 120.537, 1 ex., 100.2 mm SL; Sumatra (Indonesia): Jambi, Batang Hari. ZRC 11819–11820, 2 ex., 72.7–78.7 mm SL; Peninsular Malaysia: Pahang, Tasek Chini. ZRC 30458, 1 ex., 92.8 mm SL; Peninsular Malaysia: Pahang, Sungai Chini. ZRC 38803, 3 ex., 61.0–62.3 mm SL; Borneo (Indonesia): Kalimantan Barat, Kapuas River drainage, Danau Basuk, lake adjacent to Kapuas immediately downriver of Jongkong. ZRC 39036, 2 ex., 82.7–84.5 mm SL; Sumatra (Indonesia): Riau, Sungai Bengkwang, tributary of Batang Kuantan (Indragiri River), 4 hours downstream of Rengat. ZRC 41678, 5 ex., 37.7–86.7; Sumatra (Indonesia): Jambi, from aquarium trade.

Ompok sabanus: FMNH 44828, 1 ex., holotype, 131.6 mm SL; FMNH 44829, 11 ex., paratypes, 101.6–117.8 mm SL; Borneo (Malaysia): Sabah, Lahad Datu district, Segama River at Segama Estate.

Table 1.—Morphometric data for *Ompok pinnatus.*

In %SL	
Head length	17.9–19.6
Head width	9.7–10.5
Head depth	11.7–13.4
Predorsal distance	26.1–28.5
Preanal length	31.9–35.3
Prepelvic length	28.9–33.2
Prepectoral length	17.9–20.0
Body depth at anus	19.7–23.4
Depth of caudal peduncle	5.0–6.0
Pectoral-spine length	11.2–13.1
Pectoral-fin length	18.0–20.9
Length of dorsal fin	21.1–24.2
Pelvic-fin length	4.2–6.1
Length of anal-fin base	66.5–69.9
Caudal-fin length	18.6–23.9
In %HL	
Snout length	32.8–37.5
Interorbital distance	43.5–47.0
Eye diameter	21.7–25.8
Maxillary barbel length	425.2–505.3
Mandibular barbel length	495.4–613.3

Ompok pinnatus, new species
Fig. 1

Ompok eugeneiatus.—Bornbusch, 1995: 44 (in part).

Ompok sp. cf. *eugeneiatus.*—Rainboth, 1996: 149; Lim et al., 1999: 383.

Holotype.—UMMZ 232679, 80.5 mm SL; Cambodia: Tonle Sap at Kompong Chhnang, fishing lot 9 in second channel E of town; W. J. Rainboth, C. Rotha & N. van Zalinga, 27 Feb 1995.

Paratypes.—UMMZ 186749, 1 ex., 67.1 mm SL; Thailand: Maharaj province, Koh Tong canal (tributary of Chao Phraya River) 17.5 km N of Ayutthaya; A. Witt & S. Tongsangah, 12 Aug–12 Sep 1964. UMMZ 232375, 2 ex., 67.4–71.5 mm SL; Cambodia: Kandal, Prek Ta Pov, 11 km S of Phnom Penh; W. J. Rainboth, 2 Feb 1995.

Diagnosis.—*Ompok pinnatus* can be distinguished from congeners in uniquely having the following combination of characters: greatly elongated dorsal fin (about 20%SL vs. 10–15%SL) and barbels (extending beyond caudal fin), head width 9.7–10.5%SL, caudal peduncle depth 5.1–6.0%SL, and 53–58 anal-fin rays.

Description.—Body and head laterally compressed. Dorsal profile of body slightly convex, descending gently from dorsal-fin origin to snout tip, and again from the posteriormost dorsal-fin ray to the caudal peduncle. Anterior profile of snout rounded, dorsal profile of nuchal region concave. Anterior pair of nostrils tubular and located anteromedial to maxillary barbel base. Posterior pair of nostrils bordered by fleshy dorsal and ventral membranes and situated posteromedial to maxillary barbel base.

Mouth terminal; gape oblique. Rictal lobes narrowly continuous at rictus and deeply subtended by submandibular groove, with upper rictal lobe lacking skin fold.

Teeth villiform. Dentary teeth in bands that narrow posteriorly, teeth extending from symphysis to near posterior end of jaw; premaxillary teeth in broader bands, teeth extending from symphysis to near posterior end of jaw. Vomerine teeth in a single crescentic band.

Maxillary barbels reaching base of caudal peduncle when extended posteriorly. Single pair of mandibular barbels present, originating slightly anterolateral to gular fold; barbels flattened for most of length, reaching beyond tips of caudal fin when extended posteriorly.

Eyes small, subcutaneous; located in middle of head; visible dorsally, and more so ventrally.

Gill membranes separate and free from isthmus. Anterior third of left and right membranes overlapping. Branchiostegal rays 9. Gill rakers short, anteriormost rakers on lower first arch small and widely spaced; 4 on epibranchial and 16–18 on ceratobranchial.

Pectoral fin with convex distal margin and 9–10 branched rays. Proximal two-thirds of first pectoral-fin element ossified into a spine without anterior and distal serrae. Pectoral spine and articulated segments of first pectoral-fin element sexually dimorphic in mature individuals. Pectoral spine of males broad and somewhat flattened dorsoventrally, dentated with 3–4 distinct posterior serrae that increase in size distally; proximal articulated segments with 4 well-developed posterior serrae, decreasing in size distally. Pectoral-fin spine in females and juveniles more slender than in adult males, without serrae on posterior edges of either spine or articulated segments.

Pelvic fin with convex distal margin and i,6 rays. Dorsal fin with pointed distal margin (first dorsal-fin ray longest), with i,3 rays; segments of first ray not ossified to form spine. Anal fin with straight distal margin and 53–58 rays; not confluent posteriorly with caudal fin. Integument over anal fin thickened proximally for slightly more than half of ray lengths; fin-ray erector muscles extending along anterior edges of anal-fin rays, ventralmost extent of muscles same as that of thickened integument. Caudal fin strongly forked; principal rays i,7,7,i. Urogenital papillae of both sexes located immediately posterior to insertion of pelvic fins. Vertebrae 12 + 36 = 48, 11 + 38 = 49 or 12 + 37 = 49. Morphometric data as in Table 1.

Color.—Head and body dark yellow, with scattered melanophores on dorsal surfaces, flanks and thickened integument over anal fin; ventral surfaces of head, breast and belly with lighter covering of scattered melanophores. Faint black midlateral line variably present, usually as series of scattered melanophores broadening at base of caudal peduncle to form dark roughly triangular spot. Maxillary and mandibular barbels dark yellow, with color gradually fading distally. Fins hyaline, with small dark-brown spots occasionally present.

Distribution.—Known only from the Chao Phraya and Mekong River drainages (in Thailand and Cambodia, respectively).

Etymology.—From the Latin pinnatus, meaning feathered or plumed. In reference to the very long dorsal fin and barbels of this species. Used as a noun.

Remarks.—The *O. eugeneiatus* group is characterised by the following combination of characters (after Bornbusch 1995): (1) cartilaginous plates supporting the mandibular barbels enlarged, roughly circular in shape, and each with a dorsolateral process that contacts the dorsal edge of the anterior ceratohyal; (2) anterior process of the hyomandibular short and extending anterodorsally to or below the level of the cranial facet; and (3) the presence of 4 dorsal-fin rays. Bornbusch (1995) examined cleared and stained material of *O. pinnatus* (which he identified as *O. eugeneiatus*), and found them to possess the characters above, thus placing *O. pinnatus* within the *O. eugeneiatus* species group. In the following discussion, detailed comparison of *O. pinnatus* with congeners will be confined largely to within the *O. eugeneiatus* group, which contains only two other nominal species: *O. eugeneiatus* and *O. sabanus*.

Ompok pinnatus differs from all congeners in having a greatly elongated dorsal fin (about 20%SL vs. 10–15%SL), and (except for *O. eugeneiatus*) barbels (extending beyond caudal fin vs. not reaching that point). It differs further from *O. sabanus* in having a narrower head (9.7–10.5%SL vs. 10.8–11.9).

Ompok pinnatus further differs from *O. eugeneiatus* in having a deeper caudal peduncle (5.1–6.0%SL vs. 3.9–4.8), shorter mandibular barbels (495.4–613.3%HL vs. 638.5–849.4) and usually fewer anal-fin rays (53–58 vs. 58–62).

Ompok eugeneiatus and *O. pinnatus* share extremely long barbels extending beyond the caudal fin (vs. extending just beyond midway along body length in *O. sabanus* and other members of the Siluridae), which is apparently derived within the *O. eugeneiatus* species group. On the basis of this unique derived character, *O. pinnatus* and *O. eugeneiatus* are hypothesized to be sister species. Given that *O. pinnatus* is restricted to the Chao Phraya and Mekong River drainages in mainland Southeast Asia, whereas *O. eugeneiatus* is found only in river drainages in central Sumatra and western Borneo, this hypothesized relationship conforms to the general biogeographic pattern in Southeast Asian siluriforms in which one sister species is found in mainland Southeast Asia (Indochina) and the other in Sundaic Southeast Asia (chiefly Sumatra and Borneo). A model of the historical biogeography of species with this pattern of distribution has been proposed by Bornbusch & Lundberg (1989), who hypothesized that the post-Pleistocene isolation of the North Sunda River system resulted in speciation.

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Literature Cited

Bornbusch, A. H. 1991. Redescription and reclassification of the silurid catfish *Apodoglanis furnessi* Fowler (Siluriformes: Siluridae), with diagnoses of three intrafamilial silurid subgroups.—Copeia 1991:1070–1084.

———. 1995. Phylogenetic relationships within the Eurasian catfish family Siluridae (Pisces: Siluriformes), with comments on generic validities and biogeography.—Zoological Journal of the Linnaean Society 115:1–46.

———, & J. G. Lundberg. 1989. A new species of *Hemisilurus* (Siluriformes, Siluridae) from the Mekong River, with comments on its relationships and historical biogeography.—Copeia 1989:434–444.

Inger, R. F. & P. K. Chin. 1959. New species of freshwater catfishes from North Borneo.—Fieldiana, Zoology 39:279–296.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology, part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Lim, P., S. Lek, S. T. Touch, S.-O. Mao, & B. Chhouk. 1999. Diversity and spatial distribution of freshwater fish in Great Lake and Tonle Sap river (Cambodia, Southeast Asia).—Aquatic Living Resources 12:379–386.

Rainboth, W. J. 1996. Fishes of the Cambodian Mekong. FAO Species Identification Field Guide for Fishery Purposes. FAO, Rome, xi+265, 27 pls.

Vaillant, L. 1902. Résultats zoologiques de l'expédition scientifique Néerlandaise au Bornéo central. Poissons.—Notes from the Leyden Museum 24:1–166.

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Halidesmus socotraensis new species and *Haliophis guttatus* (Forsskål), new records of congrogadine fishes from the Socotra Archipelago (Perciformes: Pseudochromidae)

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Abstract.—*Halidesmus socotraensis* is described from six specimens, 39.6–69.5 mm SL, from the Socotra Archipelago, western Indian Ocean. It is distinguished from all other congrogadine species in having the following combination of characters: three lateral lines (dorsal, middle and ventral complexes); ventral lateral line branched on abdomen, with unpaired median section on ventral midline; and upper lateral line without anterodorsal branch on to nape. *Haliophis guttatus* is also newly recorded from the Socotra Archipelago on the basis of 15 specimens.

The Socotra Archipelago in the western Indian Ocean at the entrance to the Gulf of Aden consists of four main islands (Fig. 1). The largest and most easterly island, Socotra, is located some 400 km south of the Arabian Peninsula and 200 km east of Cape Guardafui, the Horn of Africa. The other islands are Abd al-Kuri in the west and the two smaller southern islands of Samha and Darsah, also known as "The Brothers".

The coastal fishes of the Socotra Archipelago were poorly known until recently. Steindachner (1902, 1903) published the first study of fishes from Socotra, based on material collected by the Austrian Expedition to Socotra and South Arabia in 1898–1899. He listed 57 species of marine and brackish-water fishes. The first detailed study of the fish fauna was a sight survey conducted by Kemp (1998), who provided an account of 215 fish species and a preliminary zoogeographical analysis.

In 1999 and 2000 the Senckenberg Research Institute, Frankfurt, conducted the Marine Habitat, Biodiversity and Fisheries Surveys in the framework of the United Nations Development Programme (UNDP) Global Environment Facility funded project "Conservation and Sustainable Use of Biodiversity of Socotra Archipelago," executed under the auspices of the Environmental Protection Council of Yemen. During two expeditions the second author collected fishes at inter- and subtidal stations throughout the archipelago. Among the collections were several specimens of the pseudochromid subfamily Congrogadinae, a group of eel-like reef fishes commonly called eel blennies or snakelets. The subfamily was revised by Winterbottom (1986) who recognised 19 species in eight genera (one with two subgenera); four additional species (and one new subgenus) have been described subsequently (Winterbottom & Randall 1994, Winterbottom 1996, Gill et al. 2000). Among the collections from the Socotra Archipelago, an additional new species referable to the western-central Indian Ocean endemic genus *Halidesmus* Günther was discovered, and specimens of the widely distributed western Indian Ocean species *Haliophis guttatus* (Forsskål) were

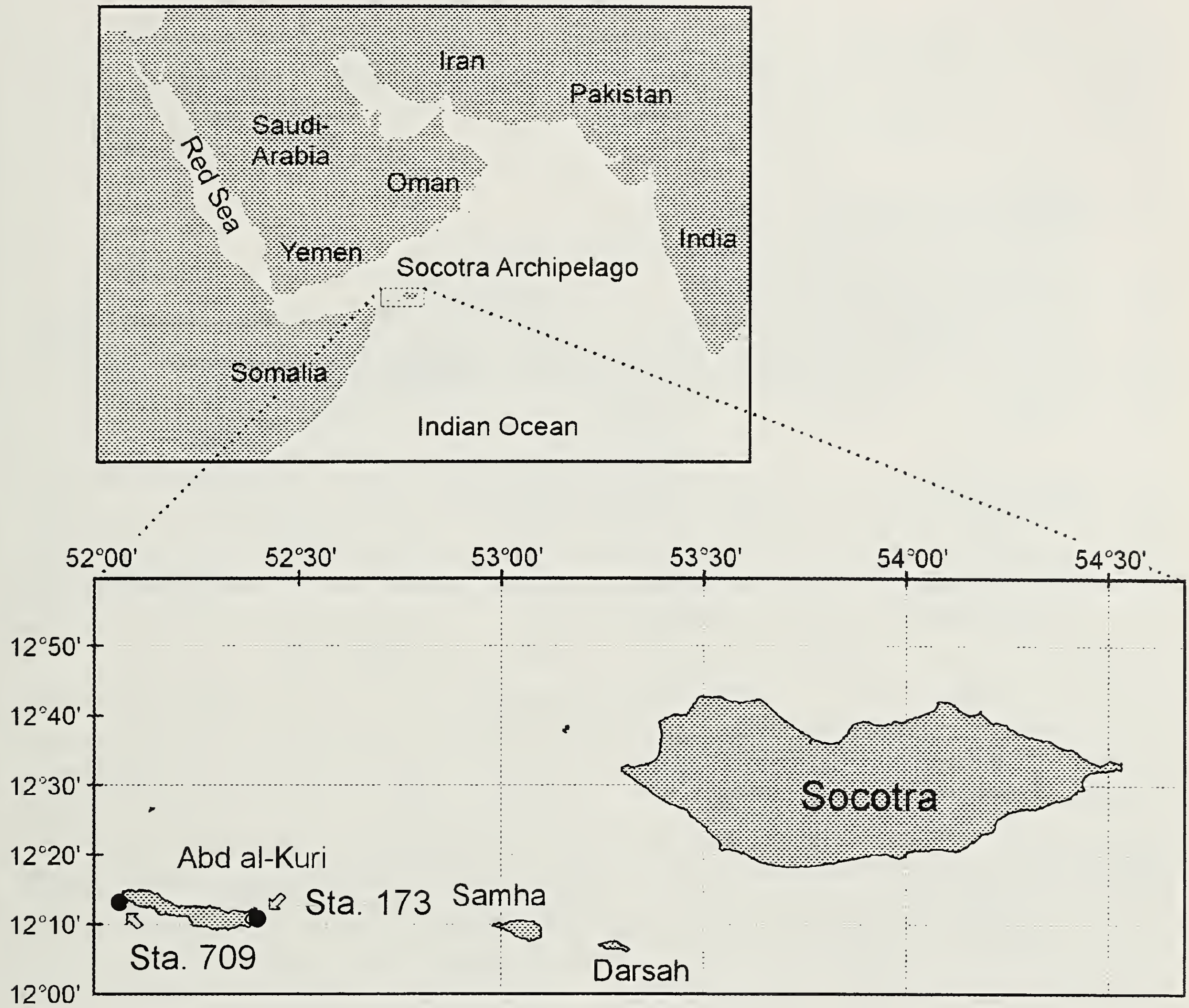

Fig. 1. Map of the Socotra Archipelago showing collection sites.

identified. The purposes of this paper are to describe the new species and to document the new record of *H. guttatus* from the Socotra Archipelago.

Materials and Methods

The nomenclature of cephalic laterosensory pores follows Gill et al. (2000). Alphabetical codes for lateral lines in the new *Halidesmus* generally follow Winterbottom (1982), except that the structure of the ventral lateral line necessitates the following modifications (Fig. 2): the apparent homolog of line G in *H. scapularis* is represented in *H. socotraensis* (and *H. polytretus*) by a median anterior section (termed G1) and a bilaterally paired posterior section (termed G2). Vertebral counts are presented in the form precaudal + caudal; the latter are defined as vertebrae bearing a haemal spine, and include the terminal urostylar complex. Terminology of ribs and intermuscular bones follows Gill (1998). Other methods of counting and measuring follow Winterbottom (1982). Institutional codes follow Leviton et al. (1985), except for NHCY-F, which is for the fish section of the Natural History Collection of Yemen. Osteological details were determined from x-radiographs. In the description of the new species, counts are given as values or value ranges for all type specimens, followed, where variation was noted, by values for the holotype in parentheses. Where counts

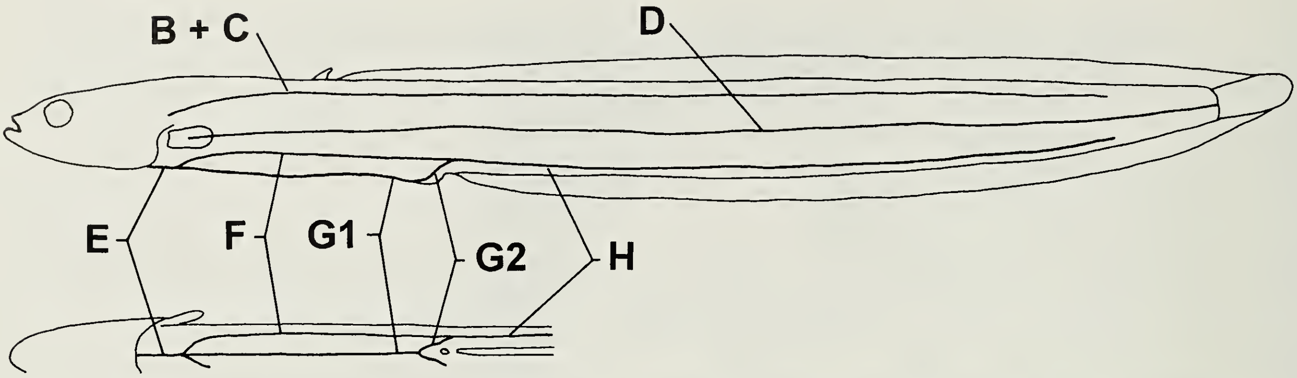

Fig. 2. Diagram of *Halidesmus socotraensis* in lateral and ventral views showing lateral-line systems and lettering scheme.

were recorded bilaterally, both counts are presented for the holotype, separated by a slash; the first count given is the left count. Ratios for morphometric characters and frequency distributions for selected meristic characters are given in Tables 1 and 2, respectively. Comparisons with other *Halidesmus* species are based primarily on data provided by Winterbottom (1982, 1986) and Winterbottom & Randall (1994).

Halidesmus socotraensis, new species
Socotran Snakelet
Figs. 2–4, Tables 1–3

Holotype.—SMF 29223, 64.3 mm SL, Socotra Archipelago, Abd al-Kuri Island, SW coast, ca. 12°13′N 52°04′E, 6–15 m, rotenone, U. Zajonz, F.N. Saeed, M. Apel and E. Zandri, 4 April 2000 (station 709).

Paratypes.—BMNH 2002.1.19.3, 1, 63.3 mm SL, ROM 72697, 1, 60.0 mm SL, SMF 29293, 3, 39.6–69.5 mm SL, all collected with holotype.

Diagnosis.—The following combination of characters distinguishes *H. socotraensis* from all other congrogadines: three lateral lines (dorsal, middle and ventral complexes); ventral lateral line branched on abdomen, with unpaired median section on ventral midline; and upper lateral line without anterodorsal branch on to nape.

Description.—Data for morphometric characters appear in Table 1.

Dorsal fin I + 58–61 (I + 61), all seg-

Table 1.—Morphometric values for *Halidesmus socotraensis* expressed as percentages of standard length (SL).

	Holotype	Paratypes				
mm SL	64.3	39.6	48.7	60.0	63.3	69.5
Soft dorsal-fin base	78.2	80.0	78.2	78.3	78.2	81.7
Anal-fin base	61.6	59.8	60.6	61.7	63.0	61.2
Snout to first dorsal	17.1	20.2	19.7	17.7	18.3	17.7
Snout to soft dorsal	19.8	22.5	22.2	19.2	19.6	20.1
Snout to anal origin	37.2	39.1	39.4	38.0	35.2	37.4
Head length	13.2	15.4	14.4	13.5	13.1	12.7
Depth at parietal	7.0	8.1	7.6	8.0	7.4	7.5
Depth at anal origin	7.9	8.8	8.8	8.7	8.5	7.5
Eye diameter	2.8	4.0	3.3	3.0	3.0	2.9
Snout length	2.8	3.3	2.9	2.8	3.0	3.2
Interorbital width	1.2	1.3	1.4	1.3	1.3	1.3
Upper jaw length	4.5	4.8	4.7	4.5	4.4	4.6
Lower jaw length	6.2	7.3	6.8	6.3	6.3	6.5
Pectoral length	5.6	5.1	4.9	4.7	5.1	?*

* fin damaged.

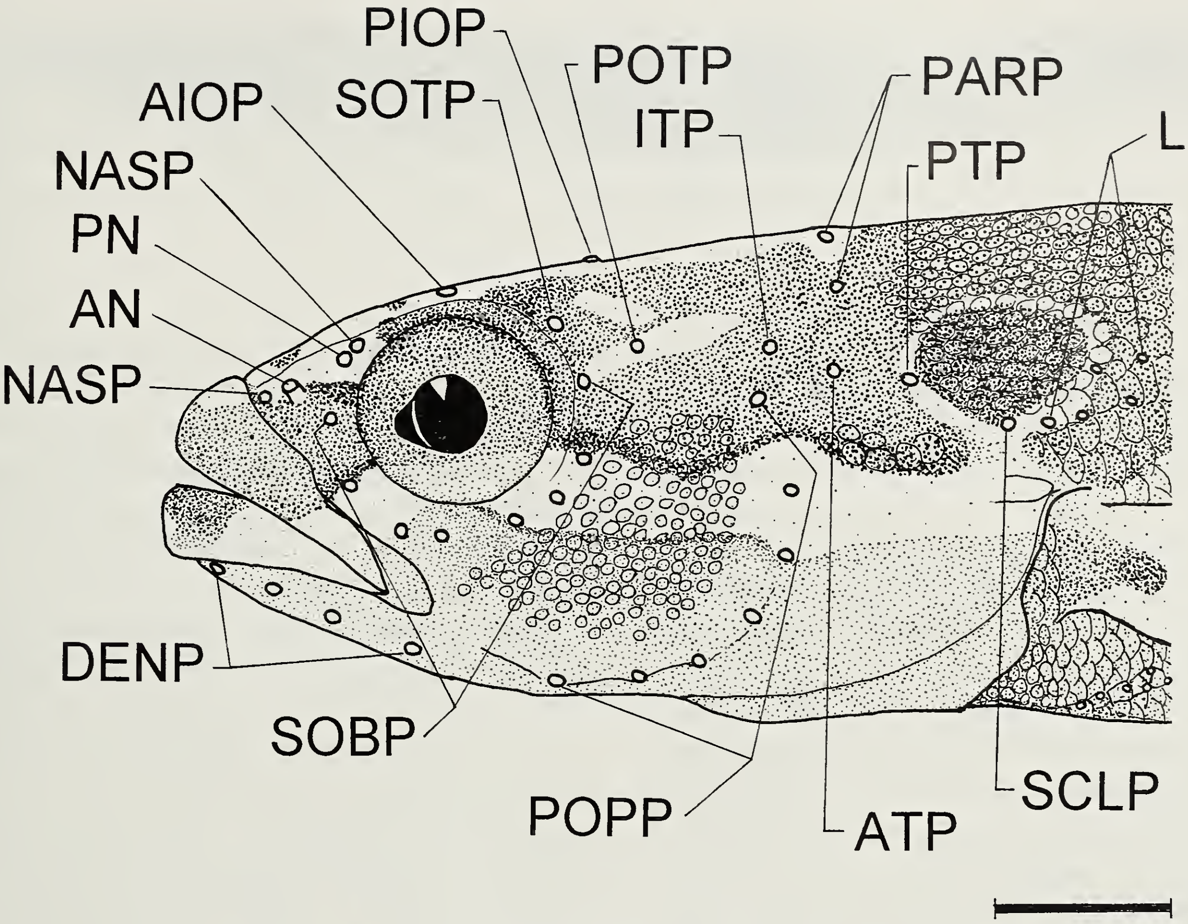

Fig. 3. *Halidesmus socotraensis,* holotype, SMF 29223, 64.3 mm SL; detail of head showing laterosensory pores, scalation and preserved pigmentation details. Abbreviations: AIOP, anterior interorbital pore; AN, anterior nostril; ATP, anterior temporal pore; DENP, dentary pores; ITP, intertemporal pore; LLP, lateral-line scale pores; NASP, nasal pores; PARP, parietal pores; PIOP, posterior interorbital pore; PN, posterior nostril; POPP, preopercle pores; POTP, posterior otic pore; PTP, posttemporal pore; SCLP, supracleithral pore; SOBP, suborbital pores; SOTP, supraotic pore. Scale bar = 2 mm.

mented rays branched; anal fin 45–48 (48), all rays branched; pectoral fins 9–10 (10/10), upper 1–2 (2/1) and lower 0–2 (1/1) rays unbranched, other rays branched; pelvic fin absent, though small rod-like pelvis present internally; caudal fin with five dorsal and five ventral principal rays, and one dorsal and one ventral procurrent rays; branched caudal fin rays 5 + 4. Caudal fin fully connected by membrane to last ray of dorsal and anal fins. Vertebrae 17–18 + 46–49 = 63–66 (17 + 49); ribs present on precaudal vertebrae 3 through 4–5 (3 through 5); epineural bones present on precaudal vertebrae 1 through 3–5? (1 through 3?; bones difficult to distinguish on x-radiographs); hypural 5 absent; hypurals 3–4 fused to one another and to urostylar complex; hypurals 1–2 fused to one another and, variably, to parhypural; epurals 1; supraneurals 2.

Cephalic sensory pore openings (Fig. 3; all pores bilateral unless otherwise indicated): nasal two, one pore just posterior to upper lip, second pore just above posterior nostril; anterior interorbital usually one, small second pore present unilaterally in one paratype, about two-thirds distance from typical anterior interorbital pore to posterior nasal pore; median (unpaired) posterior interorbital one, positioned above or slightly behind vertical through posterior edge of eye, additional posterior interorbital pore present in one paratype, displaced laterally in line with right side anterior interorbital pore; supraotic one; posterior otic usually one, two pores present unilaterally in one paratype; suborbital usually eight,

Fig. 4. *Halidesmus socotraensis*, holotype, SMF 29223, 64.3 mm SL, Abd al-Kuri Island, Socotra Archipelago.

nine unilaterally in one paratype; preopercular seven; dentary usually four, three unilaterally in one paratype; intertemporal usually one, two unilaterally in two paratypes; parietal two, canals from left and right side of head not communicating in midline; anterior temporal one; posttemporal usually one, two unilaterally in one paratype; supracleithral one.

Gill membranes fused to one another ventrally but free posteriorly from isthmus; branchiostegal rays 6; outer (anterior) gill rakers on first arch 2 + 6–7 (examined in three largest paratypes only); pseudobranch filaments 6–7 (examined in three largest paratypes only). Lateral-line system complex (Fig. 2), with pores on either dorsal or ventral margins of lateral-line scales (or in the case of median lateral lines, on either left or right margins of lateral-lines scales): line A absent; line B + C (bilateral) with 186–210 (210/206) pored scales, extending from shoulder to beneath vertical through base of segmented dorsal ray 49–54 (51/51); line D (bilateral) with 177–205 (202/197) pored scales, extending from just behind upper edge of pectoral-fin base along midside to or almost to caudal-fin base, not connecting anteriorly with line B + C; line E (median) with 6–12 (9) pored scales, extending from just beneath branchiostegal membranes to vertical beneath pectoral-fin base; line F (bilateral) with 78–90 (90/89) pored scales, extending posterodorsally from junction of lines E and G1 almost to pectoral fin, then along lower part of abdomen to junction with line G2; line G1 (median) with 59–63 (62) pored scales, extending from junction with lines E and F along ventral edge of abdomen to just in front of anus; line G2 (bilateral) with 10–14 (11/14) pored scales, connecting posterior terminus of line G1 with junction of lines F and H; line H (bilateral) with 125–152 (152/147) pored scales, extending from junction of lines F and G2 along lower part of body to vertical through base of anal ray 36–42 (41/42).

Olfactory capsule with two openings; anterior opening a short tube, positioned about midway between posterior opening and edge of lip; posterior opening with slightly raised rim, positioned near anterodorsal rim of orbit (Fig. 3). Cheek, upper edge of operculum (above horizontal through opercular spine) and body with small cycloid scales, those on upper part of operculum imbedded and inconspicuous; predorsal scales extending anteriorly to parietal commissure (Fig. 3).

Teeth in outer row of premaxilla and dentary conical, recurved anteriorly, decreasing in size and becoming laterally compressed posteriorly, numbering 11–12 in the premaxilla and 13–15 in the dentary; single row of small conical teeth present anteriorly on premaxilla and dentary immediately behind outer row teeth; vomer edentate; palatine edentate.

Live coloration: Not recorded.

Preserved coloration (Figs. 3, 4): Head and body dark brown, with indistinct to distinct paler mottling, which may align to form diffuse bars or reticulations; lower part of head and abdomen pale brown; dark grey-brown stripe extending from midside of lower lip through midside of upper lip to mid-anterior edge of eye, then behind mid-posterior edge of eye to upper edge of operculum; dark grey-brown stripe edged ventrally with creamy white stripe; large pale-edged, dark grey-brown spot on shoulder; creamy white median stripe or series of spots extending from tip of upper lip to origin of dorsal fin; dorsal fin dark greyish brown with series of alternating small dark grey-brown and pale brown spots on base of fin, spots encroaching slightly on to body; anal and caudal fins dark greyish brown, sometimes with several pale brown or dark grey-brown spots; pectoral fin pale brown, with small dark grey-brown spot on middle of fin base.

Comparisons.—The presence of three lateral lines on the body (dorsal, middle and ventral complexes) places the new species in the genus *Halidesmus.* There are four other species currently recognised in the genus (Winterbottom, 1982, 1986; Winterbottom & Randall, 1994): *H. scapularis* Günther from South Africa; *H. polytretus* Winterbottom from Kenya; *H. coccus* Winterbottom & Randall from southern Oman; and *H. thomaseni* (Nielsen) from Masirah Island (southeastern Oman) to Karachi (Pakistan) and the Bay of Bengal. Characters distinguishing the four species are summarized in Table 3.

Halidesmus is divisible into two apparent monophyletic groups, which are diagnosed by characters that are uniquely derived among pseudochromids. The first, which consists of *H. coccus* and *H. thomaseni,* is diagnosed by a single synapomorphy (fleshy crest on the snout and interorbital area). The other, which consists of *H. socotraensis, H. scapularis* and *H. polytretus,* is diagnosed by two synapomorphies (ventral lateral line with complex branching on abdomen; lateral-line pores opening to either ventral or dorsal margins of scales).

Halidesmus socotraensis differs from *H. scapularis* in the following features: pelvic fins absent (versus pelvic-fin rays usually I,2–3, fins rarely absent); lateral line A absent (versus present); lateral line D with 177–205 pores, not joining C (versus with 157–179 pores, joining C); lateral lines E and G median (versus bilateral); medial parietal pores bilaterally paired (versus single median pore); caudal, anal and dorsal fins fully confluent (versus united near fin-ray bases only); and total vertebrae 63–66 (versus 66–69).

Halidesmus socotraensis differs from *H. polytretus* in the following: lateral line A absent (versus present); pores in lateral line D 177–205 (versus 204–216); cheek, nape and opercular scales present (versus absent); preopercular pores 7 (versus 9); suborbital pores 8–9, usually 8 (versus 11–13); posterior interorbital pores usually 1, rarely 2 (versus 2); principal caudal fin rays 5 + 5 (versus 6 + 5); and gill rakers 2 + 6–7 (versus 1 + 5).

Relationships among *H. socotraensis, H. scapularis* and *H. polytretus* are ambiguous. The presence of lateral-line A is unique among congrogadines to *H. scapularis* and *H. polytretus* and suggests a sister relationship between the two species. Conversely, the presence of a median section of the lower lateral line is unique to *H. polytretus* and *H. socotraensis,* and suggests relationship between those two species. These relationships will be tested in a forthcoming study of the phylogeny and historical biogeography of *Halidesmus* by the second author.

Habitat and distribution.—All known specimens were collected at a single station in a small enclosed bay on the SW coast of Abd al-Kuri (Fig. 1, Sta. 709). The site is characterised by highly diverse assemblages of large massive and encrusting corals, and an associated diverse fish community.

Etymology.—The specific epithet refers to the known distribution of the species.

Haliophis guttatus (Forsskål)
Barred Snakelet
Fig. 5, Table 2

Haliophis guttatus is known from throughout the Red Sea to the northern Gulf of Aden, southern Oman, the east coast of Africa between Kenya and Mozambique, and the west coast of Madagascar (Winterbottom 1984, Winterbottom & Randall 1994). Fifteen specimens were collected by the second author and associates in the Socotra Archipelago. The morphology of

Fig. 5. *Haliophis guttatus*, SMF 29198, 59.5 mm SL, Abd al-Kuri Island, Socotra Archipelago.

these specimens agrees well with published descriptions of the species (e.g., Winterbottom, 1984, 1986; Randall, 1995). Winterbottom (1984) noted that the species exhibits geographic variation in several meristic and morphometric characters, which he interpreted as a step cline, with the step occurring between about 27°N and 20°N in the northern Red Sea. Frequency distributions of counts relevant to this phenomenon are provided for the Socotran specimens in Table 2. Unfortunately, the specimens are somewhat distorted and difficult to measure accurately; therefore, we do not provide relevant morphometric details. Generally, meristic values agree well with data presented by Winterbottom for specimens from the southern Arabian area (central and southern Red Sea and Gulf of Aden), except for counts of precaudal vertebrae, which more closely approached values for specimens from Mozambique and Madagascar. However, sample sizes for many of the localities reported by Winterbottom are small (often five or fewer specimens).

Material.—SMF 29224, 1: 64.8 mm SL, Socotra Archipelago, Abd al-Kuri Island, SW coast, ca. 12°13′N 52°04′E, 6–15 m, rotenone, U. Zajonz, F.N. Saeed, M. Apel and E. Zandri, 4 April 2000 (station 709); SMF 29198, 7: 38.0–79.5 mm SL, NHCY-F uncataloged, 7: 43.2–66.0 SL, Socotra Archipelago, Abd al-Kuri Island, E coast, Ras Anjara bay, ca. 12°10′N 52°22′E, 3–9 m, rotenone, U. Zajonz and M. Apel, 8 April 1999 (station 173).

Discussion

The fish surveys of 1999 and 2000 comprised 18 large sampling stations scattered all around the Socotra Archipelago. Samples of congrogadine species were obtained only at Abd al-Kuri, whereas pseudochromids of the subfamilies Pseudochrominae (six species of *Pseudochromis* Rüppell) and

Table 2.—Frequency distributions for selected meristic characters of *Halidesmus socotraensis* and *Haliophis guttatus* from the Socotra Archipelago. Bilateral counts of pectoral rays are included.

	Segmented dorsal rays								Anal rays							
	42	43	44	//	58	59	60	61	34	35	36	//	45	46	47	48
socotraensis	—	—	—		1	1	3	1	—	—	—		1	—	1	4
guttatus	2	9	4		—	—	—	—	5	7	3		—	—	—	—

	Pectoral rays			Total caudal rays				Precaudal vertebrae				
	9	10	11	12	13	14	15	13	14	//	17	18
socotraensis	4	8	—	6	—	—	—	—	—		5	1
guttatus	1	2	27	—	—	4	11	13	2		—	—

	Caudal vertebrae							Total vertebrae							
	36	37	//	46	47	48	49	49	50	51	//	63	64	65	66
socotraensis	—	—		1	—	3	2	—	—	—		1	—	2	3
guttatus	4	11		—	—	—	—	3	11	1		—	—	—	—

Table 3.—Summary of characters distinguishing *Halidesmus* species.

Character	*socotraensis*	*polytretus*	*scapularis*	*coccus*	*thomaseni*
Pores in lateral lines	open to ventral or dorsal scale margins	open to ventral or dorsal scale margins	open to ventral or dorsal scale margins	open to posterior scale margins	open to posterior scale margins
Ventral lateral line	branched	branched	branched	unbranched	unbranched
Line A	absent	present	present	absent	absent
Line D	with 177–205 pores; doesn't join C	with 204–216 pores; doesn't join C	with 157–179 pores; joins C	with 173–194 pores; doesn't join C	with 160–198 pores; doesn't join C
Lines "E" and "G"	median	median	bilaterally paired	N/A	N/A
Cheek scales	present	absent	present	absent	present
Nape scales	present	absent	present	absent	present
Opercular scales	present	absent	absent	absent	present
Preopercular pores	7	9	7–8, usually 8	7	7
Suborbital pores	8–9, usually 8	11–13	7–8, usually 8	8	8
Medial parietal pores	bilaterally paired	bilaterally paired	median, singular	bilaterally paired	bilaterally paired
Posterior interorbital pores	1–2, usually 1	2	1	1	1
Fleshy crest	weak or absent	weak or absent	weak or absent	well-developed, convex	well-developed, concave
Dorsal fin	I + 58–61	I + 57–58	I + 60–63	I + 64–68	I + 58–64
Anal fin	45–48, usually 48	45–46	48–51	52–55	45–50
Pectoral fin	9–10	9–10	8–10, usually 9	9–12	7–9
Pelvic fin	absent	absent	usually I,2–3, rarely absent	absent	absent
Caudal fin	1, 5, 5, 1	0–1, 6, 5, 0–1	Usually 2, 5, 5, 2	2, 5, 6, 2	1, 5, 5, 1
Caudal, anal and dorsal fins	fully confluent	fully confluent	membranes united basally only	fully confluent	fully confluent
Vertebrae	17–18 + 46–49 = 63–66	16 + 47–48 = 63–64	16–18 + 49–53 = 66–69	17–18 + 51–55 = 69–73	16–18 + 46–50 = 64–68
Gill rakers	2 + 6–7	1 + 5	2–3 + 6	2–3 + 5–6	1–2 + 7–8

Pseudoplesiopinae (two species of *Chlidichthys* Smith) were collected from other islands as well. It seems possible that Abd al-Kuri receives a higher influx of pelagic eggs and larvae from East Africa through the Somali current compared to the other islands, enriching the fish communities. In particular along the south and east coasts there are isolated biodiversity "hotspots," which may act like traps for recruits by providing shelter and suitable habitats (U. Zajonz, unpubl. data). Both sites where congrogadines were collected host particularly rich fish and coral assemblages as compared to other areas visited at Socotra. The fish species compositions were exceptionally rich, suggesting that there is limited faunal exchange between these patches and the wider archipelago, at least of closely reef-associated species.

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Literature Cited

Gill, A. C. 1998. Homology of the anterior vertebrae, ribs, and dorsal fin pterygiophores and rays in congrogadine fishes (Perciformes: Pseudochromidae).—Copeia 1998:1041–1045.

———, R. D. Mooi, & J. B. Hutchins. 2000. Description of a new subgenus and species of the fish genus *Congrogadus* Günther from Western Australia (Perciformes: Pseudochromidae).—Records of the Western Australian Museum 20: 69–79.

Kemp, J. M. 1998. Zoogeography of coral reef fishes of the Socotra Archipelago.—Journal of Biogeography 25:919–933.

Leviton, A. E., R. H. Gibbs, Jr, E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Randall, J. E. 1995. Coastal Fishes of Oman. Crawford House Publishing, Bathurst, 439 pp.

Steindachner, F. 1902. Wissenschaftliche Ergebnisse der südarabischen Expedition in den Jahren 1898 bis 1899. Fische von Südarabien und Socotra.—Anzeiger der Akademie der Wissenschaften Wien 39(24):316–318.

———. 1903. Fische aus Südarabien und Sokótra.—Denkschriften der Kaiserlichen Akademie der Wissenschaften, Wien 71:123–168. [dated 1902, but actually published in 1903]

Winterbottom, R. 1982. A revision of the congrogadid fish genus *Halidesmus* (Pisces: Perciformes), with the description of a new species from Kenya and a list of the species included in the family.—Canadian Journal of Zoology 60:754–763.

———. 1984. Revision of the congrogadid *Haliophis* (Pisces: Perciformes), with the description of a new species from Indonesia, and comments on the endemic fish fauna of the northern Red Sea.—Canadian Journal of Zoology 63:209–217.

———. 1986. Revision and vicariance biogeography of the subfamily Congrogadinae (Pisces: Perciformes: Pseudochromidae).—Indo-Pacific Fishes 9:1–34, pl. I. [dated 1985, but actually published 1986]

———. 1996. A new species of the congrogadin genus *Rusichthys* from southern Oman (Perciformes; Pseudochromidae), with notes on its osteology.—Canadian Journal of Zoology 74: 581–584.

———, & J. E. Randall. 1994. Two new species of congrogadins (Teleostei; Pseudochromidae), with range extensions for four other species.—Canadian Journal of Zoology 72:750–756.

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Calocidaris micans (Cidaridae) and *Pseudoboletia maculata* (Toxopneustidae): additions to the sea urchin fauna (Echinodermata: Echinoidea) of the Gulf of Mexico

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Abstract.—Two sea urchins (*Calocidaris micans, Pseudoboletia maculata*) were collected and photographed in the Gulf of Mexico between 1978 and 1998. These constitute new records for their distributions. *Calocidaris micans* has been reported previously off the northwestern coast of Cuba, in the Yucatan Channel, and off Barbados. One of our specimens was photographed and collected in the northeastern Gulf of Mexico off Alabama at 100 m. Unpublished museum holdings (USNM) add a second record off Louisiana at 129–144 m. *Pseudoboletia maculata* is distributed in the Pacific Ocean from Ceylon to Japan, in the South Atlantic only at Ascension and St. Helena islands, and in the North Atlantic from Venezuela, Barbados, and off the Atlantic coast of the United States from Florida to North Carolina. An unpublished document of a federal agency reported this sea urchin from the western Gulf of Mexico. Our collections and photographs from off Pensacola, Florida, at ca. 40 m depth revealed that *P. maculata* occurs there in mixed-species aggregations with the echinoid *Lytechinus variegatus.* These records bring the echinoid fauna of the Gulf of Mexico to 61 species, only one of which is endemic and 39 of which have West Indian-Caribbean distributions. Although these records probably are not range extensions within recorded human history, they might represent a post-glacial (re)invasion of the Gulf of Mexico within the last 9000 yr as patchily distributed live-bottom biotopes at intermediate depths became available. These depths and biotopes—poorly sampled in the past—have become more accessible for survey using current sampling technology.

In his review of the echinoid fauna of the Gulf of Mexico, Serafy (1979) listed 89 species, an increase of 23 species from Clark's (1954) list. Serafy pointed out that many of Clark's species are not part of the Gulf fauna proper but have been collected only on its periphery, belonging instead to faunas of the Caribbean, Bahamas, eastern Florida, and the Florida Keys; Serafy's list is annotated to reflect the species restricted to adjacent waters. Apparent inconsistencies in Serafy's two tabulated lists give 53–57 species of echinoid in the Gulf of Mexico proper: *Cidaris abyssicola* (Cidaridae), *Araeolampas atlantica* (Echinothuridae), and *Pourtalesia miranda* (Pourtalesiidae) are not marked as peripheral species, although their distributions would make them so by his criteria; *Echinometra viridis* is listed only as peripheral in his table 1 perhaps by lapsus because Serafy recorded it later in table 2 from several regions within the Gulf. Hulings's (1955) report of *E. viridis* from the northwestern Gulf of Mexico confirmed the presence of this species, although Pomory (2002) does not list it from the Texas coast. If, then, some interpretation is allowed, the known echinoid fauna of the Gulf stands at 54 species based on Serafy (1979), although numerous misidentifications reported by Turner & Norlund (1988) are cause to question Gulf records of *Brissopsis elongata.*

Defenbaugh (1976) identified specimens of *Echinocardium* from the northern Gulf of Mexico as the European species *E. cordatum* and *E. flavescens* rather than as *E. laevigaster* reported by Clark (1954) and Serafy (1979). Harry (1979) believed that Defenbaugh's specimens were misidentified. Serafy (1979) did not list the toxopneustid *Pseudoboletia maculata,* which was recorded by Pawson (1978) from southeastern Florida and listed and illustrated from the western Gulf of Mexico (Texas A&M University 1981). The reanalysis of *Mellita quinquiesperforata* by Harold & Telford (1990) resulted in its restriction as a western Gulf species and in the elevation of *M. quinquiesperforata tenuis* to species in the eastern Gulf. Hopkins et al. (1991) added *Tretocidaris bartletti* from the northern Gulf off the coast of Alabama; this species was one of Serafy's (1979) peripheral species. Most recently, the record of *Cidaris abyssicola* off the northern coast of the Yucatan Peninsula by Barbosa-Ledesma et al. (2000) places this echinoid well within the boundaries of the Gulf; and these authors also found *Cidaris rugosa* off the western coast of the Yucatan Peninsula and *Stereocidaris ingolfiana* off the northern coast.

In the present report, we confirm *Pseudoboletia maculata* as a part of the Gulf echinoid fauna with the find of a dense aggregation off western Florida, and we add *Calocidaris micans* from one specimen off Alabama and a second off Louisiana. These additions bring to 61 the echinoid species recorded from the Gulf of Mexico.

Materials and Methods

Sea urchins were obtained for this study from Continental Shelf Associates, Inc., Jupiter, Florida, U.S.A., under contract with the U.S. Department of the Interior, Minerals Management Service (*Calocidaris micans*) (Continental Shelf Associates, Inc., & Texas A&M University 2001) and with Chevron U.S.A., Inc., New Orleans, Louisiana (*Pseudoboletia maculata*) (Continental Shelf Associates, Inc. 1996a, 1996b); from the Texas Cooperative Wildlife Collection of Texas A&M University (TAMU); and from the National Museum of Natural History (USNM) of the Smithsonian Institution. Details of collecting localities are given under descriptions of the material. Other records for the Western Atlantic Ocean are based on holdings of USNM, Museum of Comparative Zoology (MCZ) of Harvard University, Harbor Branch Oceanographic Museum (HBOM) of Harbor Branch Oceanographic Institution, California Academy of Sciences, and the Museum of Natural History (BMNH) in London. In most cases, the specimens were examined by us.

Calocidaris micans was collected off Louisiana, U.S.A., with the manipulator arm of R/V *Johnson-Sea-Link I* submersible operated by HBOI in 1989. R/V *Edwin Link* served as the tender.

The R/V *Tommy Munro* served as the tender during survey photography and specimen collection of *C. micans* off Alabama, U.S.A., in 1998. Photographic data and the voucher specimen were collected using a Benthos® open frame SeaROVER remotely operated vehicle (ROV) equipped with color-imaging scanning sonar, manipulator arm, video and 35-mm still cameras, quartz-halogen lamps, and a strobe. The Photosea® underwater still camera and strobe were triggered manually by the onboard scientist. The voucher specimen of *C. micans* was collected using the ROV manipulator arm.

Pseudoboletia maculata was photographed and collected from the East Flower Garden Bank in the NW Gulf of Mexico by Texas A&M University in 1978. The submersible DRV *Diaphus* was equipped with video and still cameras, a manipulator arm, sediment scoop, and suction sampler (Texas A&M University 1981).

The M/V *Mr. Offshore* was used during survey operations by Continental Shelf Associates, Inc., off Pensacola, Florida, U.S.A., in 1992 and 1993. *Pseudoboletia maculata* was photographed from a towed multicamera system with both video and 35-mm still cameras. Still photographs were taken with a Benthos® 1000 underwater camera and strobe. Specimens were collected by a 7.5-m semi-balloon "mongoose" trawl.

Results

Order Cidaroida Claus, 1880
Family Cidaridae Gray, 1825
Genus *Calocidaris* H. L. Clark, 1907
Calocidaris micans (Mortensen, 1903)
(Figs. 1–2)

Porocidaris sharreri Agassiz, 1880:71 (part.).

Dorocidaris micans Mortensen, 1903:23 (original description), 28 (list).

Calocidaris micans: Mortensen, 1928:312–314 (for complete synonymy, key, description), text-fig. 19-2.—Clark, 1954: 374 (list).—Fell, 1966:U333 (diagnosis).—Phelan, 1970:7–9 (key, description), text-fig. 2, pls. 2, 3.—Serafy, 1979: 10, 14, 109 (key, geographic and bathymetric distributions).

Non-*Calocidaris micans*: Downey, 1968:62 (see note in Phelan 1970:16).

Material examined.—Gulf of Mexico: USNM E47929, 1 spec., dry, 65/76 mm test height/test diameter (TH/TD), R/V *Edwin Link,* R/V *Johnson-Sea-Link I,* dive 2585, Green Canyon, off Louisiana, U.S.A., 27°44′37″N, 91°7′54″W, 129–144 m, 5 Sep 1989; USNM 1002220, 1 spec., alcoholic, 58/73 mm TH/TD, R/V *Tommy Munro* and remotely operated vehicle, Continental Shelf Associates, Inc., job 1600, cruise 3, site 4, sample 335, off Alabama, U.S.A., 29°19′39″N, 87°46′7.8″W, 100 m, manipulator arm, 28 Aug 1998.—Western Atlantic Ocean: MCZ 283, 1 spec., dry, 41/58 mm TH/TD, USCSS *Blake,* sta. 297, off Barbados, 123 fm [225 m], 1879; USNM 10705, 1 spec., alcoholic, 28 mm TD, R/V *Albatross,* sta. 2348, Straits of Florida, off Havana, Cuba, 23°10′39″N, 82°20′21″W, 211 fm [386 m], 20 Jan 1885; USNM 10717, 2 spec., dry and alcoholic, 48 mm TD (dry), 50 mm TD (alcoholic), R/V *Albatross,* sta. 2354, Yucatan Channel, off Cozumel Island, Mexico, 20°59′30″N, 86°23′45″W, 130 fm [238 m], 22 Jan 1885; MCZ 7720, 1 spec., dry, 41/58 mm TH/TD, R/V *Atlantis,* sta. 3305, off Playa Baracoa, Havana Province, Cuba, 330 fm [604 m], 23 Mar 1939; USNM E13068, 1 spec., dry, 77 mm TD, R/V *Gerda,* cruise 6433 (30th biological cruise), sta. 388, NW corner of Little Bahama Bank, Bahamas, 27°18′0″N, 79°12′0″W, 320 m, 19 Sep 1964; USNM E13069, 2 of 3 spec., dry, 53 and 70 mm TD, R/V *Gerda,* cruise 6717, sta. 899, Arrowsmith Bank, Yucatan Channel, off Yucatan Peninsula, Mexico, 20°57′0″N, 86°34′0″W, 40–165 m [one tag reads "102 m"], 10 Sep 1967; USNM E13025, 1 of 2 spec., dry, 56 mm TD, R/V *Pillsbury,* cruise 6802, sta. 595, Arrowsmith Bank, Yucatan Channel, off Yucatan Peninsula, Mexico, 21°8′30″N, 86°27′0″W, 33–586 m, 15 Mar 1968; USNM E13067, 3+ spec., dry, 17, 34, and 70 mm TD, R/V *Pillsbury,* cruise 7001, sta. 1141, off S coast of Great Inagua Island, Bahamas [one tag reads "Caribbean, nr. Haiti"], 20°52′0″N, 73°14′0″W, 403–458 m, 13 Jan 1970; HBOM 72:307, 1 spec., dry, 37/46 mm TH/TD, R/V *Seward Johnson,* cruise 118, R/V *Johnson-Sea-Link II,* dive 579, W of Nassau Harbor, New Providence, Bahamas, 25°7.1′N, 77°26.1′W, 488 m, manipulator, 30 Mar 1981; HBOM 72:339, 1 spec., alcoholic, 46/58 mm TH/TD, R/V *Johnson-Sea-Link I,* dive 1306, off Wood Cay, N of Grand Bahama Island, Bahamas, 274 m, manipulator, 7 Dec 1982; USNM E32546, 1 spec., dry, 57 mm TD, R/V *Seward Johnson,* cruise 157, R/V *Johnson-Sea-Link I,* dive 1357, W of Wood Cay, Bahamas, 26°42′36″N, 79°1′42″W, 244–309 m, 14 Jun 1983; USNM E32551, 1 spec., dry, 62 mm TD, R/V *Seward Johnson,* cruise 157, R/V *Johnson-Sea-Link I,* dive 1359, W of Wood Cay, Bahamas, 26°42′48″N, 79°9′30″W, 618–624 m, 15 Jun 1983; USNM E32547, 1 spec., dry, 37 mm TD, R/V *Seward Johnson,* cruise 159, R/V *Johnson-Sea-Link I,* dive 1498, French Bay, San Salvador Island, Bahamas, 23°56′0″N, 74°32′54″W, 436–468 m, 21 Oct 1983; USNM E32550, 1 spec., dry, 50 mm TD, R/V *Seward Johnson,* cruise 159, R/V *Johnson-Sea-Link I,* dive 1500, off Cockburn Town, San Salvador Island, Bahamas, 24°2′48″N, 74°32′30″W, 1600 ft [488 m], 22 Oct 1983; USNM E32548, 1 spec., dry, 34 mm TD, R/V *Seward Johnson,* cruise 159, R/V *Johnson-Sea-Link I,* dive 1506, Bonefish Bay, San Salvador Island, Bahamas, 24°4′42″N, 74°33′6″W, 914 ft [279 m], 25 Oct 1983; USNM E32606, 1 spec., alcoholic, 16 mm TD, R/V *Seward Johnson,* cruise 161, R/V *Johnson-Sea-Link II,* dive 805, off Sandy Point, Great Abaco Island, Bahamas, 25°36′12″N, 76°44′30″W, 473 m, 7 Apr 1984; USNM E32580, 1 spec., dry, 48 mm TD, R/V *Seward Johnson,* cruise 161, R/V *Johnson-Sea-Link II,* dive 807, S of Rock Point, Great Abaco Island, Bahamas, 25°59′30″N, 77°24′6″W, 300 m, 8 Apr 1984; USNM E32511, 1 spec., dry, 73 mm TD, R/V *Seward Johnson,* cruise 161, R/V *Johnson-Sea-Link II,* dive 816, Chub Cay, Berry Islands, Bahamas, 25°23′42″N, 77°54′30″W, 226 m, 14 Apr 1984; HBOM 72:505, 1 spec., dry, 24/34 mm TH/TD, R/V *Seward Johnson,* R/V *Johnson-Sea-Link I,* dive 2001, San Salvador Island, Bahamas, 24°13.6′N, 74°29.5′W, 572 m, manipulator, 21 Apr 1987; HBOM 72:498, 1 spec., dry, 43/54 mm TH/TD, R/V *Seward Johnson,* R/V *Johnson-Sea-Link I,* dive 2007, San Salvador Island, Bahamas, 23°0.7′N, 74°33.0′W, 263 m, manipulator, 24 Apr 1987; HBOM 72:743, 1 spec., dry, 48/63 mm TH/TD, R/V *Seward Johnson,* R/V *Johnson-Sea-Link II,* dive 1738, 2.46 nm off Needham's Point, bearing 044°, Barbados, 200–207 m, manipulator, 20 Apr 1989.

Other sources.—In addition to specimens examined by us, we have relied on station data for *Calocidaris micans* deposited in California Academy of Sciences, HBOM, and BMNH.

Descriptions of stations and material.—The specimen of *C. micans* (USNM E47929) taken off the coast of Louisiana at 129–144 m depth was collected by submersible. The following description of the site is based on notes written by S. D. Cairns (in litt.) during the dive. Bottom temperature was 17°C. The site was a ridge oriented from northwest to southeast with a slope of 45° at least on one side. The slope was partly composed of large, flat, imbricated, calcareous slabs that Cairns compared to plates of deep-reef *Agaricia.* The substratum consisted also of gravel and of rocks of various sizes and shapes. A variety of scleractinian and antipatharian corals were observed or collected (Cairns et al. 1993), including a new species of black coral (Opresko & Cairns 1992). Other material collected were three slit shells, another unspecified gastropod, and a crinoid; collection of *C. micans* was not mentioned in Cairns's field notes.

The specimen at hand had a test diameter (TD) of 76 mm and a test height (TH) of 65 mm, giving the test a high globose shape (TH:TD = 0.86) typical of *C. micans.* All primary spines above the ambitus were broken except one (137 mm long; = 1.8 TD); Phelan (1970) reported that primary spines of *C. micans* can be up to 3 TD, although more commonly they are up to 1.5 TD. In addition to morphology of the test and pedicellariae (Mortensen 1928, Phelan 1970), all primary spines had the smooth porcelaneous surface (Fig. 1B, C) that is unique to this species (Phelan 1970). The spines were free of epizoics. Although cidaroid spines are known to harbor epizoics (Hyman 1955), the spines of most *C. micans*

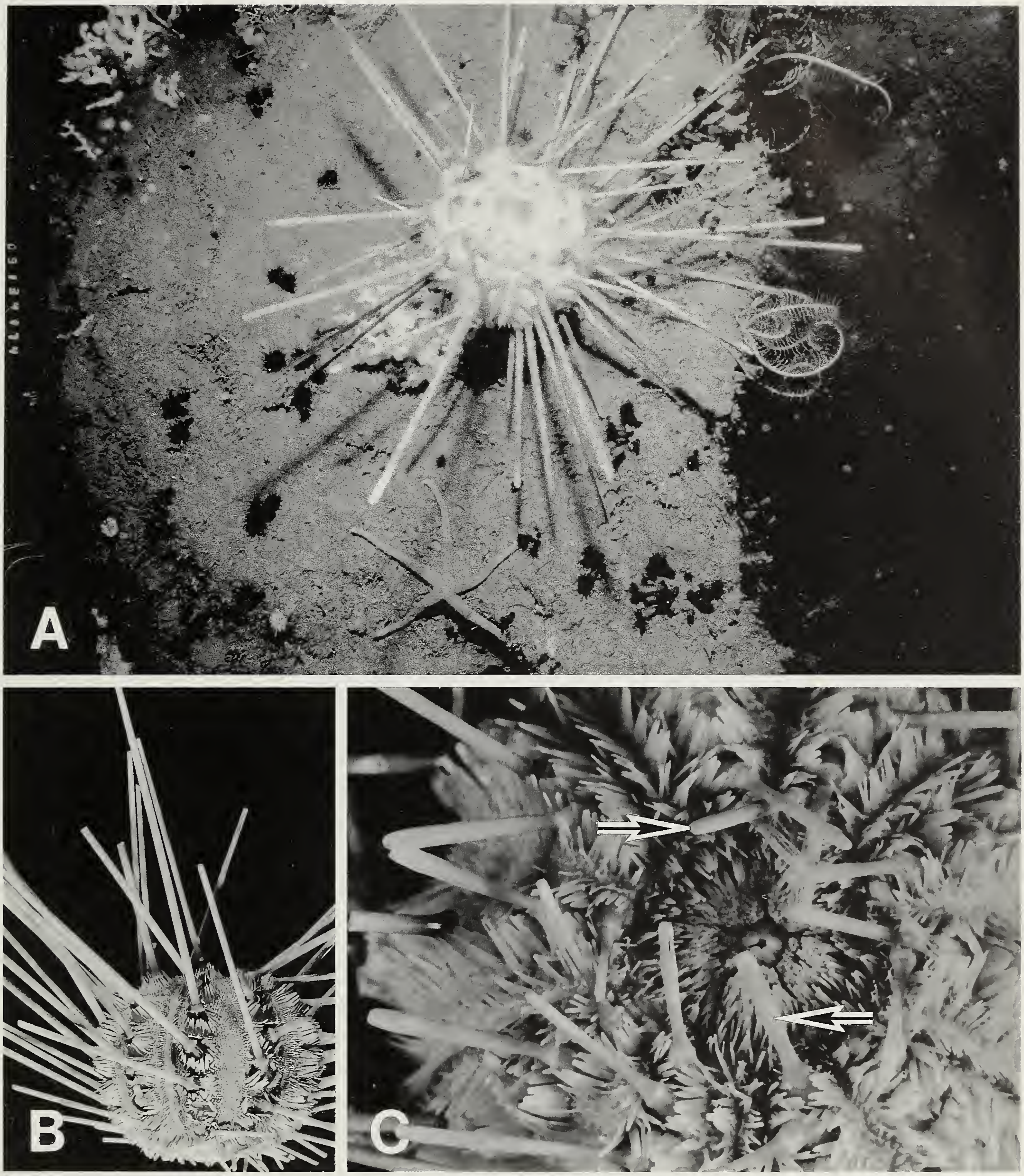

Fig. 1. *Calocidaris micans.* A. USNM 1002220 on ledge at collection site off Alabama, with a colony of the hard coral *Madrepora carolina* to left, the hard coral *Madracis myriaster* to the upper left, two unidentified comatulid crinoids to the right, several individuals of the black ahermatypic coral *Rhizopsammia manuelensis,* and the seastar *Chaetaster nodosus* at the bottom; note epizoics on some of the primary spines of the echinoid; courtesy of Continental Shelf Associates, Jupiter, Florida. B. USNM E47929, showing long, terete, smooth primary spines on ambitus and near apex of test. C. USNM 1002220, oral surface, showing smooth oral primary spines (arrows).

examined by us were rarely covered with epizoics.

The specimen of *C. micans* (USNM 1002220) was photographed and collected off Alabama, U.S.A., at 100 m depth on a high-relief (>2 m) hard-bottom feature described by Ludwick & Walton (1957) as a trend of discontinuous reef-like pinnacles located near the edge of the continental shelf between the Mississippi River delta and DeSoto Canyon. The sampling site was the apex of a relatively large ridge gradually sloping to the west-southwest and to the north. Visually and numerically dominant taxa at the site were hard corals (*Rhizopsammia manuelensis, Madracis myriaster, Madrepora carolina*), soft corals [*Ctenocella* (*Ellisella*) spp., *Nicella* spp.], antipatharians (*Antipathes* spp.), crinoids, basketstars, and various unidentified ahermatypic hard corals.

The in-situ photograph (Fig. 1A) of the specimen at hand showed it on a ledge that was lightly coated with sediment. Associated fauna visible in the photograph were a variety of anthozoans, crinoids, a seastar, and a galatheid crab. Most primary spines at and above the ambitus were broken, and little additional damage was inflicted upon collection of the specimen. The animal in life had pale yellow interambulacra and paler ambulacra, scrobicular spines, and regenerating primary spines. The primary spines otherwise were medium brown, much darker basally, and largely unbanded. Many primary spines of the live specimen exhibited a fuzzy coating, presumably of epizoics; but the only obvious epizoics on the alcoholic specimen were occasional patches of the foraminiferan *Homotrema rubra.* Among other *C. micans* examined, one specimen from Barbados (HBOM 72:743) had spines with barnacles and tubicolous polychaetes. The test of the specimen from Alabama was globose (TH:TD = 0.79).

Remarks.—*Calocidaris micans* was first collected off Barbados (Fig. 2) at 225 m depth by USCSS *Blake* in 1879 and was one of three specimens in Agassiz's (1880) type material of *Porocidaris sharreri.* [It was not collected again off Barbados for 110 yr when one specimen (HBOM 72:743) was collected by T. Askew at a depth of 200–207 m.] In 1885, R/V *Albatross* took two specimens each from the Straits of Florida (337–386 m) and the Yucatan Channel (238 m). One specimen from the Straits of Florida (NHM 1898.5.3.583) is Mortensen's (1903) holotype of *Dorocidaris micans.* It was in his report on echinoids of the Danish Ingolf Expedition that Mortensen (1903) pointed out Agassiz's (1880) error. Clark (1907:211) erected *Calocidaris* for *D. micans,* naming it presumably because it was "the most beautiful echinoid I have ever seen," an evaluation with which Mortensen (1910) later concurred. Clark (1907) characterized his new genus partly by the smooth, highly polished, porcelain-like primary spines (Fig. 1B) and by the absence of serrations (spinules) even on the oral primaries (Fig. 1C). Phelan (1970) viewed the morphology of the primary spines as diagnostic of *Calocidaris,* pointing out that all other cidaroids have serrations on at least some primaries. Although Clark (1925) later synonymized his *Calocidaris* with *Cidaris,* Mortensen (1928) retained *Calocidaris,* as have echinoid systematists since then. The genus remained monotypic and Recent until Cutress (1980) described *Calocidaris palmeri* from the Middle Miocene of Cuba; Cutress (1980) considered *C. micans* to have descended directly from *C. palmeri* in a process paralleled in *Cidaris* and *Tretocidaris.* For decades, the few specimens of *C. micans* were known only from the Greater and Lesser Antilles.

The cruises of R/V *Gerda* and *Pillsbury* in 1964–1970 collected more specimens from the Yucatan Channel (33–586 m) but added the Bahamas (320–458 m) to its distribution (Fig. 2). Many Bahamian specimens were collected during cruises of R/V *Seward Johnson* and R/V *Edwin Link* using the *Johnson-Sea-Link* submersibles in 1981–1998 at depths of 226–624 m. Not until 1989, 110 yr after its original discovery off Barbados, was *C. micans* taken from

Fig. 2. Distribution of *Calocidaris micans* based on museum records and literature. Each plot might represent multiple nearby records.

the Gulf of Mexico, off Louisiana at a depth of 129–144 m. The second Gulf specimen was photographed in situ (Fig. 1A) and collected in 1998 off Alabama at 100 m. Both specimens were from the northern Gulf of Mexico, well within Serafy's (1979) criteria for inclusion; they are among the largest (73 and 76 mm TD) known specimens of *C. micans* and from among the shallowest stations (<150 m).

Order Temnopleuroida Mortensen, 1942
Family Toxopneustidae Troschel, 1872
Genus *Pseudoboletia* Troschel, 1869
Pseudoboletia maculata Troschel, 1869
(Figs. 3–5)

Pseudoboletia maculata Troschel, 1869:96 (original description).

Pseudoboletia atlantica Clark, 1912:344 (original description), 345 (key).

Pseudoboletia occidentalis Clark, 1921: 115–118, pl. II (original description).

Pseudoboletia maculata: Mortensen, 1943: 528 (key), 532–534 (for complete synonymy, description), pl. XLII, figs. 4, 5; pl. LV, figs. 2, 5, 6, 16, 17, 21.—Pawson, 1978:3–5 (listed), 7 (description), 17–20 (description).—Continental Shelf Associates, Inc., 1979 (station data).—Texas A&M University, 1981:99 (ecology, station data), fig. X-10 (in situ), table X-C-29 (listed).—Duke University Marine Laboratory, 1982:tables 5.9, 5.13, Appendix 20 (listed).—Rowe & Gates, 1995:258 (systematics, distribution).—Continental Shelf Associates, Inc., 1996a:148 (ecology).—Continental Shelf

Associates, Inc., 1996b:15, 17 (ecology), table 1 (listed), pl. B-12.

Pseudoboletia atlantica: Mortensen, 1943: 528 (key), 534–538 (synonymy, description), pl. XXXII, figs. 1–5; pl. XXXIX, fig. 6; pl. XL, fig. 6; pl. XLII, figs. 1–3; pl. XLIII, figs. 1, 2; pl. XLIV, fig. 1; pl. LV, figs. 1, 3, 19, 20.

Pseudoboletia occidentalis: Mortensen, 1943:528 (key); 538–540 (synonymy, description).

?*Lytechinus variegatus*: Continental Shelf Associates, Inc., 1996a:table 5.4 (part., listed).

Material examined.—Gulf of Mexico: TAMU 3-1809, 1 spec., alcoholic, 27/51 mm test height/test diameter (TH/TD), DRV *Diaphus,* cruise 78-G9-D5, dive 5 [night dive], submersible, East Flower Garden, 27°53′N, 93°38′W, 160–190′ [49–58 m], 30 Oct 1978 [one tag reads "9/30/78"]; USNM 1002222, 1 spec., dry, 34/66 mm TH/TD, M/V *Mr. Offshore,* Continental Shelf Associates, Inc., job 1390.3 for Chevron, Destin Dome Unit, survey 2, trawl 22, off Pensacola, Florida, U.S.A., 29°59′N, 87°11′W, 112′ [34 m], 9 Oct 1992; USNM 1002298, 2 spec., dry, 29/58 & 32/65 mm TH/TD, M/V *Mr. Offshore,* Continental Shelf Associates, Inc., job 1390.3 for Chevron, Destin Dome Unit, survey 2, trawl 22, off Pensacola, Florida, U.S.A., 29°59′N, 87°11′W, 112′ [34 m], 9 Oct 1992; USNM 1002299, 1 spec., alcoholic, 42/81 mm TH/TD, M/V *Mr. Offshore,* Continental Shelf Associates, Inc., job 1390.5 for Chevron, Destin Dome Unit, survey 4, trawl 43, sample QSA 2, off Pensacola, Florida, U.S.A., 29°56.25′N, 87°14.3′W, 126′ [38 m], 18 Apr 1993.—Other Atlantic sites: USNM E4531, 1 spec. [holotype of *Pseudoboletia occidentalis* Clark, 1921], dry, 28/54 mm TH/TD, State University of Iowa Barbados-Antigua Expedition, 1918, off Barbados, 30–100 fm [55–183 m], 1918; MCZ 7583, 2 spec., dry, 32/70 & 43/94 mm TH/TD, coll. T. Mortensen, off St. Helena, ca. 15°58′12″S, 5°46′36″W [our estimate from Mortensen (1933)], 50 m, Feb 1930; USNM E5953, 1 spec., dry, 42/89 mm TH/TD, coll. T. Mortensen, off St. Helena, ca. 15°58′12″S, 5°46′36″W [our estimate from Mortensen (1933)], 20 m, Feb 1930; USNM E12353, 4 spec., dry, 31/63–39/79 mm TH/TD, R/V *Pillsbury,* cruise 6806, sta. 736, off Venezuela, 10°57′0″N, 65°52′0″W, 38–85 fm [69–155 m], 22 Jul 1968; USNM E16096, 1 spec., dry [crushed], coll. by "F.M. for A. Loveridge," James Bay, St. Helena, 14 Aug 1968; USNM E11732, 1 spec., dry, 39/82 mm TH/TD, coll. by "F.M. for A. Loveridge," wreck of *Papanui,* James Bay, St. Helena, 1 Feb 1969; USNM E20593, 1 spec., dry, 5.8/12 mm TH/TD, R/V *Pillsbury,* cruise 6907, sta. 878, east of St. Vincent, St. Vincent and the Grenadines [other tags read "off of Saint Lucia" and "off Windward Is"], 13°11′18″N, 61°6′30″W, 37–40 m, 6 Jul 1969; USNM E16204, 1 spec., dry, 39/85 mm TH/TD, coll. Rick Guest, off Hillsboro Beach, Florida, U.S.A., 70′ [21 m], 7 Mar 1974; USNM E16202, 1 spec., dry, 30/60 mm TH/TD, coll. R. Guest, off Hollywood, Florida, U.S.A., 65′ [20 m], spring 1974; USNM E16203, 1 spec., dry, 33/74 mm TH/TD, coll. R. Guest, off Hollywood, Florida, U.S.A., 65′ [20 m], 6 May 1974; USNM E16246, 2 spec. [1 crushed], 33/75 mm TH/TD, coll. M. Telford, Carlisle Bay, Barbados, 40′ [12 m], 1976; HBOM 72:278, 1 spec., dry, 34/74 mm TH/TD, Continental Shelf Associates, Inc., sta. James Island-380, sample 14A-a, Charleston, South Carolina, U.S.A., from 32°34.9′N, 78°34.8′W to 32°35.2′N, 78°35.0′W, 53 m, biological dredge, 2 Oct 1978; USNM E29871, 1 spec., dry, 35/75 mm TH/TD, R/V *Dan Moore,* Living Marine Resources Study, sta. OS05 (field no. 818118), off North Carolina, U.S.A., 33°48′42″N, 76°34′12″W, 102 m, trawl, 14 May 1981; USNM E32267, 2 spec., alcoholic, 73 & 74 mm TD, R/V *Dan Moore,* Living Marine Resources Study, sta. OS05 (field no. 818169), off North Carolina, U.S.A., 33°49′0″N, 79°34′0″W, 69 m [one tag reads "33°49.1′ 76°34.0′ 66 m"], trawl, 10 Aug 1981; USNM E29626, 1 spec., alcoholic, 68 mm TD, R/V *Dan Moore,* Living Marine Resources Study, sta. OS05 (field no. 818171), off North Carolina, U.S.A., 33°49′30″N, 76°34′0″W, 63 m, trawl, 11 Aug 1981; USNM E30528, 7 spec. [1 crushed], alcoholic, 66–85 mm TD, R/V *Dan Moore,* Living Marine Resources Study, sta. OS05 (field no. 818179), off North Carolina, U.S.A., 33°49′24″N, 76°33′24″W, 68 m, trawl [W. W. Kirby-Smith, in litt.; but museum records indicate "Smith-MacIntyre grab"], 11 Aug 1981.

Other sources.—In addition to specimens examined by us, we have relied on station data for other *Pseudoboletia maculata* deposited in BMNH and HBOM.

Descriptions of stations and material.—*Pseudoboletia maculata* were photographed on and collected from the NW rim of DeSoto Canyon off Pensacola, Florida, in 1992–1993 on a soft substratum that supported a biotal assemblage referred to as a "sand bottom algal community" (Continental Shelf Associates, Inc. 1996a, 1996b). The sand bottom algal community was visually dominated by calcareous red algae (Corallinaceae and *Peyssonnelia inamoena*) and closely associated with coarse substratum consisting of coralline algal rubble, shell debris, and coarse sand. The substratum supporting the sand bottom algal community produced a relatively strong acoustic side-scan sonar reflection, indicating a coarse grain size and relatively high shell content (Marine Technical Services, Inc. 1985; John E. Chance & Associates 1991a, 1991b, 1992).

The presence of abundant algae on the sand substratum in water depths of approximately 30–55 m supported relatively dense aggregations of grazing echinoids (*Astropyga magnifica, Eucidaris tribuloides, Lytechinus variegatus, P. maculata, Stylocidaris affinis*). *Pseudoboletia maculata* was only observed in mixed-species aggregations with the echinoids *Lytechinus variegatus* and *Eucidaris tribuloides* (Fig. 3A). Other biota observed and collected with *P. maculata* included the free-living hard coral *Oculina tenella,* the scallop *Pecten ravenelli,* and rock shrimp *Sicyonia brevirostris.* The algal density within the area exhibited high variability (Continental Shelf Associates, Inc. 1996a) probably due to seasonal changes in light or temperature in combination with other oceanographic conditions. *Peyssonnelia inamoena,* the dominant alga closely associated with the presence of *P. maculata,* has been observed to vary seasonally in density in other areas where it is found (Schneider 1976).

Eight non-overlapping photographs showed 1–18 *P. maculata* per frame, with occasional *Eucidaris tribuloides* and possible *L. variegatus* (Fig. 3A). Many *P. maculata* had debris on their tests. Maculae were not visible in the photographs, but the large size and low hemispherical shape of most of the urchins distinguished them as *P. maculata* rather than *L. variegatus.* Many of the *P. maculata* were clumped, sometimes with spines in contact with neighbor's spines; but, elsewhere, animals were several test diameters apart.

Four *Pseudoboletia maculata,* test diameters 58–81 mm, were collected at two stations 5 nm apart in a sand bottom algal community. The specimens were mixed with *Lytechinus variegatus* (USNM 1002300 and 1002301), which has a proportionately higher test than *P. maculata* (Fig. 4). Only one of the four specimens had maculae (Fig. 3B), which occurred in three cycles: one cycle of pigmented spots subapical in the interambulacra; two cycles of spots, one just above and one just below the ambitus, each cycle consisting of five large interambulacral and five small ambulacral maculae. Each macula was formed by a group of primary and secondary spines, most primary spines dark brown basally, fading to pale green medially and white distally. Otherwise, the spines and test were white. Our observations of spine coloration agree with those of Koehler (1908), Mortensen (1943), and Pawson (1978).

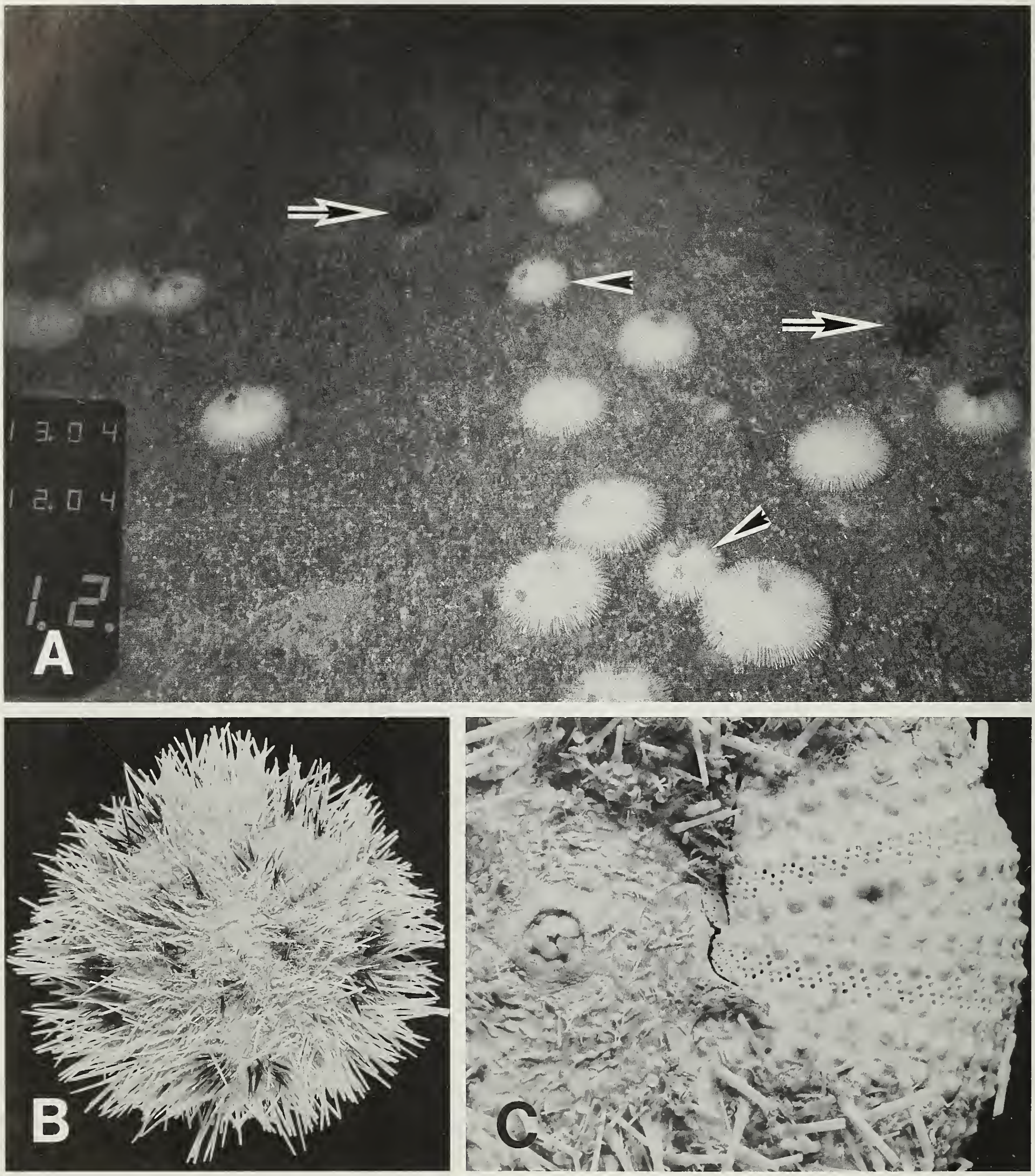

Fig. 3. *Pseudoboletia maculata.* A. Photograph of collection site off Pensacola, Florida, showing an aggregation of *P. maculata* with two possible *Lytechinus variegatus* (arrowheads; based on size and shape) and two *Eucidaris tribuloides* (arrows); courtesy of Continental Shelf Associates, Jupiter, Florida. B. USNM 1002299, specimen from off Pensacola, Florida, showing maculae. C. USNM 1002222, specimen from off Pensacola, Florida, showing pore pairs in arcs of four and spination of plates in the buccal membrane.

In addition to the material off Florida, one specimen (TAMU 3-1809) of *P. maculata* was collected by T. J. Bright in 1978 on a night submersible dive at 49–58 m on the western side of East Flower Garden Bank, a salt dome in the western Gulf of Mexico. The cidaroid *Stylocidaris affinis* was the only other echinoid recorded from the dive (Texas A&M University 1981). Submersible observations revealed high densities of *P. maculata, Arbacia punctulata,* and the asteroid *Linckia nodosa* at 46–76 m, and one photograph taken in 1979 of the sea floor showed 46–50 *P. maculata* on

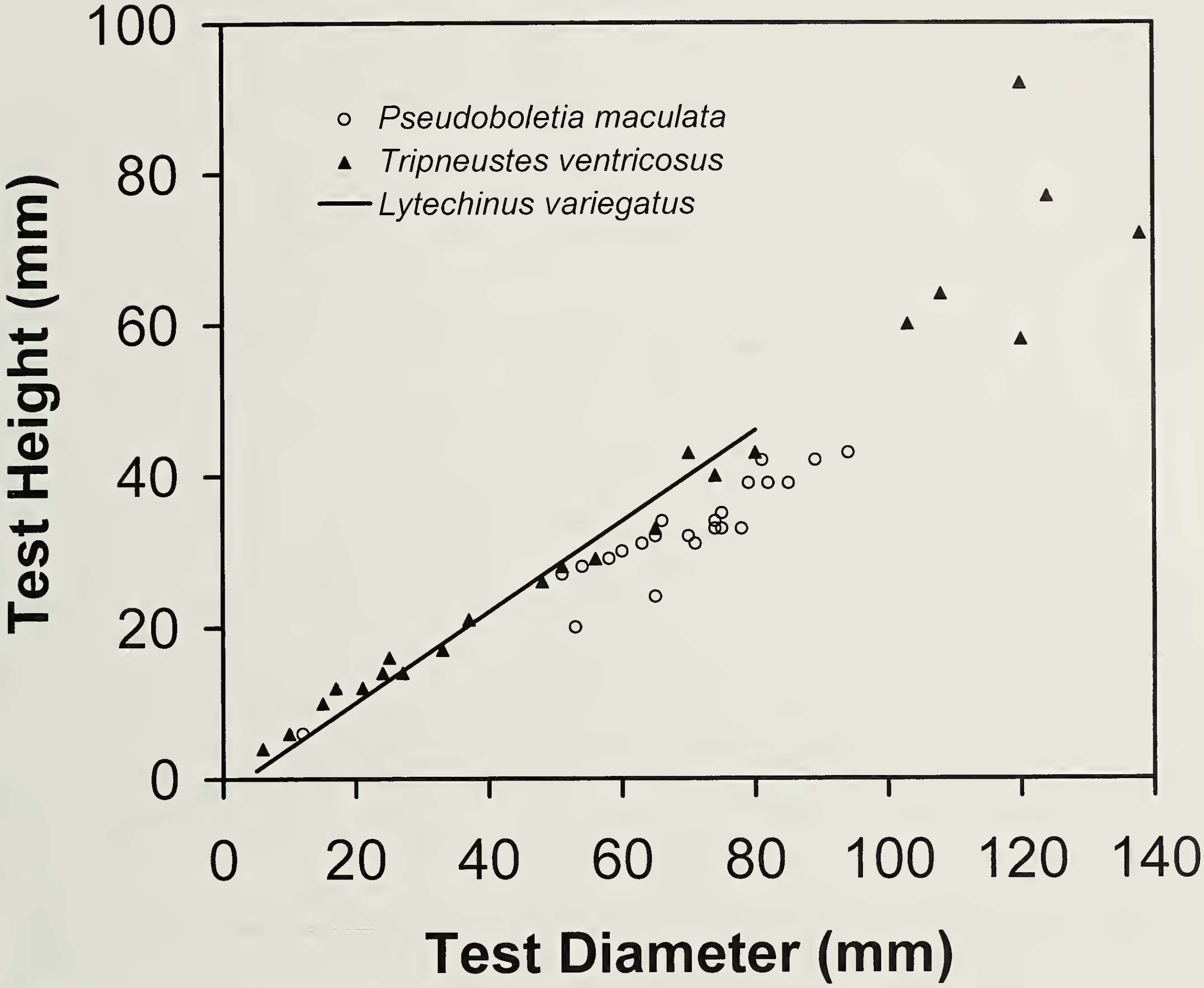

Fig. 4. Test dimensions for three species of toxopneustid echinoid. Data for *Pseudoboletia maculata* are from our material examined, Clark (1925), and Koehler (1908). Data for *Tripneustes ventricosus* are from Mortensen (1943). The line plots Serafy's (1979) equation for *Lytechinus variegatus* using test diameters of his smallest and largest specimens.

a "nodule-covered bottom" at 59 m depth (Texas A&M University 1981). Many of the sea urchins in the photograph held debris on their tests, and spines of most were in contact with those of neighboring urchins. Based on test diameter (51 mm) of specimen TAMU 3-1809, the density of the aggregation was up to 300 m^{-2}. Maculae were not visible on *P. maculata* in the photograph nor on the specimen at hand.

Although the presence of maculae is not a reliable character in *Pseudoboletia maculata* from the Atlantic Ocean (Mortensen 1943, Pawson 1978), other characters readily distinguish this species from other common toxopneustids, viz., *Lytechinus variegatus* and *Tripneustes ventricosus.* The test has a low, hemispherical, subpentagonal shape, with the ratio of test height (TH) to test diameter (TD) generally <0.50 (Fig. 4) in contrast to the higher dome-shaped test of *L. variegatus* (Serafy 1979) and even more depressed than the test of the similar *T. ventricosus,* at least in the range TD = 50–90 mm. *Pseudoboletia* is the only toxopneustid genus bearing spinelets on the buccal plates and other ossicles of the buccal membrane (Fig. 3C); Mortensen (1943) described this condition as a "bearded appearance." The compound plates of the ambulacral series are trigeminate (three pore-pairs) in *Lytechinus* and *Tripneustes* and

Fig. 5. Distribution of *Pseudoboletia maculata* in the Atlantic Ocean and adjacent waters based on museum records and literature. Each plot might represent multiple nearby records. Inset shows records for Ascension Island and St Helena in the South Atlantic Ocean.

polyporous (four or five pore pairs) in *Pseudoboletia* (Fig. 3C); and the compound plates bear one primary tubercle and spine each in *Lytechinus* and *Pseudoboletia* but one primary spine only every three or four compound plates in *Tripneustes* (Mortensen 1943, Serafy 1979).

Remarks.—Pseudoboletia maculata (s.s.) has a far broader distribution (Fig. 5) than does *Calocidaris micans* (Fig. 2) and is almost pantropical, absent only from the eastern tropical Pacific Ocean. Mortensen (1943) recognized four species of *Pseudoboletia*: *P. atlantica* Clark, 1912 (S Atlantic Ocean), *P. indiana* (Michelin, 1862) (Madagascar to Hawaii), *P. maculata* Troschel, 1869 (Ceylon to Philippines), *P. occidentalis* Clark, 1921 (West Indies). Pawson (1978) included all Atlantic specimens in *P. maculata,* designated *P. occidentalis* as a junior synonym, and recognized two subspecies based on the number of pore pairs in each ambulacral arc: *P. maculata atlantica* Clark, 1912 (five pore pairs, S Atlantic), *P. maculata maculata* Troschel, 1869 (four pore pairs, West Indies). More recently, Liao & Clark (1995) synonymized *P. maculata* with *P. indiana,* effectively rendering *Pseudoboletia* monotypic; but they did not address the taxonomy of the genus in the Atlantic basin, and others (Rowe & Gates 1995, Lane et al. 2000, Liao 2001) have retained the distinction between species. For their lack of comprehensive treatment, we reject the synonymy of Liao & Clark (1995) and tentatively adopt that of Pawson (1978), assigning material from the Gulf of Mexico to *P. maculata*

maculata because of the presence of four pore pairs per arc (Fig. 3C). The genus must, however, be re-evaluated, particularly with the application of molecular techniques, some of which have already been applied to animals from the western Pacific Ocean (Matsuoka 1985, 1986, 1987; Yoshino et al. 1989).

Pseudoboletia maculata has long been known from the Indian and Pacific oceans (Mortensen 1943), sometimes in communities with other grazing echinoids (Shimabukuro 1991). The earliest possible specimens from the Atlantic Ocean might have been taken prior to 1875 by J. C. Melliss off St. Helena (Mortensen 1933), but the first definite record was Koehler's (1908) two specimens taken by R/V *Scotia* in 1904 off Ascension Island at 40 fm [73 m]. Koehler's (1908) description of the two specimens formed the basis for Clark's (1912) new species *P. atlantica.* [A specimen collected by E. W. Alexander off St. Helena is designated by museum records as "holotype" of *P. atlantica* H. L. Clark, 1912 (BMNH 1949.1.18.3). It has a label signed by H. L. Clark and dated "1924," but the meaning of the date is unclear. Clark (1925) described the specimen but did not list it among the 111 echinoid types in the British Museum (Natural History).] A second possible discovery at St. Helena was by J. T. Cunningham in 1909 (Mortensen 1933), mistaken for *Tripneustes ventricosus* (reported as *T. esculentus*) perhaps because of the low, hemispherical, subpentagonal test bearing fine, short spines. Mortensen (1933, 1943) collected at least 12 *P. maculata atlantica* off St. Helena in 1930 "in patches in great numbers" from a depth of 20 m (Mortensen 1933:467; tags written in Mortensen's own hand read "20 m" for USNM E5953 but "50 m" for MCZ 7583) on a bottom of small stones, *Lithothamnion,* and "loose *Furcellaria*-like algae," with which the urchins covered their tests. In 1968–1969, A. Loveridge took additional specimens from St. Helena (USNM E11732, E16096).

Pseudoboletia was first collected in the West Indies in 1918 by C. C. Nutting during the Barbados-Antigua Expedition (Fig. 5). The single specimen (USNM E4531), taken off Barbados "in all probability" from 30–100 fm [55–183 m], is the holotype of Clark's (1921) *P. occidentalis* [but not listed by Downey (1968)], which Pawson (1978) synonymized with *P. maculata maculata.* Clark (1921:117) hailed this specimen as "certainly one of the most noteworthy results of the Barbados-Antigua Expedition," and he expressed surprise that the species had not been taken in earlier expeditions. Additional records include two more specimens from Barbados collected at 12 m (the shallowest Atlantic record) by M. Telford in 1976 (USNM E16246) and one near St. Vincent in 1969 by R/V *Pillsbury* (USNM E20593). Four specimens from the Caribbean Sea collected in 1968 off Venezuela by R/V *Pillsbury* (USNM E12353) were listed by Pawson (1978), along with records off the SE coast of Florida, U.S.A., (USNM E16202, E16203, E16204) in 1974 at 20–21 m. An additional unpublished specimen from Key Largo, Florida, was taken in 1979 on an algal bottom at 51 m (HBOM 72:252). In 1978—the same year in which the first specimens were found in the Gulf of Mexico—three specimens were collected off the coast of South Carolina, U.S.A., at 53–55 m (HBOM 72:278, 72:867); and in 1981, at least 21 specimens were collected in 12 of 24 trawl samples off North Carolina, U.S.A., at depths of 63–102 m (USNM E29626, E29871, E30528, E32267; at least 10 in collection of W. W. Kirby-Smith, in litt.), representing the northernmost Atlantic records to date. The North Carolinian *P. maculata* inhabited " 'live bottom' rock outcrops with scattered sand in between" (W. W. Kirby-Smith, in litt.; Duke University Marine Laboratory 1982). The community was dominated in biomass by echinoderms, which clustered at a high level (≥ 0.7) of constancy along with sponges and decapod crustaceans. Crustose corallines were the only algae reported from the station, and a ridge-trough system at 100 m depth included rubble with large "lithothamnion balls" (Duke University Marine Laboratory 1982). It is surprising that Project SEAMAP (National Marine Fisheries Service & Florida Department of Natural Resources) took no *P. maculata* in 1983–1985 and 1987 from its 450 trawl and dredge stations at 11–549 m between Stuart (27°10′N) and Fernandina Beach (30°42′N), Florida (R. L. Turner, unpubl.).

Discussion

These records of *Calocidaris micans* and *Pseudoboletia maculata* bring the echinoid fauna of the Gulf of Mexico to 61 species (Table 1), add 2 West Indian-Caribbean species to its fauna, and further reduce its level of echinoid endemism. Of the 47 species that inhabit the continental shelf (0–200 m), 39 species (83%) have West Indian-Caribbean distributions. Serafy (1979) recorded *C. micans, Cidaris rugosa,* and *Stereocidaris ingolfiana* as slope species, but *Calocidaris micans* occurs at 100–144 m in the Gulf of Mexico and *Cidaris rugosa* at 46 m (Barbosa-Ledesma et al. 2000); although Barbosa-Ledesma et al. (2000) did not report the depth for their *S. ingolfiana,* their station coordinates plot well within the 100-m isobath on the continental shelf north of the Yucatan Peninsula. Serafy (1979) considered *Brissopsis alta* to be the only echinoid endemic to the Gulf of Mexico. Since his work was published, *B. alta* has been collected at 12 stations sampled by R/V *Delaware II* and R/V *Chapman* during Project SEAMAP in 1984–1987 between 27°49′N (off Sebastian Inlet, Florida) and 30°20′N (off Jacksonville, Florida) at depths of 177–411 m in the Atlantic Ocean (R. L. Turner, unpubl.). But the addition of *Mellita tenuis,* restricted to the eastern Gulf of Mexico (Harold & Telford 1990), retains the level of endemism at 1 species out of 61 (<2%). Cutress (1980) considered *Calocidaris* to be the only cidaroid genus, Recent or fossil, endemic to the Caribbean Sea; but our records of *C. micans* from the Gulf of Mexico and the Bahamas eliminate the endemic standing of the genus.

We believe that the new records do not represent range extensions but rather increased sampling effort using recent technology (SCUBA, submersibles, ROVs, camera sleds), in some cases in high-relief live-bottom biotopes that were avoided by earlier naturalists, except for the occasional use of rock dredges. This thought parallels those of Hendler & Miller (1984) and Hendler & Turner (1987) for four new species of deep-reef ophiuroids from the Caribbean Sea and Gulf of Mexico. Clark (1921:118) in the description of his new *Pseudoboletia occidentalis* remarked, "It is strange that neither the 'Blake,' the 'Hassler,' nor the 'Albatross,' nor any other collector in the West Indies, has met with the genus but the reason may be that the vessels mentioned did nearly all their collecting outside the 100 fms. line while the other collectors have done very little dredging at any depth. The teeming area between 10 and 100 fms. has scarcely been touched as yet."

Cutress (1980) postulated the extinction of many genera of cidaroid from the Caribbean after the Cretaceous due to lowered salinity, reduced temperature, and heavy sedimentation from terrigenous sources. These conditions might have prevailed also in the Gulf of Mexico more recently during the Wisconsin Glacial Epoch of 100,000–14,000 B.P. (reduced temperature) and with the subsequent postglacial flow of meltwater from the Laurentide ice sheet via Lake Agassiz down the Mississippi River basin in the last 14,000 yr (reduced temperature and salinity, heavy sedimentation, altered surface currents; Broeker et al. 1989, Pielou 1991, Gore 1992, Williams et al. 1998). Only in the last 9000 yr might Caribbean echinoids have invaded the Gulf of Mexico to inhabit new biotopes of the recently flooded continental shelf. Live-bottom echinoids such as *Calocidaris micans* and *Pseudoboletia maculata* would have found suitable habitat only in patches of high relief

Table 1.—Echinoids of the Gulf of Mexico, modified from Serafy (1979). Taxa marked with an asterisk (*) are additions to Serafy (1979). Species in Serafy's (1979) list that remain peripheral are excluded. Geographic distribution beyond the Gulf of Mexico: AA, amphiatlantic; BH, Bahamas; CA, Caribbean and Antillean; ET, eurythermal temperate (Cape Cod south); FK, Florida Keys & SE Florida; MT, Mediterranean; NA, N Atlantic; PT, pantropical; SA, S Atlantic; WA, W Atlantic; WT, warm temperate (Cape Hatteras south).

Taxon	Distribution		Additional sources
	Bathymetric (m)	Geographic	
Order Cidaroida			
Family Cidaridae			
*Cidaris abyssicola**	36–800	CA ET FK	Phelan (1970), Serafy & Fell (1985) Barbosa-Ledesma et al. (2000)
*Cidaris rugosa**	46–790	CA FK WT	Phelan (1970) Barbosa-Ledesma et al. (2000)
*Calocidaris micans**	100–624	BH CA	Present study
Eucidaris tribuloides tribuloides	0–800	BH CA FK SA WT	
*Stereocidaris ingolfiana**	100–1750	AA CA FK	Phelan (1970) Barbosa-Ledesma et al. (2000)
Stylocidaris affinis	23–1000	AA BH CA FK MT WT	
*Tretocidaris bartletti**	48–625	CA FK	Phelan (1970), Hopkins et al. (1991)
Order Echinothuroida			
Family Echinothuridae			
Araeosoma belli	130–1020	CA FK	
Araeosoma fenestratum	160–1180	AA CA FK WT	Mortensen (1935), Serafy & Fell (1985)
Hygrosoma petersii	200–3700	AA CA ET FK	Mortensen (1935)
Phormosoma placenta			
P. placenta placenta	50–3700	AA	Mortensen (1935)
P. placenta sigsbei	200–1800	CA WA	Mortensen (1935)
Order Diadematoida			
Family Diadematidae			
Diadema antillarum	0–400	AA BH CA FK SA WT	
Astropyga magnifica	11–88	CA FK WT	
Centrostephanus longispinus rubicingulus	33–310	CA FK SA WT	Pawson & Miller (1983)
Family Aspidodiadematidae			
Plesiodiadema antillarum	720–3000	AA CA FK SA WT	Mortensen (1940), Serafy & Fell (1985)
Order Salenioida			
Family Saleniidae			
Salenia goesiana	90–540	CA FK	

Table 1.—Continued.

Taxon	Distribution		Additional sources
	Bathymetric (m)	Geographic	
Order Arbacioida			
Family Arbaciidae			
Arbacia punctulata	0–225	BH CA ET FK	
Coelopleurus floridanus	65–2380	CA ET FK SA	Pawson (1978), Serafy & Fell (1985)
Podocidaris sculpta	230–730	CA FK	
Order Temnopleuroida			
Family Temnopleuridae			
Genocidaris maculata	12–420	AA CA ET FK MT	
Family Toxopneustidae			
Lytechinus euerces	55–777	CA FK WT	
Lytechinus variegatus			
L. variegatus carolinus	0–75	BH FK WT	
L. variegatus variegatus	0–250	BH CA FK SA	
Lytechinus williamsi	5–92	CA FK	Hendler et al. (1995)
*Pseudoboletia maculata maculata**	12–155	CA FK PT SA WT	Pawson (1978), present study
Tripneustes ventricosus	0–55	AA CA FK SA WT	Hendler et al. (1995)
Order Echinoida			
Family Echinometridae			
Echinometra lucunter lucunter	0–45	AA CA FK SA WT	Hendler et al. (1995)
Echinometra viridis	0–40	CA FK	Hulings (1955)
Order Holectypoida			
Family Echinoneidae			
Echinoneus cyclostomus	5–570	CA FK PT SA	Pawson (1978)
Order Clypeasteroida			
Family Clypeasteridae			
Clypeaster chesheri	20–101	CA FK	
Clypeaster prostratus	15–75	CA FK WT	
Clypeaster ravenelii	50–230	CA FK WT	
Clypeaster rosaceus	0–285	CA FK WT	Hendler et al. (1995)
Clypeaster subdepressus	5–210	CA FK SA WT	

Table 1.—Continued.

Taxon	Distribution		Additional sources
	Bathymetric (m)	Geographic	
Family Fibulariidae			
Echinocyamus grandiporus	150–2500	AA CA FK	Mortensen (1948)
Family Mellitidae			
Mellita quinquiesperforata	0–180	CA SA	Harold & Telford (1990)
*Mellita tenuis**	0–3		Harold & Telford (1990)
Leodia sexiesperforata	0–60	CA FK WT	
Encope aberrans	12–90	BH FK WT	
Encope michelini	3–90	FK WT	
Order Cassiduloida			
Family Echinolampadidae			
Echinolampas depressa	37–310	CA FK	
Conolampas sigsbei	130–800	CA FK	
Order Spatangoida			
Family Hemiasteridae			
Hemiaster expergitus	380–4833	AA CA FK NA	Mortensen (1950)
Sarsiaster griegii	1900–3120	FK NA	Kier & Lawson (1978)
Family Schizasteridae			
Schizaster orbignyanus	26–500	BH CA ET FK	
Agassizia excentrica	43–900	CA FK	
Hypselaster brachypetalus	750–1750	CA	Mortensen (1951)
Hypselaster limicolus	30–340	CA	
Moira atropos	0–445	CA FK SA WT	
Family Aeropsidae			
Aceste bellidifera	550–5220	AA CA FK NA SA	Mortensen (1950)
Family Brissidae			
Brissus unicolor	0–240	AA CA FK MT SA	Pawson (1978), Hendler et al. (1995)
Brissopsis alta	45–310	FK	Chesher (1968)
Brissopsis atlantica	26–641	BH CA FK	Chesher (1968)
Brissopsis elongata elongata(?)	3–270	CA	
Meoma ventricosa ventricosa	2–200	BH CA FK	Hendler et al. (1995)
Plagiobrissus grandis	1–210	BH CA FK SA	
Plethotaenia spatangoides	150–619	BH CA ET FK	Chesher (1968)

Table 1.—Continued.

Taxon	Distribution		Additional sources
	Bathymetric (m)	Geographic	
Family Loveniidae			
Echinocardium laevigaster	40–220	FK WT	
Homolampas fragilis	360–3550	CA FK	
Family Asterostomatidae			
Archaeopneustes hystrix	38–1610	CA FK	Mortensen (1950)
Palaeobrissus hilgardi	150–1025	CA FK	
Paleopneustes cristatus	76–805	CA FK	

and other locations less prone to sediment accumulation. These events might be factors that explain the strong Caribbean influence and low endemism of the Gulf of Mexico echinoid fauna.

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Literature Cited

Agassiz, A. 1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Caribbean Sea in 1878–79, and along the Atlantic coast of the United States during the summer of 1880, by the U.S. Coast Survey Steamer "Blake," Commander J. R. Bartlett, U.S.N., commanding. IX. Preliminary report on the Echini.—Bulletin of the Museum of Comparative Zoology at Harvard College, in Cambridge 8:69–84.

Barbosa-Ledesma, I. F., F. A. Solís-Marín, & A. Laguarda-Figueras. 2000. New records for cidaroid echinoids (Echinodermata: Echinoidea) of the Gulf of Mexico, Mexico.—Revista de Biología Tropical 48:721.

Broecker, W. S., J. P. Kennett, B. P. Flower, J. T. Teller,

S. Trumbore, G. Bonani, & W. Wolfli. 1989. Routing of meltwater from the Laurentide Ice Sheet during the Younger Dryas cold episode.—Nature 341:318–321.

Cairns, S. D., D. M. Opresko, T. S. Hopkins, & W. W. Schroeder. 1993. New records of deep-water Cnidaria (Scleractinia & Antipatharia) from the Gulf of Mexico.—Northeast Gulf Science 13: 1–11.

Chesher, R. H. 1968. The systematics of sympatric species in West Indian spatangoids: a revision of the genera *Brissopsis, Plethotaenia, Paleopneustes,* and *Saviniaster.*—Studies in Tropical Oceanography 7:1–168.

Clark, A. H. 1954. Echinoderms (other than holothurians) of the Gulf of Mexico.—Fishery Bulletin of the Fish and Wildlife Service 55:373–379.

Clark, H. L. 1907. The Cidaridae.—Bulletin of the Museum of Comparative Zoology at Harvard College 51:165–230.

———. 1912. Hawaiian and other Pacific echini. The Pedinidae, Phymosomatidae, Stomopneustidae, Echinidae, Temnopleuridae, Strongylocentrotidae, and Echinometridae.—Memoirs of the Museum of Comparative Zoology at Harvard College 34(4):1–179.

———. 1921. Report on the Echinoidea collected by the Barbados-Antigua Expedition from the University of Iowa in 1918.—University of Iowa Studies in Natural History 9(5):103–121.

———. 1925. A catalogue of the Recent sea-urchins (Echinoidea) in the collection of the British Museum (Natural History). British Museum (Natural History), London, 250 pp.

Claus, C. F. W. 1880. Grundzüge der Zoologie: zum wissenschaftlichen Gebrauche. Fourth edition, volume 1. N. G. Ellwert, Marburg, 822 pp.

Continental Shelf Associates, Inc. 1979. South Atlantic hard bottom study. Report to U.S. Department of the Interior, Bureau of Land Management, Washington, D.C., Contract AA551-CT8-25. Continental Shelf Associates, Inc., Jupiter, Florida, 356 pp.

———. 1996a. Baseline environmental surveys for the Destin Dome Unit. Report to Chevron U.S.A., Inc., New Orleans, Louisiana. Continental Shelf Associates, Inc., Jupiter, Florida, 155 pp. & appendices.

———. 1996b. Photodocumentation surveys of Destin Dome area blocks 12, 13, 14, 15, 16, 54, 55, 56, 57, 99, and 100. Report to Chevron U.S.A., Inc., New Orleans, Louisiana. Continental Shelf Associates, Inc., Jupiter, Florida, 80 pp. & appendices.

———, & Texas A&M University. 2001. Mississippi/Alabama pinnacle trend ecosystem monitoring, final synthesis report. Report to U.S. Department of the Interior, Geological Survey, Biological Resources Division, Kearneysville, West Virginia, Contract USGS/BSR—2001-0007 & U.S. Department of the Interior, Minerals Management Service, Gulf of Mexico OCS Region, New Orleans, Louisiana, OCS Study MMS 2001-080. Continental Shelf Associates, Inc., Jupiter, Florida, & Texas A&M University, Geochemical and Environmental Research Group, College Station, 415 pp. & appendices.

Cutress, B. M. 1980. Cretaceous and Tertiary Cidaroida (Echinodermata: Echinoidea) of the Caribbean area.—Bulletins of American Paleontology 77(309):1–215.

Defenbaugh, R. E. 1976. A study of the benthic macroinvertebrates of the continental shelf of the northern Gulf of Mexico. Unpublished Ph.D. dissertation, Texas A&M University, College Station, 476 pp.

Downey, M. E. 1968. Catalog of Recent echinoid type specimens in the U.S. National Museum Smithsonian Institution and the Museum of Comparative Zoology Harvard University.—Smithsonian Institution, United States National Museum Bulletin, 264:1–99.

Duke University Marine Laboratory. 1982. Final report. South Atlantic OCS area living marine resources study. Year II. Volume II. An investigation of live-bottom habitats off North Carolina. Report to U.S. Department of the Interior, Minerals Management Service, Contract AA551-CT1-18. Duke University Marine Laboratory, Beaufort, North Carolina, 143 pp. & appendices.

Fell, H. B. 1966. Cidaroids. Pp. U312–U339 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, part U, Echinodermata 3(1). University of Kansas Press & Geological Society of America, New York, 367 pp.

Gore, R. H. 1992. The Gulf of Mexico. Pineapple Press, Sarasota, Florida, 384 pp.

Gray, J. E. 1825. An attempt to divide the Echinida or sea-eggs into natural families.—Annals of Philosophy 10/26:423–431.

Harold, A. S., & M. Telford. 1990. Systematics, phylogeny and biogeography of the genus *Mellita* (Echinoidea: Clypeasteroida).—Journal of Natural History 24:987–1026.

Harry, H. W. 1979. Echinoderms recorded from the northwestern Gulf of Mexico. H. W. Harry, Bellaire, Texas, 58 pp.

Hendler, G., & J. E. Miller. 1984. *Ophioderma devaneyi* and *Ophioderma ensiferum,* new brittlestar species from the western Atlantic (Echinodermata: Ophiuroidea).—Proceedings of the Biological Society of Washington 97:442–461.

———, ———, D. L. Pawson, & P. M. Kier. 1995. Sea stars, sea urchins, and allies: echinoderms of Florida and the Caribbean. Smithsonian Institution Press, Washington, 391 pp.

———, & R. L. Turner. 1987. Two new species of *Ophiolepis* (Echinodermata: Ophiuroidea) from the Caribbean Sea and Gulf of Mexico, with notes on ecology, reproduction, and morphology.—Natural History Museum of Los Angeles County Contributions in Science 395:1–14.

Hopkins, T. S., J. F. Valentine, J. B. McClintock, K. Marion, & S. A. Watts. 1991. Community patterns of echinoderms associated with substrate and depth in the northern Gulf of Mexico. Pp. 231–239 *in* T. Yanagisawa, I. Yasumasu, C. Oguro, N. Suzuki, & T. Motokawa, eds., Biology of Echinodermata: proceedings of the Seventh International Echinoderm Conference, Atami, 9–14 September 1990. A. A. Balkema, Rotterdam, 590 pp.

Hulings, N. C. 1955. An investigation of the benthic invertebrate fauna from the shallow waters of the Texas coast. Unpublished M.A. thesis, Texas Christian University, Fort Worth, 87 pp.

Hyman, L. H. 1955. The invertebrates, volume 4, Echinodermata: the coelomate Bilateria. McGraw-Hill Book Co., New York, 763 pp.

John E. Chance & Associates, Inc. 1991a. Hazard study of block 15 (OCS-G-8321) and block 16 (OCS-G-8322) Destin Dome area. Report to Chevron U.S.A., Inc., New Orleans, Louisiana. John E. Chance & Associates, Inc., Lafayette, Louisiana, 11 pp. & appendices.

———. 1991b. Archeological and hazard study of block 12 (OCS-G-8320), block 13 (OCS-G-10418), block 14 (OCS-G-10419), and block 57 (OCS-G-6407), Destin Dome area. Report to Chevron U.S.A., Inc., New Orleans, Louisiana. John E. Chance & Associates, Inc., Lafayette, Louisiana, 29 pp. & appendices.

———. 1992. Hazard study of the eastern half of block 100 (OCS-G-6411), Destin Dome area. Report to Chevron U.S.A., Inc., New Orleans, Louisiana. John E. Chance & Associates, Inc., Lafayette, Louisiana, 12 pp. & appendices.

Kier, P. M., & M. H. Lawson. 1978. Index of living and fossil echinoids 1924–1970.—Smithsonian Contributions to Paleobiology 34:1–182.

Koehler, R. 1908. Astéries, ophiures et échinides de l'Expédition Antarctique Nationale Écossaise—Transactions of the Royal Society of Edinburgh 46(Pt. III, 22):529–649.

Lane, D. J. W., L. M. Marsh, D. VandenSpiegel, & F. W. E. Rowe. 2000. Echinoderm fauna of the South China Sea: an inventory and analysis of distribution patterns.—The Raffles Bulletin of Zoology 2000(Supplement 8):459–493.

Liao, Y. 2001. Echinodermata. Pp. 386–399 *in* Z. Huang, ed., Marine species and their distribution in China's seas [J. Lin, translator]. Krieger Publishing Co., Malabar, Florida, 599 pp.

———, & A. M. Clark. 1995. The echinoderms of southern China. Science Press, Beijing, 614 pp.

Ludwick, J. C., & W. R. Walton. 1957. Shelf edge calcareous prominences in the northeastern Gulf of Mexico. Bulletin of the American Association of Petroleum Geologists 41:2054–2101.

Marine Technical Services, Inc. 1985. A high-resolution geophysical report on blocks 55, 56, 57, 99, and 100, Destin Dome area. Report to Conoco, Inc., Algiers, Louisiana. Marine Technical Services, Inc., Stafford, Texas, 13 pp. & appendices.

Matsuoka, N. 1985. Biochemical phylogeny of the sea-urchins of the family Toxopneustidae.—Comparative Biochemistry and Physiology 80B: 767–771.

———. 1986. Further immunological study on the phylogenetic relationships among sea-urchins of the order Echinoida.—Comparative Biochemistry and Physiology 84B:465–468.

———. 1987. Biochemical study on the taxonomic situation of the sea-urchin, *Pseudocentrotus depressus*.—Zoological Science 4:339–347.

Michelin, M. H. 1862. Echinides et Stellérides. Annexe A (7 pp.) *in* L.-C. Maillard, Notes sur l'Île de la Réunion (Bourbon). Dentu, Paris.

Mortensen, T. 1903. Echinoidea (Part I).—The Danish Ingolf-Expedition 4(1):1–193.

———. 1910. On some West Indian echinoids.—Smithsonian Institution, United States National Museum Bulletin 74:1–31.

———. 1928. A monograph of the Echinoidea, volume 1, Cidaroidea. C. A. Reitzel, Copenhagen, 551 pp.

———. 1933. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 66. The echinoderms of St. Helena. (Other than crinoids.)—Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København 93:401–473.

———. 1935. A monograph of the Echinoidea, volume 2, Bothriocidaroida, Melonechinoida, Lepidocentroida, and Stirodonta. C. A. Reitzel, Copenhagen, 647 pp.

———. 1940. A monograph of the Echinoidea, volume 3(1), Aulodonta. C. A. Reitzel, Copenhagen, 370 pp.

———. 1942. New Echinoidea (Camarodonta). Preliminary notice.—Videnskabelige Meddelelser fra Dansk naturhistorisk Forening i København 106:225–232.

———. 1943. A monograph of the Echinoidea, volume 3(2), Camarodonta I: Orthopsidae, Glyphocyphidae, Temnopleuridae and Toxopneustidae. C. A. Reitzel, Copenhagen, 533 pp.

———. 1948. A monograph of the Echinoidea, volume 4(2), Clypeastroida: Clypeastridae, Arachnoididae, Fibulariidae, Laganidae and Scutellidae. C. A. Reitzel, Copenhagen, 471 pp.

———. 1950. A monograph of the Echinoidea, volume 5(1), Spatangoida 1. C. A. Reitzel, Copenhagen, 432 pp.

———. 1951. A monograph of the Echinoidea, volume 5(2), Spatangoida 2. C. A. Reitzel, Copenhagen, 593 pp.

Opresko, D. M., & S. D. Cairns. 1992. New species of black coral (Cnidaria: Antipatharia) from the northern Gulf of Mexico.—Northeast Gulf Science 12:93–97.

Pawson, D. L. 1978. The echinoderm fauna of Ascension Island, south Atlantic Ocean.—Smithsonian Contributions to the Marine Sciences, No. 2: i–iv, 1–31.

———, & J. E. Miller. 1983. Systematics and ecology of the sea-urchin genus *Centrostephanus* (Echinodermata: Echinoidea) from the Atlantic and eastern Pacific Oceans.—Smithsonian Contributions to the Marine Sciences, 20:1–15.

Phelan, T. 1970. A field guide to the cidaroid echinoids of the northwestern Atlantic Ocean, Gulf of Mexico, and the Caribbean Sea.—Smithsonian Contributions to Zoology 40:1–67.

Pielou, E. C. 1991. After the ice age: the return of life to glaciated North America. University of Chicago Press, Chicago, 366 pp.

Pomory, C. M. 2002. A guide to the shallow-water Echinodermata of the Texas coast. University of Texas Press, Austin (in press).

Rowe, F. W. E., & J. Gates. 1995. Zoological catalogue of Australia, volume 33, Echinodermata. CSIRO Australia, Melbourne, 510 pp.

Schneider, C. W. 1976. Spatial and temporal distributions of benthic marine algae on the continental shelf of the Carolinas.—Bulletin of Marine Science 26:133–151.

Serafy, D. K. 1979. Echinoids (Echinodermata: Echinoidea).—Memoirs of the Hourglass Cruises 5(3):1–120.

———, & F. J. Fell. 1985. Marine flora and fauna of the northeastern United States. Echinodermata: Echinoidea. NOAA Technical Report NMFS 33:i–iii, 1–27.

Shimabukuro, S. 1991. *Tripneustes gratilla* (sea urchin). Pp. 313–328 *in* S. Shokita, K. Kakazu, A. Tomori, & T. Toma, eds., Aquaculture in tropical areas [M. Yamaguchi, translator]. Midori Shobo Company, Ltd., Tokyo, 360 pp.

Texas A&M University. 1981. Northern Gulf of Mexico topographic features study, final report, volume 3. Report to U.S. Department of the Interior, Bureau of Land Management, Outer Continental Shelf Office, New Orleans, Louisiana, Contract AA551-CT8-35. Texas A&M University, College of Geosciences, Department of Oceanography, College Station, 130 pp., C-1–C-34.

Troschel, F. H. 1869. Über einige neue Seeigel.—Sitzungsberichte und Verhandlungen des naturhistorischen Vereines der preussischen Rheinlande 26:96.

———. 1872. Die Familie der Echinocidariden.—Archiv für Naturgeschichte. 38:293–356.

Turner, R. L., & C. M. Norlund. 1988. Labral morphology in heart urchins of the genus *Brissopsis* (Echinodermata: Spatangoida), with an illustrated revised key to western Atlantic species.—Proceedings of the Biological Society of Washington 101:890–897.

Williams, M., D. Dunkerley, P. De Deckker, P. Kershaw, & J. Chappell. 1998. Quaternary environments, Second edition. Arnold Publishers, London, 329 pp.

Yoshino, K.-I., H. Kajiura, K. Nomura, T. Takao, Y. Shimonishi, M. Kurita, M. Yamaguchi, & N. Suzuki. 1989. A halogenated amino acid-containing sperm activating peptide and its related peptides isolated from the egg jelly of sea urchins, *Tripneustes gratilla, Pseudoboletia maculata, Strongylocentrotus nudus, Echinometra mathaei* and *Heterocentrotus mammillatus*.—Comparative Biochemistry and Physiology 94B:739–751.

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The genus *Chrysopetalum* Ehlers, 1864 (Annelida: Polychaeta: Chrysopetalidae) in the Pacific coast of Panamá

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Abstract.—The family Chrysopetalidae is represented in the Pacific coast of Panamá by three genera: *Bhawania* Schmarda, 1961, *Paleanotus* Schmarda, 1961 and *Chrysopetalum* Ehlers, 1864. Up to now, the latter genus was represented by a single species, *Chrysopetalum occidentale* Johnson, 1897. During a study carried out at the National Park of Coiba (Pacific coast of Panamá), three species of this genus were found: *C. occidentale* and two new species: *C. elegantoides* n. sp. and *C. maculata* n. sp. In this paper the two new species are described and a key for identification is provided. *Chrysopetalum elegantoides* closely resembles the descriptions of *C. elegans* Bush, 1900 and *C. ehlersi* Gravier, 1901. The paleae and neurosetae are very similar to those of *C. elegans,* but specimens from Coiba lack interramal glands like *C. ehlersi. Chrysopetalum elegantoides* differs from *C. ehlersi* principally in the tips of paleae and the length of the blades of the neurosetae. *Chrysopetalum maculata* differs from all others within the genus in having a wide body and broad paleae and in the lack of spines. The most similar species is *C. heteropalea* Perkins, 1985; both species lack spines (*sensu* Perkins) and have several symmetrical paleae; but the paleae of the *C. maculata* are ornamented with knobs, lacking the transverse ridges that are typical of *C. heteropalea.* The presence of *C. occidentale* in the area is verified.

Polychaetous annelids are poorly known in the Panamanian Pacific, and only few studies in this area have provided records of these marine animals (Monro 1928a, 1928b, 1933a, 1933b; Fauchald & Reimer 1975; Fauchald 1977a; López et al. 1997). Investigators from the Laboratorio de Invertebrados y Biología Marina of the Universidad Autónoma de Madrid have been working at the National Park of Coiba since 1996 in order to increase the knowledge of the marine fauna in general (San Martín et al. 1997), and the polychaetes in particular (Capa et al. 2001a, 2001b, 2001c, San Martín et al. 1998).

The diversity of genera and species of the family Chrysopetallidae in the Panamanian Pacific appears to be low; only three genera: *Bhawania* Schmarda, 1961, *Paleanotus* Schmarda, 1961 and *Chrysopetalum* Ehlers, 1864, and four species: *B. goodei* Webster, 1884, *B. riveti* (Gravier, 1908), *P. chrysolepis* Schmarda, 1861 and *C. occidentale* Johnson, 1897, have been reported. The present paper increases the knowledge of this family in the area offering a description of two new species of *Chrysopetalum,* as well as verifies the presence of *C. occidentale.*

The National Park of Coiba (7°10′ to 7°53′N and 81°32′ to 81°56′W) is a marine-terrestrial area, protected since 1991. It is a set of a large amount of islands and islets, the largest being the one which gives the name to the Park. The study of the fauna and flora of this Park is very important issue for several reasons: the eastern central Pacific has a special biogeographical interest due to its past connection with the present Caribbean (Laverde-Castillo 1986); the lack of human impact; and the few studies carried out in the area.

Material and Methods

The samples were collected during four expeditions carried out between Jun 1996 and Sep 1998. Different substrata were sampled: blocks of dead coral (*Pocillopora* spp.), epibionts from dead gorgonians (*Pacifigorgia* sp.) and living oysters (*Hyotisa hyotis*) and coarse sand. Samples were collected in three different ways: the blocks of dead coral *Pocillopora* spp. (approximately 4 kg) were sampled by SCUBA and immediately put into a bag, the blocks were then placed in sea water for 24 h in order to induce the organisms to leave the coral cavities due to short supply of oxygen; the remainder of the organisms were extracted by fragmenting the branched blocks; the polychaetes associated with dead gorgonians and living oysters were sampled by SCUBA, by removing the substrata and scraping off their surfaces; and for sampling the polychaetes in coarse sand, a corer 9.5 cm diameter and 1 liter volume was used, and the sediment was washed through a 0.25 mm gauge mesh sieves.

The samples were fixed in a 10% formaldehyde-seawater solution and preserved in a 70% alcohol solution. For identification a Olympus SZ30 stereomicroscope and Olympus CH30 optical microscope were used. Parapodia from most of the specimens were removed and slide mounts were made in glycerine gel. The drawings were made to scale, with a drawing tube, in a Nikon Optiphot optical microscope equipped with interference contrast optics (Nomarsky). Scanning electron micrographs (SEM) were made using standard procedure. The specimens in 70% alcohol were introduced gradually in solutions more concentrated in acetone. The specimens were critical-point dried in carbon dioxide, coated with gold and viewed through a SEM Phillips XL-30 system, in the SEM unit at the Universidad Autonoma de Madrid. The specimens are deposited in the Museo Nacional de Ciencias Naturales de Madrid (MNCNM), Spain.

The sample sites, co-ordinates and habitats are provided in Table 1. In 14 samples studied, a total of 65 specimens of Chrysopetalids were identified belonging to only one genus, *Chrysopetalum*, and three species.

Results

Genus *Chrysopetalum* Ehlers, 1864

Type species.—*Chrysopetalum fragile* Ehlers, 1864.

Diagnosis.—Medium in size, up to 65 segments. Prostomium rounded, partially retracted into anterior segments (about posterior margin of the fourth segment), with two pairs of eyes generally in rectangular disposition, anterior pair larger than posterior ones. A pair of elongate ventral palps. Pair of long lateral antennae emerging ventrally on anterior margin of dorsal surface, and short median antenna, fusiform, originating behind anterior eyes. Caruncle attached on posterior dorsal margin of prostomium, smaller than prostomium, sphaeroidal, and reaching the end of fifth setiger. Ventral mouth opening with triangular or rounded cover, extending from anterior margin of fifth segment. Peristomium reduced, only visible as lip covering the mouth. First two segments each with pair of dorsal and ventral cirri, similar to those following segments. First segment asetigerous, second segment only with notosetae. From third segment, parapodia birramous with notopodial paleae (modified notosetae) and compound spinigerous neurosetae on anterior segments, changing to compound falcigerous neurosetae through posterior segments. Dorsal cirri with long cirrophores and long cirrostyles with wide basis and filiform distal part. Ventral cirri shorter, but similar in shape. Dorsum partially covered by flatened paleae, distally serrated, with

Table 1.—Collection sites, coordinates, habitats, depths and weight/volumes of the studied samples.

Sampled substrate	Samples	Coordinates	Station	Depth	Weight/volume
Dead coral samples	CM2FEB97	7°49′N, 81°46′W	Isla de Uvas	3 m	—
Dead coral samples	CM3FEB97	7°41′50″N, 81°38′25″W	Isla del Canal de Afuera	6 m	4000 g
Dead coral samples	CM4FEB97	7°24′20″N, 81°41′W	Ensenada María	3 m	4200 g
Dead coral samples	CM2NOV97	7°38′30″N, 81°41′40″W	Playa Rosario	2.5 m	4100 g
Dead coral samples	CM4NOV97	7°24′20″N, 81°41′W	Ensenada María	5.8 m	4400 g
Dead coral samples	CM5NOV97	7°49′N, 81°46′W	Isla de Uvas	6 m	4000 g
Dead coral samples	CM1SEP98	7°35′30″N, 81°42′30″W	Isla de Granito de Oro	2 m	3000 g
Dead coral samples	CM4SEP98	7°24′20″N, 81°41′W	Ensenada María	2 m	3600 g
Dead coral samples	CM5SEP98	7°38′30″N, 81°41′40″W	Playa Rosario	1.2 m	3900 g
Gorgonian epibionts	CUAL8JUN96	7°38′N, 41°47′10″W	Islote Santa Cruz	11 m	—
Hyotisa hiotis epibionts	CUAL2FEB97	7°36′40″N, 81°49′30″W	Islote San Martín	14 m	—
Hyotisa hiotis epibionts	CUAL5FEB97	7°36′10″N, 81°50′10″W	Punta Cirilo	4–9 m	—
Below rocks	CUAL8FEB97	7°41′50″N, 81°38′25″W	Isla del Canal de Afuera	4–6 m	—
Coarse sand	AR1SEP98	7°39′N, 81°41′40″W	Bajo Mali Rock	10 m	1 liter

internal longitudinal ribs and transverse chambers. Paleae of middle segments forming at least three groups arranged in semicircular or straight row, covering dorsum, extending from bundles occupying 0.5 to 0.67 of segmental width, serrated on both margins. Some species with an additional row of anterior spines. Middle group paleae consisting of two or three irregular transversely arranged rows of long and slender paleae originated in up to eight developmental centers, median paleae symmetrical, each with up to 12 internal longitudinal ribs, lateral ones with tips asymmetrical, bent toward middle of group. Lateral group paleae consisting of up to 10 more slender, symmetrically tipped, laterally orientated paleae, also with internal ribs. Midline group paleae arranged in longitudinal to slightly oblique row of up to six; each bent medially and posteriorly, shorter, slender than middle group paleae, with almost symmetrical tips. Compound falcigers with blades decreasing in size dorsally to ventrally, unidentate, with hooded tips and serrated margins. Pygidium with pair of anal cirri similar to dorsal cirri (Perkins 1985, San Martín in press).

Chrysopetalum elegantoides new species
Figs. 1, 2

Material examined.—Holotype: CM2NOV97 (MNCN 16.01/8531a), paratypes: CM2FEB97(2) (MNCN 16.01/8352), CM3FEB97(1) (MNCN 16.01/8533), CM4FEB97(21) (MNCN 16.01/8534), CM2NOV97(5) (MNCN 16.01/8531b), CM4NOV97(2) (MNCN 16.01/8535), CM5NOV97(1) (MNCN 16.01/8536), CM1SEP98(6) (MNCN 16.01/8537), CM5SEP98(1) (MNCN 16.01/8539), CUAL8JUN96(1) (MNCN 16.01/8541), CUAL2FEB97(1) (MNCN 16.01/8541), CUAL5FEB97(8) (MNCN 16.01/8543).

Additional material examined.—CM3FEB97(fragments), CM4FEB97(fragments), CUAL8FEB97(fragments).

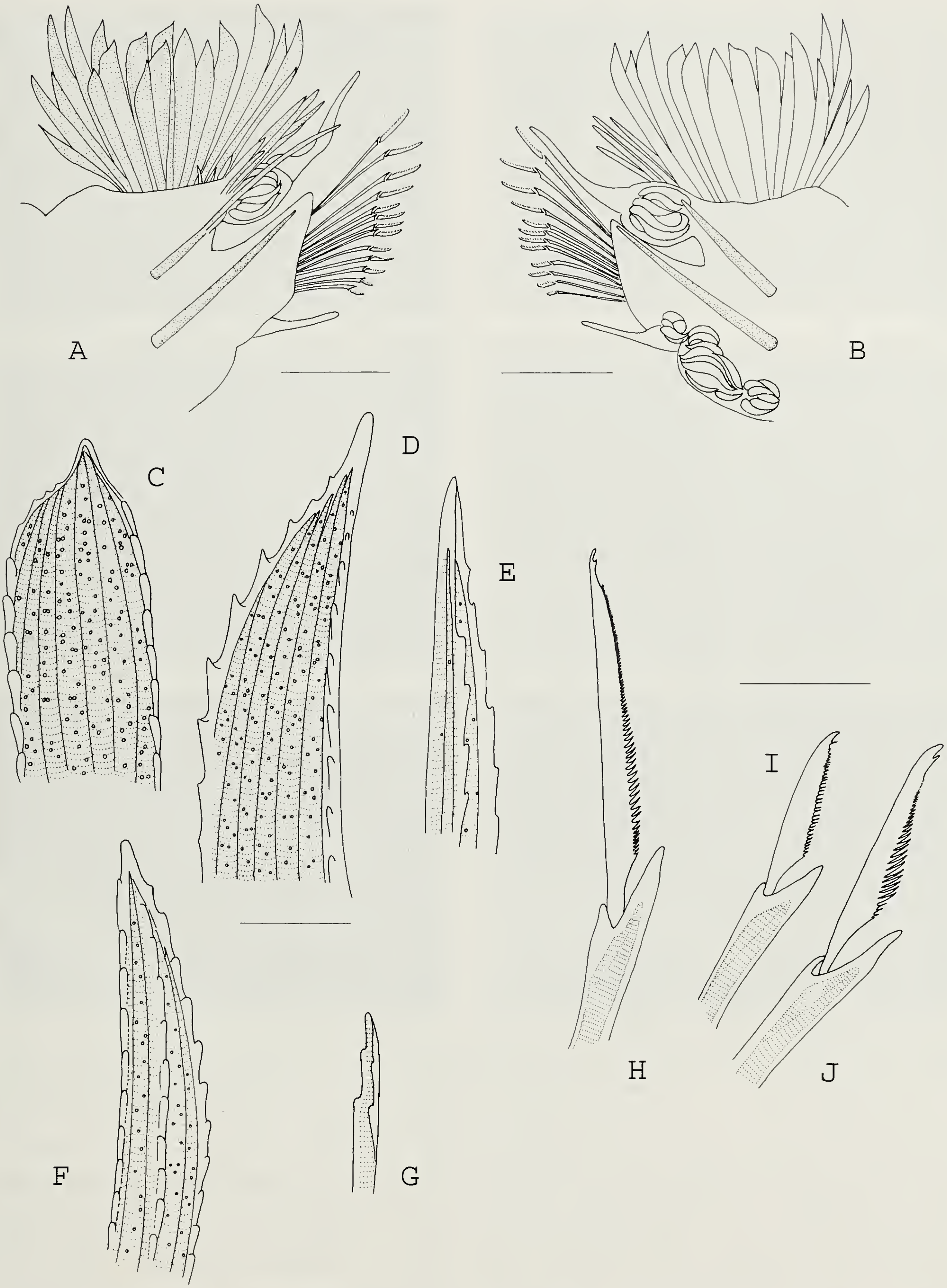

Fig. 1. *Chrysopetalum elegantoides* n. sp. Paratype CM1SEP98. A: Right parapodium, setiger 33, anterior view; B: Same, posterior view; C: Tip of symmetrical palea, middle group; D: Tip of palea, lateral part, middle group; E: Palea, lateral group; F: Palea, midline group; G: Spine, anterior group; H: Upper compound falcigerous neuroseta, middle segments; I: Lower compound falciger; J: Middle compound falciger. Scale A, B: 68.25 μm; C–J: 20 μm.

Other material examined.—Chrysopetalum elegans MNCN16.01/4107, MNCN 16.01/4194, MNCN16.01/4201, MNCN 16.01/4195 from Cuba, loaned by de Museo Nacional de Ciencias Naturales de Madrid. *Chrysopetalum elhersi* 1941.4.4.238 and A39 from Red Sea, 1969.192 from Kuwait and 1961.8.14 from Mombassa; lounded by the Natural History Museum, London and the Museum National d'Histoire Naturelle de Paris.

Description.—Only two complete specimens (the holotype and one paratype in sample CUAL3FEB97). Holotype 8 mm long, 0.6 mm wide with 58 segments. Complete paratype 6 mm long, 0.5 mm wide, with 37 segments. Prostomium oval, slightly longer than wide. Some specimens having three pairs of eyes, with two posterior pairs slightly superimposed, anterior pair sometimes very close to each other but also separated in other specimens. Caruncle smaller than prostomium. Notosetae consisting of paleae and spines. Paleae serrated on their margins, without hoods on middle and midline groups, dorsal surface moderately knobbed (Figs. 1C–F, 2B). Middle group paleae of midbody numbering 20–30; middle, symmetric paleae with eight or nine internal longitudinal ribs and conical tapered tips (Figs. 1C, 2C); lateral middle group paleae asymmetrical with tips directed to middle ones, with eight internal ribs (Fig. 1D); central paleae shorter than lateral paleae in middle group. Middline group paleae about seven, each with denticulated surface midrib (Fig. 1F). Lateral group paleae gradually more slender and smaller from the principal group to the anteriomedial spines (Fig. 1E). Three spines slender and denticulated in each parapodia on anterior group (Fig. 1G). Neuropodia with characteristic setae (Fig. 1H–J). Parapodial gland in the base of dorsal and ventral cirrostyles and in the inferior part of neuropodia (Fig. 1A–B).

Remarks.—Two very similar species with slender paleae have been previously described: *C. elegans* Bush, 1910 and *C. ehlersi* Gravier, 1901. *Chrysopetalum elegans* differs from *C. ehlersi* in having well developed interramal glands with spindles of fibers, as well as in having wider neurosetal blades (Perkins 1985). The geographical distribution of these two species is also different: *C. elegans* has been reported from the Caribbean (Bermuda and Cuba), Gulf of Mexico, and Florida, whereas *C. ehlersi* has been reported from the Indian Ocean (Gulf of Aden, Persian Gulf and Kenia). *Chrysopetalum elegantoides* n. sp. from Coiba has cirrophoral glands but lacks interramal glands, although it is very similar to *C. elegans* in the shape of the paleae and the width of the neurosetae. The specimens from Coiba have been compared with specimens of *C. elegans* from Cuba (San Martín 1986). The specimens of *C. elegans* from Cuba have very conspicuous interramal glands, confirming that this character has value for segregating species (Perkins 1985). Comparisons have also been made with specimens of *C. elhersi* 1941. Specimens from Kuwait and Mombasa are not *C. ehlersi,* and perhaps represent an undescribed species. They differ from *C. ehlersi* in having conspicuously broader hooded paleae, whereas the specimens from the Red Sea perfectly agree with the original description (Gravier 1901). *Chrysopetalum elegantoides* shares with *C. ehlersi* the absence of an interramal gland and the similar shape of acute paleae, but they differ in several features: the median antenna in C. *elegantoides* is shorter than those in the specimens of *C. ehlersi*; *C. elegantoides* has proportionally more slender paleae than does *C. ehlersi,* which is more evident in the middle group and the lateral group paleae (Figs. 1C, E, 3C, E); the tips of the paleae are sharper in *C. elegantoides* (Fig. 1D) than in those of *C. ehlersi* (Fig. 3D); midline group paleae have the denticulated midrib displaced laterally in *C. ehlersi* (Fig. 3F) and centered in *C. elegantoides* (Fig. 1F); the bidentation of neurosetae appears to be more pronounced in *C. elegantoides* (Figs. 1H–J, 2E, F) than in *C. ehlersi* (Fig.

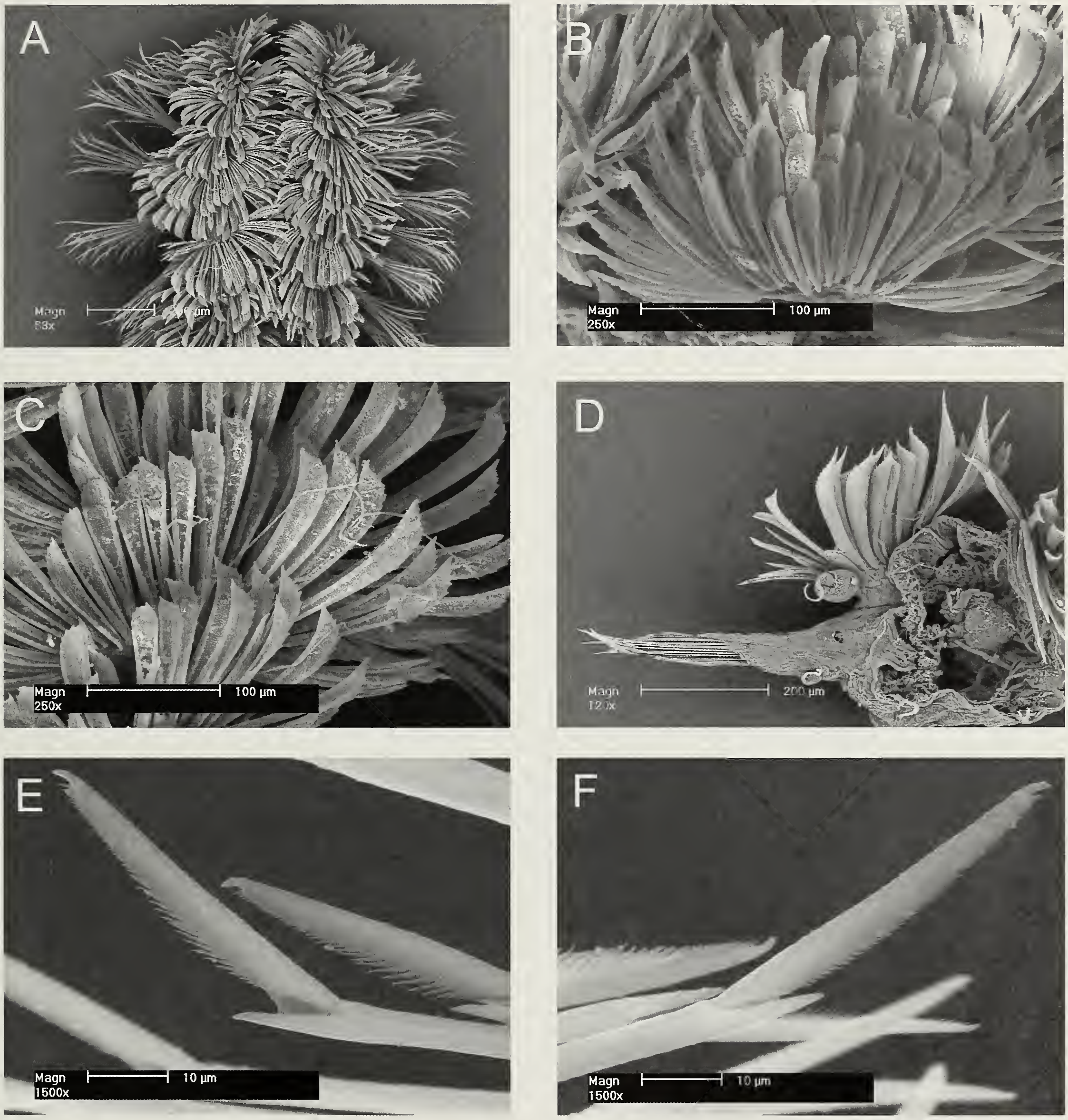

Fig. 2. *Chrysopetalum elegantoides* n. sp. Scanning electron micrographs (SEM). A: Anterior end, dorsal view; B: Paleae, anterior setigers; C: Paleae, middle setigers; D: Middle parapodium, posterior view; E–F: Compound falciger neurosetae.

3G–I); the neurosetal blades are shorter but they have the same width (they measure 44, 35 and 15 μm long in *C. elegantoides,* in the superior, median and inferior setae of a midbody parapodium respectively, and 57, 41 and 20 μm long in *C. ehlersi,* respectively. The cirrophoral gland is relatively larger in *C. elegantoides* than in *C. ehlersi* (Figs. 1A, B, 2D, 3A, B).

The presence of three pairs of eyes has been reported before on other species: Bush (in Verrill 1900) found some specimens with six eyes in the syntypes of *C. elegans,* although Perkins (1985) reported only two pairs.

Etymology.—The specific name is given because of the similarity between this species and *C. elegans* (*-oides* = similar to, in greak) which lives on the other side of the Isthmus of Panamá.

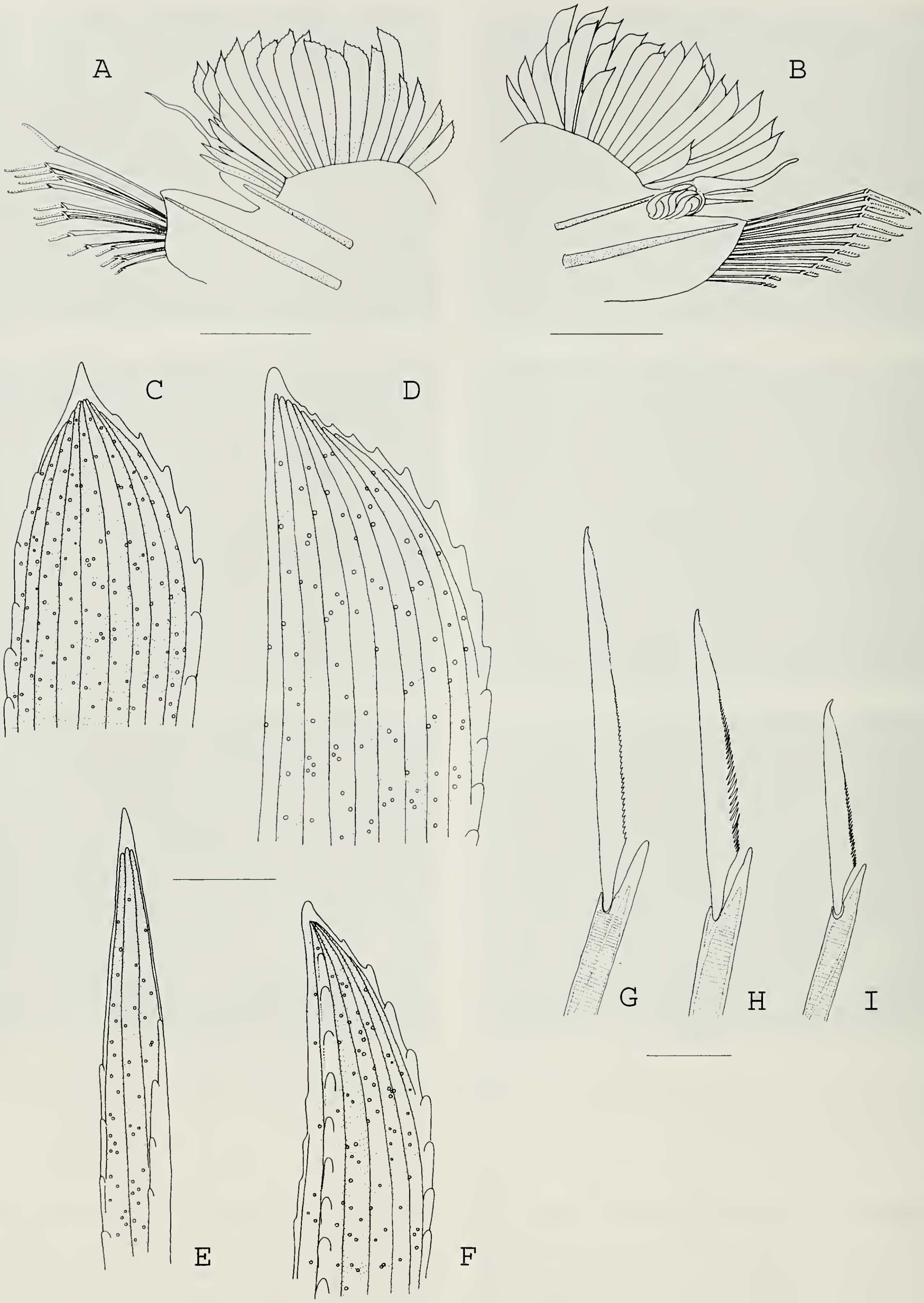

Fig. 3. *Chrysopetalum ehlersi*. NHML ZK 1941.4.4.238. A: Parapodium middle segment anterior view; B: Same, posterior view; C: Tip of palea, central part of middle group; D: Same, from lateral part; E: Palea, lateral group; F: Palea, midline group; G: Upper compound falcigerous neuroseta; H. Middle compound falciger; I: Lower compound falciger. Scale A, B: 0.195 mm; C–I: 20 μm.

Fig. 4. *Chrysopetalum maculata* n. sp. AR1SEP98. A: Anterior end, dorsal view; B: Anterior end without paleae, dorsal view; C: Right parapodium, middle segment, anterior view; D: Left parapodium, middle segment, posterior view. Scale A: 0,195 mm; B: 0,18 mm; C, D: 97,5 μm.

Habitat.—Blocks of dead *Pocillopora* spp.

Geographical distribution.—Pacific coast of Panamá.

Chrysopetalum maculata, new species
Figs. 4–6

Material examined.—Holotype: AR1 SEP98(1) (MNCN 16.01/8530a), paratypes: AR1SEP98(3) (MNCN 16.01/8530b).

Additional material examined.—AR1SEP98(10).

Description.—Holotype anterior fragment 4.12 mm long, 1 mm wide without setae, 30 segments; largest paratype anterior fragment, 2.76 mm long, 0.8 wide, 23 segments. Fragile, broad body, white to pale brown. Silver to gold-colored paleae fans, often flecked with brown spots, covering worm completely, median paleae interlock-

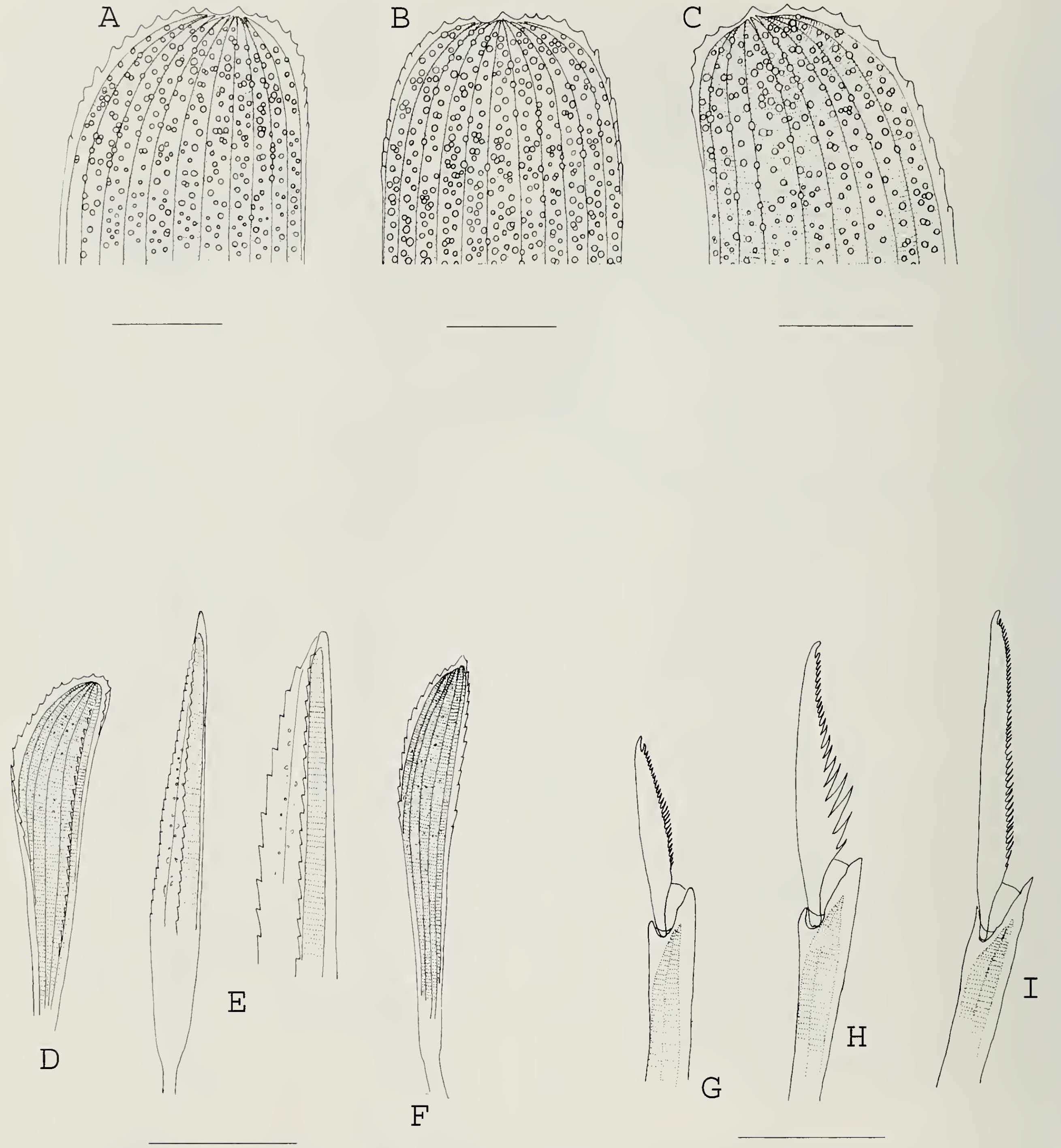

Fig. 5. *Chrysopetalum maculata* n. sp. AR1SEP98. A, C: Tips of paleae from lateral part of middle group, middle segment; B: Tip of palea from central part of middle group, middle segment; D: Palea, midline group; E: Paleae, lateral group; F: Palea, lateral group G: Lower compound falciger neuroseta; H: Middle compound falciger; I: Upper compound falciger. Scale A–C: 20 μm; D: 48 μm; E: 20 μm; F: 48 μm; G–I: 20 μm.

ing at mid-line, forming distinct convex median ridge (Fig. 4A). Prostomium wider than long, with two pairs of garnet eyes, some specimens with an additional central eye. Palps about twice longer than wide (Fig. 4B). Rounded caruncle with cilia (Fig. 6B). Mouth covering semioval (Fig. 6A), eversible proboscis with two stylets. Notosetae consisting of only very broad paleae, anterior group spines absent. Middle group paleae of middle segments about 20–22, with dorsal surface strongly knobbed, with 9–12 internal longitudinal ribs (Fig. 5A–C) and, sometimes, with hooded tips; various symmetrical paleae in the centre of the fan (Fig. 6D). Midline group bearing about five

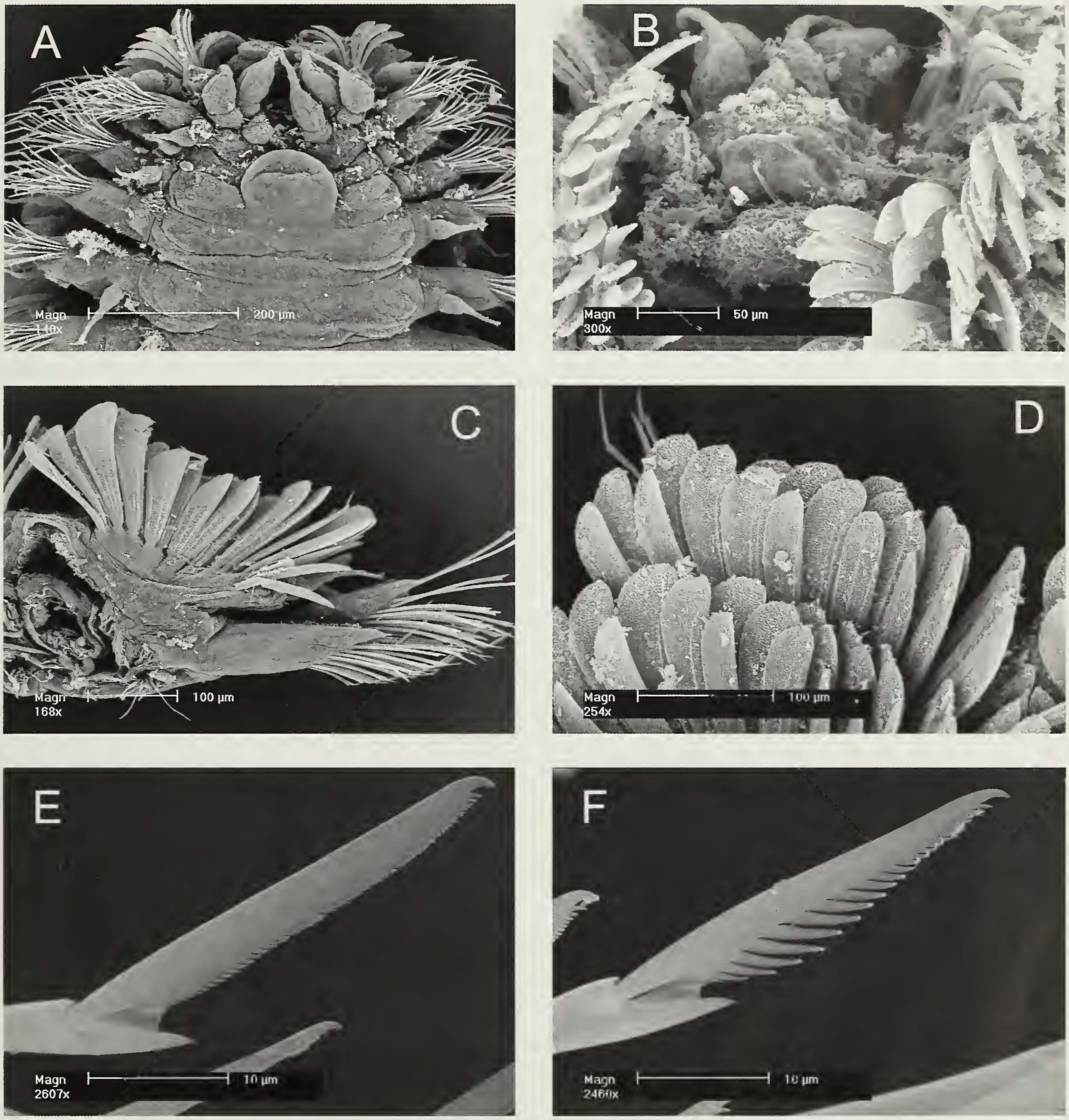

Fig. 6. *Chrysopetalum maculata* n. sp. AR1SEP98. (SEM). A: Anterior end, ventral view; B: Ciliated caruncula; C: Left parapodium, middle segment, anterior view; D: Tips of paleae from middle group, middle segment; E: Upper compound falciger neuroseta; F: Middle compound falciger neuroseta.

paleae with denticulate midrib and six longitudinal ribs (Fig. 5D). Lateral group consisting of one long, broad and acutely tipped palea with five or six longitudinal ribs, originating near acicula (Fig. 5F) and two or three more slender, shorter paleae originating laterally (Fig. 5E, 4C). Compound falcigerous neurosetae numbering 20 to 30 with blades moderately long. Upper few blades distinctly longer than adjacent ones, gradually shorter ventrally. Dorsal blades 55 μm long, with short and coarse serration (Figs. 5I, 6E); middle blades 38 μm long, with long and stout serration (Figs. 5H, 6F); ventral blades 28 μm long, with fine, moderately long serration (Fig. 5G). Interramal region of middle parapodia ciliated on anterior side. Glands containing spindles of fibers in dorsal cirrophore (Fig. 4D).

Remarks.—*Chrysopetalum maculata* n. sp. resembles the general aspect of the species of the genus *Arichlidon* Russell, 1998, because of considerably broad shape of the body and paleae, as well as the golden color of the paleae with brown scale spots. However, the diagnostic characters place this species in the genus *Chrysopetalum. Chrysopetalum maculata* differs from other species of the genus in having very broad knobbed paleae and in lacking spines on the notopodia of middle segments. *Chrysopetalum remaneii* Perkins, 1985 and *C. hernancortezae* Perkins, 1985, have very narrow paleae and notopodial spines. *Chrysopetalum elegans* Bush, 1900 also possesses very narrow paleae and their typical interramal glands could not be observed in the studied specimens. *Chrysopetalum debile* (Grube, 1855), *C. occidentale* Johnson, 1897, *C. floridanum* Perkins, 1985, and *C. euripalea* Perkins, 1985, have also narrow paleae, and tips of the paleae are displaced and have notopodial spines. The definition of *C. elongatum* (Grube, 1856) is conflicting and not clear (Perkins 1985) since drawings and descriptions are incomplete. The most similar species is *C. heteropalea* Perkins, 1985, because both *C. maculata* and *C. heteropalea* lack notopodial spines, posses dorsal cirrophoral glands, the anterior side of middle parapodia in the interramal region is ciliated, and the shapes of neurosetae and paleae are similar. The tips of the paleae of *C. heteropalea* are also displaced as in *C. maculata* and both present symmetrical paleae in the centre of the middle group. Paleae of *C. heteropalea* are considerably narrower, with 8 longitudinal ribs and lack knobs in their dorsal surface; instead, there is ornamentation consisting of numerous and irregular transversals ribs that is not present in *C. maculata. Chrysopetalum heteropalea* has also visible glands in the neuropodia and ventral cirrophores, which have not currently been found in specimens of *C. maculata.* Neurosetae are similar in both species, although *C. maculata* does not present the typical lowest compound falciger that occurs in *C. heteropalea* and middle compound falcigers are slightly different. The caruncle of *C. maculata* is ciliated, differing from that described by Perkins (1985) for *C. heteropalea.*

Etymology.—The species name derives from the latin *macula* (=spot), in reference to the numerous dark spots on the surface of paleae.

Habitat.—Intertidal coarse sand.

Geographical distribution.—Pacific coast of Panamá.

Chrysopetalum occidentale Johnson, 1897
Fig. 7

Chrysopetalum occidentale Johnson, 1897: 161, pl. 5, figs 15, 16, pl. 6, Figs. 17–19; Monro 1933a: 19; Hartman 1961: 56, 57; 1968: 185, 186, Figs. 1–5; Fauchald & Reimer 1975: 82; Fauchald 1977a: 71, Figs. 18 a–c; 1977b: 10, Perkins 1985: 869–871, Figs. 3, 4.

Material examined.—CM1 SEP98 (1+ 1 fragment), CUAL8FEB97 (1 fragment).

Remarks.—Only one anterior fragment of 15 setigers and two middle fragments were collected. The specimens agree generally with the description of Perkins (1985). The anterior fragment lacks the median and left antennae, and we can not compare these structures with Perkins' description (1985). Middle group paleae have obtuse tips and eight to ten internal ribs (Fig. 7C, D). Midline group paleae have the denticulated midrib slightly displaced laterally (Fig. 7F). Lateral group paleae are slender (Fig. 7E). Blades of compound falcigerous neurosetae are bidentate, gradually decreasing in size dorsally to ventrally (Fig. 7G, H).

Perkins (1985) established some differences between the specimens from California and those from Mexico. The number of paleae in the middle group of specimens from the first locality is between 35 and 40 and in Mexico they have a maximum of 30 paleae. In Coiba, the specimens found have

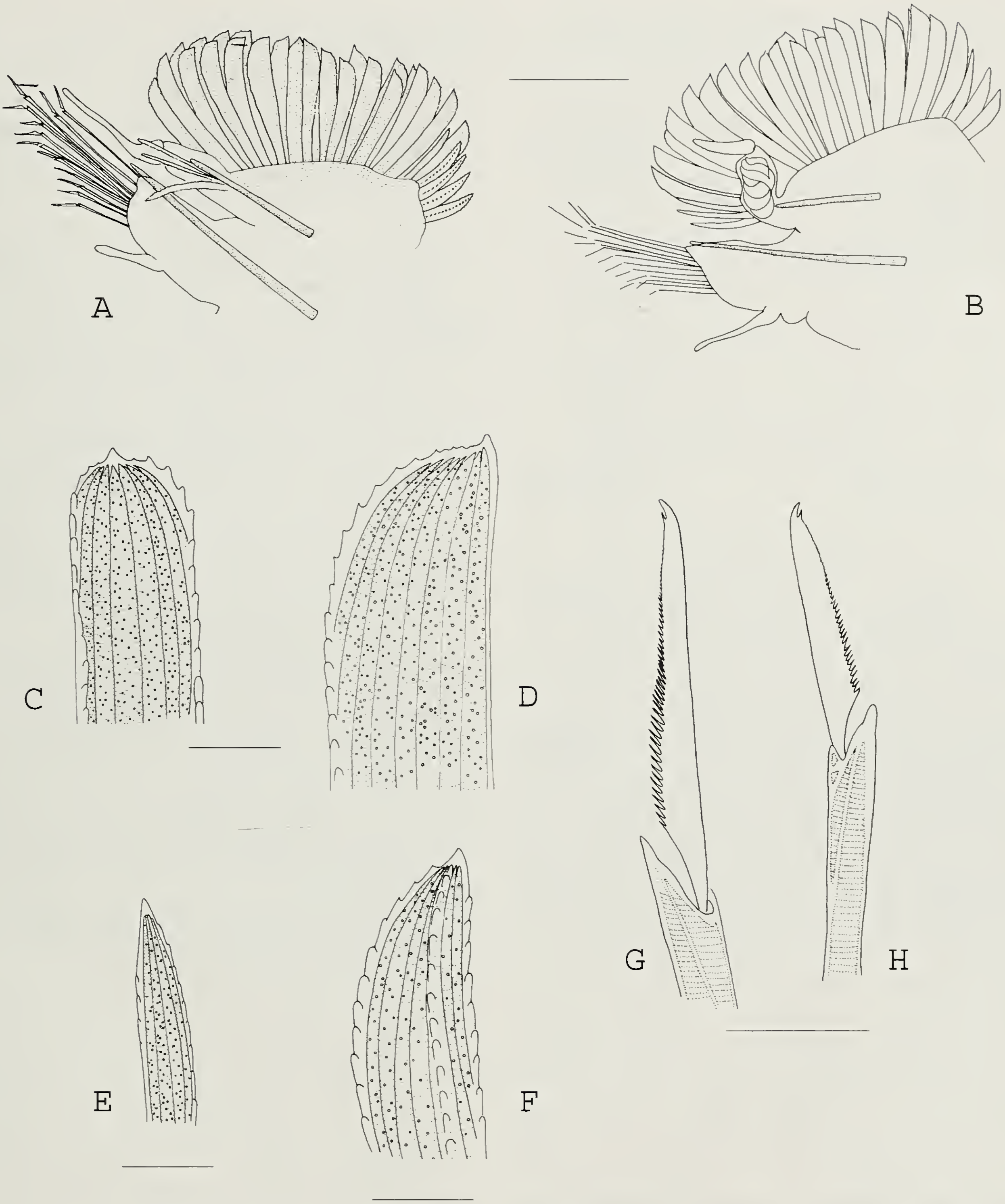

Fig. 7. *Chrysopetalum occidentale*. CM1SEP98. A: Left parapodium, setiger 14, anterior view; B: Right parapodium, same setiger, posterior view; C: Palea, middle group, central part; D: Palea, middle group, lateral part; E: Palea, lateral group; F: Palea, midline group; G: Upper compound falciger neuroseta; H: Lower compound falciger. Scale A, B: 0.195 mm; C–H: 20 μm.

between 15 and 24 paleae in the middle group (Fig. 7A, B). Midline group paleae number about six in California and about four in Coiba.

Type locality.—California.

Habitat.—Rocks (Hartman 1968), holdfast (Perkins 1985), intertidal (Fauchald 1977a), dead coral (*Pocillopora* spp.).

Geographical distribution.—According to Perkins (1985) the distribution of this species is localized in the East Pacific, from the southern California to Panamá.

Key to *Chrysopetalum* Species in the Panamanian Pacific

1a. Anterior group of paleae and spines (*sensu* Perkins 1985) absent. Body and paleae very broad. .... *C. maculata* n. sp.
1b. Anterior group of paleae and spines present 2
2a. Middle group paleae with acute tips (see Fig. 2C–F), and narrow subterminal region, without hoods or remnants in the distal end of paleae .... *C. elegantoides* n. sp.
2b. Middle group paleae with obtuse tips (see Fig. 8C–F) and enlarged subterminal region, hoods or remnants generally present .... *C. occidentale*

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Literature Cited

Capa, M., G. San Martín, & E. López. 2001a. Syllinae (Syllidae: Polychaeta) del Parque Nacional de Coiba, Panamá.—Revista de Biología Tropical 49(1):103–115.

———, ———, & ———. 2001b. Autolytinae, Eusyllinae y Exogoninae (Syllidae: Polychaeta) con comentarios sobre la ecología y la biogeografía de la familia Syllidae del Parque Nacional de Coiba, Panamá.—Revista de Biología Tropical 49(2):621–628.

———, ———, & ———. 2001c. Description of a new species of *Parasphaerosyllis* (Polychaeta: Syllidae: Syllinae).—Proceedings of the Biological Society of Washington 114(1):280–284.

Ehlers, E. 1864. Die Borstenwürmer (Annelida Chaetopoda) nach systematischen und anatomischen Unterschungen dargestelt. Leipzig, Wilhelm Engelmann, xx + 1–268, pls. 1–11.

Fauchald, K. 1977a. Polychaetes from intertidal areas in Panamá, with a review of previous sallow-waters records.—Smithsonian Contributions to Zoology 221:1–81.

———. 1977b. The Polychaete worms. Definitions and keys to the orders, families and genera.—Natural History Museum of Los Angeles Country, Sciences Series 28:1–188.

———, & A. A. Reimer. 1975. Clave de poliquetos panameños con la inclusión de una clave para todas las familias del mundo.—Boletín del Instituto Oceanográfico Universidad de Oriente Cumana 14(1):71–94.

Gravier, M. C. 1901.Contribution a l'etude des annelides polychetes de la Mer Rouge.—Nouvelles Archives du Museum Paris, ser. 4. 3:147–268, pls. 7–10.

Grube, E. 1855. Beschreinbungen neuer oder wenig bekannter Anneliden.—Archib für Naturgeschichte, Berlin 21:81–136, pls. 3–5.

———. 1856. Annulata Örstediana. Enumeratio Annulatorum, quae in itinere per Indiam occidentalem et Americam centralem 1845–1848 suscepto legit cl. A. S. Örsted, adjectis speciebus nonnullis a cl. H. Kröyero in itinero ad Americam meridionalem collectis. Pt. 1.—Videnskabelige Meddeleser fra den naturhistoriske Forening i Kjobenhavn, vol. for 1856:44–62.

Hartman, O. 1961. Polychaetes annelids from California.—Allan Hancock Pacific Expeditions 25:1–226.

———. 1968. Atlas of the Errantiate Polychaetous Annelids from California. University of Southern California, Los Angeles. 828 p.

Johnson, H. P. 1897. A preliminary account of the marine annelids of the Pacific Coast, with descriptions of new species, part 1. The Euphosynidae, Amphinomidae, Palmyridae, Polynoidae, and Sigalionidae.—Proceedings of the California Academy of Sciences, ser. 3, Zoology 1:153–199.

Laverde-Castillo J. 1986. Lista anotada de los poliquetos (Annelida) registrados para el Pacífico Colombiano con notas preliminares de su zoogeografía.—Actualidades Biológicas 15(58):123–130.

López, E. G. San Martín,P. Cladera, & M. Capa. 1997. Fauna de Anélidos Poliquetos del Parque Nacional de Coiba (Panamá). In: S. Castroviejo (ed.). Flora y Fauna del Parque Nacional de Coiba (Panamá). p 57–73.

Monro, C. C. A. 1928a. Polychaeta of the Families Polynoidae and Acoetidae from the vicinity of the Panamá Canal, collected by Dr, C. Crosland and Dr. Th. Mortesen.—Journal of the Linnean Society of London 36:553–576.

———. 1928b. Papers from Dr. Mortensen's Pacific Expedition 1914–16, 45.On the Polychaeta collected by Dr. Th. Mortensen off the coast of Panamá.—Videnskabelige Meddelelser fra Dansk Naturhisurisk Forening 85:75–103.

———. 1933a. The Polychaeta Errantia collected by Dr. C. Crossland at Colón in the Panamá region and the Galapagos Islands during the expedition of the "St. George".—Proceedings of the Zoological Society of London:1–96.

———. 1933b. The Polychaeta Sedentaria collected by Dr. C. Crossland at Colón in the Panamá region and the Galápagos Islands during the expedition of the "St. George".—Proceedings of the Zoological Society of London:1039–1092.

Perkins, T. 1985. *Chrysopetalum, Bhawania* and two new genera of Chrysopetalidae (Polychaeta). Principally from Florida.—Proceedings of the Biological Society of Washington 98:856–915.

San Martín, G. 1986. Anélidos poliquetos procedentes de la I expedición cubano-española a la isla de la Juventud y archipiélago de los Canarreos. Familias Chysopetalidae y Amphinomidae.—Revista de Investigaciones Marinas 7(1):17–30.

———. In press. Anélidos poliquetos. Chrysopetalidae. *In* Fauna Ibérica. Ramos, M. A. et al., eds., Museo Nacional de Ciencias Naturales, CSIC, Madrid.

———, E. López, M. S. Redondo, M. Capa, P. Cladera, & A. Laborda. 1997. El bentos marino del Parque Nacional de Coiba (Panamá). Pp. 33–55 *in* S. Castroviejo, ed., Flora y Fauna del Parque Nacional de Coiba (Panamá), AECI, Madrid, 534 pp.

———, E. López, & A. I. Camacho. 1998. First record of a freshwater Pisionidae (Polychaeta): description of a new species from Panama with a key to the new species of *Pisione*.—Journal of Natural History 32:1115–1127.

Schmarda, L. K. 1861. Neue wirbellose Thiere beobachtet und gesammelt auf einer Reise um die Erde 1853 bis 1857, vol. 1. Turbellarien, Rotatorien und Anneliden, Pt. 2.—Leipzig, Wilhelm Engelmann, Pp. 1–164. 22 pls.

Verrill, A. E. 1900. Adittions to the Turbellaria, Nemertina, and Annelida of the Bermudas, with the revision of some new England genera and species.—Transactions of the Connecticut Academy of Arts and Sciences 10:595–671.

Watson-Russell, C. 1998. Description of *Arichlidon* new genus and two new species from Australia; *Bhawania reyssi* redescribed and assigned to *Arichlidon* (Chrysopetalidea: Polychaeta).—Beagle 14:159–176.

Webster, H. E. 1884. The Annelida from Bermuda, collected by Mr. G. Brown Goode.—Bulletin of United States National Museum 25:307–327, pls. 7–12.

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Annotated checklist of decapod crustaceans of Atlantic coastal and continental shelf waters of the United States

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Abstract.—The decapod crustacean assemblage inhabiting estuarine, neritic and continental shelf waters (to 190 m) of the temperate eastern United States is diverse, with 391 species reported from Maine to Cape Canaveral, Florida. Three recognized biogeographic provinces (Boreal in part, Virginian and Carolinian) are included in this region. The assemblage contains 122 shrimp species (28 penaeids, 2 stenopodids, and 92 carideans), 10 thalassinideans, 8 lobsters, 61 anomurans and 190 brachyurans. Since previous compilation of this fauna, 12 additional species have been described, including four carideans, one callianassid, four anomurans, and three brachyurans. Range extensions into the region have been reported for another five species (*Parapenaeus americanus, Scyllarides aequinoctialis, Petrolisthes armatus, Dromia erythropus, Clythrocerus nitidus*). One species, *Hemigrapsus sanguineus,* has been introduced and become established throughout intertidal environments from southern Maine to northern North Carolina. Six species previously recorded from this region are no longer considered to occur there. Two of these species occur south of the Carolinian biogeographic province, three others are now known to occur only in the Pacific Ocean, and one species previously considered as likely to occur in the region has never actually been recorded there. Scientific nomenclature for all species recorded from the region is updated and referenced. Geographic distributions are summarized for each species incorporating recent published information where available.

The decapod crustacean assemblage (shrimps, lobsters, and crabs) inhabiting estuarine, neritic and continental shelf waters (to 190 m) of the temperate eastern United States is diverse and fairly well known. The most recent comprehensive review of this fauna (Williams 1984) recognized 342 species of decapods and listed 14 extralimital species (species thought to occur incidentally in the region). Williams' (1984) monograph is widely used and continues to be the best available reference for decapod crustaceans of the east coast of the United States. However, in the nearly 20 years since publication of Williams (1984), knowledge regarding shallow water (≤190 m) decapods in this region has advanced. Numerous changes in taxonomy and/or systematic placement of species occurring in this region have also been published in papers scattered throughout the literature.

Objectives of this paper are to re-evaluate the taxonomic status and to update nomenclature for the 342 nominal species of decapods treated by Williams (1984). The list of species he presented is updated by inclusion of all decapods now known to occur in this region based on recently published information. Emendations to Williams' original list include (1) the addition of species in this region described after Williams' publication, (2) adding of species newly reported from the region as published range extensions and introductions, and (3) removal of species no longer considered to occur in the region based on published range revisions. The emended list also includes 13 species listed in Williams (1984) as extralimital, as well as 16 other species that Williams (1984) did not treat, but which previously had been recorded from this region.

Methods

This compilation largely follows the classification and arrangement of Martin & Davis (2001). Based on other recent systematic studies (cited below), some species and genera have been moved to different families, and other species have been reassigned to different genera. Where new systematic information has necessitated changes, updated nomenclature with relevant references is provided, together with a cross-reference to names used in Williams (1984). Symbols preceding species listings highlight the following changes between Williams (1984) and the present compilation: ▶ denotes new additions to the decapod assemblage; ★ denotes changes in nomenclature and/or systematic placement. Additionally, distributional information is reported for each species that occurs in the region with recently published range revisions incorporated and referenced. Justification explaining changes in systematic placement of taxa, together with appropriate reference sources, are provided in a remarks section when relevant.

The region of coverage in the present work is the same as that in Williams (1984), spanning depths from shallow water to the 100-fathom (ca. 190 m) depth contour in three biogeographic provinces. These provinces, defined by marine climatic zones (Williams 1984, Engle & Summers 1999), are, from north to south, Boreal (represented by the region from Maine to north of Cape Cod, Massachusetts), Virginian (Cape Cod, Massachusetts, to Cape Hatteras, North Carolina) and Carolinian (Cape Hatteras, North Carolina, to Cape Canaveral, Florida). Williams (1984) commented that inclusion or exclusion of some species from his list was subjective. For example, he regarded some species as extralimital (i.e., their center of distribution was outside the region) and did not consider them to be part of the assemblage despite the fact that they had been recorded from the region. Williams' treatment of extralimital taxa has proved to be problematic and confusing especially in attempts to summarize decapod crustacean diversity of the region. To alleviate this confusion, the present work does not consider species as extralimital (sensu Williams). Based on available distributional information, the present compilation treats species as either occurring in the geographic region and thus included in the list, or as not occurring in the region and thus excluded.

Systematic Account

Order Decapoda Latreille, 1802
Suborder Dendrobranchiata Bate, 1888
Infraorder Penaeidea Rafinesque, 1815
Superfamily Penaeoidea Rafinesque, 1815
▶ Family Aristeidae Wood-Mason, 1891

Remarks.—Pérez Farfante & Kensley (1997) diagnosed the family and genera, presented a key to the genera based on morphological characters, and illustrated important diagnostic characters for the genera included in their study.

▶ *Aristaeomorpha foliacea* (Risso, 1827)

Remarks.—Species diagnosis and figures are provided in Pérez Farfante (1988) and Rodríguez (1993). This species occurs between 170–1300 m (Pérez Farfante 1988).

Known range.—Western Atlantic: Massachusetts to Florida, Gulf of Mexico, Caribbean Sea to Venezuela (Pérez Farfante & Kensley 1997), and Brazil (D'Incao 1998); Eastern Atlantic: Bay of Biscay to Western Sahara; Azores; Madeira; Canary Islands; Mediterranean Sea; Indo-West Pacific:

South Africa to Mozambique; Madagascar; Réunion Island; Maldive Islands; Sri Lanka; Indonesia; Philippines; Taiwan; Japan; Australia; New Zealand; New Caledonia; Wallis and Futuna Islands; Fiji (Pérez Farfante & Kensley 1997).

Family Penaeidae Rafinesque, 1815

Remarks.—Dall et al. (1990) provided a comprehensive account of many aspects of penaeid systematics, biology and ecology. Pérez Farfante & Kensley (1997) diagnosed the family and genera, presented a key to the genera based on morphological characters, and illustrated important diagnostic characters for the genera included in their study. Former subgenera (*Farfantepenaeus* and *Litopenaeus*) of the more inclusive *Penaeus* were raised to full generic status by Pérez Farfante & Kensley (1997). Results of some molecular phylogenies (Baldwin et al. 1998, Gusmão et al. 2000) have failed to support elevation of these subgenera to genera, however, an alternative hypothesis of relationships proposed in the molecular phylogeny of Maggioni et al. (2001) supported conclusions of Pérez Farfante & Kensley (1997) derived from their analysis of morphological characters. *Trachypenaeus,* as previously defined and as listed in Williams (1984), was shown to be a complex of five genera (Pérez Farfante & Kensley 1997). Only one of these five genera, *Rimapenaeus* Pérez Farfante & Kensley, 1997, is represented in the region by a single species.

★ *Farfantepenaeus aztecus* (Ives, 1891)

Penaeus (*Farfantepenaeus*) *aztecus* Ives.—Williams, 1984:24.

Known range.—Western Atlantic: Martha's Vineyard, Massachusetts, to Florida; Gulf of Mexico to Yucatán (Williams 1984, Pérez Farfante & Kensley 1997).

★ *Farfantepenaeus brasiliensis* (Latreille, 1817)

Penaeus (*Farfantepenaeus*) *brasiliensis* Latreille.—Williams, 1984:28.

Remarks.—This species occurs in shallow water to 366 m (Caetano da Costa et al. 2000), but more frequently at depths of less than 60 m (D'Incao 1998).

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to Florida Keys; southern Gulf of Mexico (off Campeche) and Yucatán; Caribbean Sea to Rio Grande do Sul, Brazil; Bermuda (Williams 1984, Pérez Farfante & Kensley 1997).

★ *Farfantepenaeus duorarum* (Burkenroad, 1939)

Penaeus (*Farfantepenaeus*) *duorarum* Burkenroad.—Williams, 1984:28.

Known range.—Western Atlantic: lower Chesapeake Bay to Florida; Gulf of Mexico to tip of Yucatán Peninsula; Bermuda (Williams 1984, Pérez Farfante & Kensley 1997).

★ *Litopenaeus setiferus* (Linnaeus, 1767)

Penaeus (*Litopenaeus*) *setiferus* (Linnaeus).—Williams, 1984:32.

Known range.—Western Atlantic: New York to St. Lucie Inlet, Florida; Gulf of Mexico to Yucatán (Williams 1984, Pérez Farfante & Kensley 1997).

Metapenaeopsis goodei (Smith, 1885)

Known range.—Western Atlantic: northeast of Cape Lookout, North Carolina, through the Florida Straits to Alabama; off Cape Catoche, Yucatán; Bahamas through the Caribbean Sea and along the coasts of Central and South America to Espírito Santo, Brazil; Bermuda (Williams 1984, Pérez Farfante & Kensley 1997, D'Incao 1998).

► *Parapenaeus americanus* Rathbun, 1901

Remarks.—Pérez Farfante & Kensley (1997) record this species from off New England. This species occurs at 37–412 m (Pérez Farfante 1977b, D'Incao 1998).

Known range.—Western Atlantic: off

New England; off Ponte Vedra, Florida; Gulf of Mexico; Bahamas; Cuba; Puerto Rico; St. Lucia; Belize; Brazil (Rio de Janeiro to Rio Grande do Sul); northern Uruguay (Pérez Farfante 1977b, Pérez Farfante & Kensley 1997, D'Incao 1998).

Parapenaeus politus Smith, 1881

Remarks.—*Parapenaeus politus* occurs over mud and sandy mud sediments at depths of 3–752 m, but is usually found between 65–275 m (Rodríguez 1993).

Known range.—Western Atlantic: Martha's Vineyard, Massachusetts, south through Gulf of Mexico, Caribbean Sea to French Guiana, and Pará, Brazil (Williams 1984, Pérez Farfante & Kensley 1997, D'Incao 1998).

► *Penaeopsis serrata* Bate, 1881

Remarks.—Species diagnosis, description, illustrations, as well as, color and size information were provided in Pérez Farfante (1980). *Penaeopsis serrata* occurs at 120–750 m, with maximum concentrations occurring between 300–450 m (Pérez Farfante 1980, Rodríguez 1993).

Known range.—Western Atlantic: New Jersey to Gulf of Mexico; Caribbean Sea to French Guiana; southern Brazil; Eastern Atlantic: Portugal to northwest coast of Africa (Pérez Farfante 1980, Pérez Farfante & Kensley 1997).

★ *Rimapenaeus constrictus* (Stimpson, 1871)

Trachypenaeus constrictus (Stimpson).—Williams, 1984:38.

Remarks.—*Rimapenaeus constrictus* is a new combination proposed by Pérez Farfante & Kensley (1997). This species occurs in shallow water to 127 m (Caetano da Costa et al. 2000).

Known range.—Western Atlantic: Nova Scotia; Chesapeake Bay to Florida Keys, Gulf of Mexico; Bermuda; Caribbean Sea to Santa Catarina, Brazil (Williams 1984, Pérez Farfante & Kensley 1997, D'Incao 1998).

Xiphopenaeus kroyeri (Heller, 1862)

Remarks.—This species occurs in shallow water to 70 m (Caetano da Costa et al. 2000).

Known range.—Western Atlantic: Virginia (Maris 1986) to Rio Grande do Sul, Brazil, including the Gulf of Mexico and Caribbean Sea (Williams 1984, Pérez Farfante & Kensley 1997, Caetano da Costa et al. 2000); Eastern Pacific: Punta Piaxtla, Sinaloa, Mexico to Paita, Peru (Pérez Farfante & Kensley 1997).

Family Sicyoniidae Ortmann, 1898

Remarks.—Pérez Farfante & Kensley (1997) provided family and generic diagnoses and illustrations of diagnostic characters.

Sicyonia brevirostris Stimpson, 1871

Known range.—Western Atlantic: Norfolk, Virginia, to Florida, through the Gulf of Mexico; Campeche and Yucatán banks; Cuba; Bahamas; Eastern Pacific: off southern Mexico (Williams 1984, Pérez Farfante & Kensley 1997).

Sicyonia burkenroadi Cobb, 1971

Known range.—Western Atlantic: Cape Lookout, North Carolina, to Florida, through the Gulf of Mexico; West Indies; Caribbean coasts of Central and South America to Bahia, Brazil (Williams 1984, Pérez Farfante & Kensley 1997).

Sicyonia dorsalis Kingsley, 1878

Known range.—Western Atlantic: Cape Hatteras, North Carolina, through the Gulf of Mexico to Texas; Caribbean coasts of Central and South America to southern Brazil (Williams 1984, Pérez Farfante & Kensley 1997, D'Incao 1998).

Sicyonia laevigata Stimpson, 1871

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to southern Florida; Gulf of Mexico; West Indies; Caribbean coasts of Mexico, Central America and South America to Rio Grande do Sul, Brazil (Williams 1984, Pérez Farfante & Kensley 1997, Caetano da Costa et al. 2000); Eastern Pacific: southern Gulf of California; Costa Rica; Panama (Pérez Farfante & Kensley 1997).

Sicyonia parri (Burkenroad, 1934)

Known range.—Western Atlantic: Beaufort, North Carolina, through the Gulf of Mexico; West Indies to São Paulo, Brazil (Williams 1984, Pérez Farfante & Kensley 1997, Caetano da Costa et al. 2000).

Sicyonia stimpsoni Bouvier, 1905

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to Florida through the Gulf of Mexico; West Indies; Caribbean coasts of Mexico, Central and northern South America to Suriname (Williams 1984, Pérez Farfante & Kensley 1997).

Sicyonia typica (Boeck, 1864)

Known range.—Western Atlantic: Wrightsville Beach, North Carolina, through the Gulf of Mexico; Cuba through the West Indies; Caribbean coasts of Central and South America to Rio Grande do Sul, Brazil (Williams 1984, Pérez Farfante & Kensley 1997, D'Incao 1998, Caetano da Costa et al. 2000).

Family Solenoceridae Wood-Mason, 1891

Remarks.—Pérez Farfante & Kensley (1997) diagnosed the family and genera, presented a key to the genera based on morphological characters, and illustrated important diagnostic characters for the genera included in their study.

▶ *Hadropenaeus affinis* (Bouvier, 1906)

Remarks.—Description, affinities, comparisons, and illustrations are included in Pérez Farfante (1977a). This species occurs between 165–570 m (Pérez Farfante 1977a).

Known range.—Western Atlantic: North Carolina to Florida; Gulf of Mexico; Caribbean; Eastern Atlantic: Cape Verde Islands (Pérez Farfante 1977a, Pérez Farfante & Kensley 1997).

▶ *Hadropenaeus modestus* (Smith, 1885)

Remarks.—Description, affinities, comparisons, and illustrations are included in Pérez Farfante (1977a). This species occurs at depths of 150–550 m (Pérez Farfante 1977a).

Known range.—Western Atlantic: Delaware to Florida, Gulf of Mexico, Bahamas, Caribbean, and northern Brazil (Pérez Farfante 1977a, Pérez Farfante & Kensley 1997).

Mesopenaeus tropicalis (Bouvier, 1905)

Known range.—Western Atlantic: northeast of Cape Lookout, North Carolina, to southern Brazil, including Gulf of Mexico (Williams 1984, Pérez Farfante & Kensley 1997).

▶ ★ *Pleoticus robustus* (Smith, 1885)

Hymenopenaeus robustus Smith.—Williams, 1984:484.

Remarks.—Williams (1984) considered this species to be extralimital. Pérez Farfante (1977a) concluded that *Hymenopenaeus* comprised a complex of genera and consequently transferred *H. robustus* and two other species (*H. muelleri* and *H. steindachneri*) to the genus *Pleoticus* Bate, 1888. Description, affinities, comparisons, and illustrations of *P. robustus* were included in Pérez Farfante (1977a) and Squires (1990). This species occurs at 70–915 m, but is most abundant between 250–475 m (Pérez Farfante 1977a, Rodríguez 1993).

Known range.—Western Atlantic: Massachusetts to Gulf of Mexico; Caribbean Sea to French Guiana (Pérez Farfante 1977a, 1988; Squires 1990; Pérez Farfante & Kensley 1997).

Solenocera atlantidis Burkenroad, 1939

Known range.—Western Atlantic: North Carolina to southern Brazil, including Gulf of Mexico and West Indies (Williams 1984, Pérez Farfante & Kensley 1997).

Solenocera necopina Burkenroad, 1939

Known range.—Western Atlantic: off Oregon Inlet, North Carolina, to Uruguay, including Gulf of Mexico and Bahamas (Williams 1984, Pérez Farfante & Kensley 1997).

Solenocera vioscai Burkenroad, 1934

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina, to Florida and Gulf of Mexico (Williams 1984, Pérez Farfante & Kensley 1997).

Superfamily Sergestoidea Dana, 1852

Family Luciferidae De Haan, 1849

Remarks.—Pérez Farfante & Kensley (1997) provided a family diagnosis and illustrated important diagnostic characters.

Lucifer faxoni Borradaile, 1915

Known range.—Western Atlantic: Long Island Sound, New York, to Rio Grande do Sul, Brazil, including Gulf of Mexico, Caribbean Sea, and Bermuda (Williams 1984, Pérez Farfante & Kensley 1997, D'Incao 1998); Eastern Atlantic: Senegal; Congo (Williams 1984, Pérez Farfante & Kensley 1997).

► *Lucifer typus* H. Milne Edwards, 1837

Remarks.—Williams (1984) did not include this species in his study because depth of occurrence was centered beyond the limits of bathymetric range he considered. *Lucifer typus* is usually found offshore (>180 m bottom depth), but occasionally is collected in shallower waters (Bowman and McCain 1967). Bowman and McCain (1967) provided information on diagnostic characters.

Known range.—Western Atlantic: Newfoundland; east coast of United States (Maine to Florida); Sargasso Sea; Brazil; Eastern Atlantic: Mediterranean Sea; Cape of Good Hope; east coast of South Africa; East-Cental Pacific: Baja California; Gulf of California to north of 4°; Indo-West Pacific: Bay of Bengal; Philippines; Queensland, Australia (Abele and Kim 1986, Pérez Farfante & Kensley 1997, D'Incao 1998).

Family Sergestidae Dana, 1852

Remarks.—Pérez Farfante & Kensley (1997) provided family and generic diagnoses and illustrations of diagnostic characters.

Acetes americanus carolinae Hansen, 1933

Remarks.—Pérez Farfante and Kensley (1997) considered subspecific designation valid.

Known range.—Western Atlantic: lower Chesapeake Bay through Gulf of Mexico to Panama; Suriname; French Guiana (Williams 1984, Pérez Farfante and Kensley 1997).

Suborder Pleocyemata Burkenroad, 1963

Infraorder Stenopodidea Claus, 1872

Family Stenopodidae Claus, 1872

Stenopus hispidus (Olivier, 1811)

Known range.—Western Atlantic: Bermuda; North Carolina to southern Florida, through the Gulf of Mexico to Fernando de Noronha and Espírito Santo, Brazil (Williams 1984, Coelho & Ramos-Porto 1998a); Central Pacific: Hawaii; Indo-West Pacific: Durban, South Africa; Red Sea; Japan; western Australia; eastern Australia through New Caledonia; New Hebrides; Lord Howe

Island; northern New Zealand to Tuamotu Archipelago (Williams 1984).

Stenopus scutellatus Rankin, 1898

Known range.—Western Atlantic: Bermuda; South Carolina; Gulf of Mexico to Fernando de Noronha and Rio Grande do Norte, Brazil (Williams 1984, Coelho & Ramos-Porto 1998a).

Infraorder Caridea Dana, 1852
Superfamily Pasiphaeoidea Dana, 1852
Family Pasiphaeidae Dana, 1852

Remarks.—Subgeneric designations within *Leptochela* are considered valid by Holthuis (1993).

Leptochela (*Leptochela*) *papulata* Chace, 1976

Known range.—Western Atlantic: Georges Bank, off Massachusetts; North Carolina to Georgia; eastern Gulf of Mexico (Williams 1984).

Leptochela (*Leptochela*) *serratorbita* Bate, 1888

Known range.—Western Atlantic: Beaufort, North Carolina, to South Carolina; western Gulf of Mexico; Florida Keys to Leeward Islands; Amapá to Pernambuco, and São Paulo, Brazil (Williams 1984, Ramos-Porto & Coelho 1998).

Leptochela (*Proboloura*) *carinata* Ortmann, 1893

Known range.—Western Atlantic: Georges Bank, off Massachusetts; South Carolina; Gulf of Mexico, through Bahamas to Alagoas, Brazil (Williams 1984, Ramos-Porto & Coelho 1998).

Pasiphaea multidentata Esmark, 1866

Known range.—Western Atlantic: southeast of Greenland to Cape Cod, Massachusetts, including Gulf of St. Lawrence and Gulf of Maine; Eastern Atlantic: Iceland; Norway to British Isles; Bay of Biscay; Mediterranean to Adriatic (Williams 1984, Squires 1990).

Superfamily Bresilioidea Calman, 1896
★ Family Disciadidae Rathbun, 1902

Remarks.—Martin & Davis (2001) recognized the family Disciadidae. Species of *Discias* were previously considered part of the Bresiliidae (Williams 1984).

Discias atlanticus Gurney, 1939

Remarks.—Criales & Lemaitre (1997) reported the discovery of this species inhabiting tubes of the polychaete *Chaetopterus variopedatus.* This represents the first reported occurrence of this symbiotic relationship for these species. These authors also discussed morphological sexual dimorphism.

Known range.—Western Atlantic: Bermuda; Savannah, Georgia; Fort Pierce, Florida; Gulf of Mexico; Guadeloupe; Colombia; Maranhão and Ceará, Brazil (Kensley 1983, Williams 1984, Criales & Lemaitre 1997, Ramos-Porto & Coelho 1998); Eastern Atlantic: Cape Verde Islands; Gabon (Williams 1984); Indian Ocean: northern Kenya (Williams 1984); Red Sea; Western Pacific: Great Barrier Reef, Australia (Kensley 1983).

► *Discias vernbergi* Boothe & Heard, 1987

Remarks.—Boothe & Heard (1987:506) described this species and provided a diagnosis, illustrations, and size and sexual maturity information. This species occurs at 54–74 m (Boothe & Heard 1987).

Known range.—Western Atlantic: Georgia; eastern Gulf of Mexico (west Florida) (Boothe & Heard 1987).

Superfamily Palaemonoidea Rafinesque, 1815
► Family Anchistioididae Borradaile, 1915

Anchistioides antiguensis (Schmitt, 1924)

Remarks.—This species was listed under family Palaemonidae, subfamily Pontoniinae, in Williams (1984). Chace (1992) provided evidence for familial separation of *Anchistioides*; Holthuis (1993) also adopted this arrangement.

Known range.—Western Atlantic: Bermuda; South Carolina; west Florida through West Indies to Maranhão, Pernambuco, and Alagoas, Brazil (Williams 1984, Ramos-Porto & Coelho 1998).

Family Gnathophyllidae Dana, 1852

Gnathophyllum modestum Hay, 1917

Known range.—Western Atlantic: Beaufort, North Carolina; Biscayne Bay, Florida (Williams 1984).

Family Palaemonidae Rafinesque, 1815

Subfamily Palaemoninae Rafinesque, 1815

Remarks.—Subgeneric designations within *Palaemonetes* are considered valid by Holthuis (1993).

Brachycarpus biunguiculatus (Lucas, 1849)

Remarks.—This species occurs from shallow water to 105 m (Ramos-Porto & Coelho 1998).

Known range.—Western Atlantic: Bermuda; Cape Fear, North Carolina; western Gulf of Mexico through West Indies to Curaçao and Old Providence Island (Williams 1984); Amapá to Espírito Santo and Fernando de Noronha Archipelago, Brazil (Ramos-Porto & Coelho 1998); Eastern Atlantic: Mediterranean; West Africa; Eastern Pacific: west American coast; Indo-Pacific (Williams 1984).

Leander tenuicornis (Say, 1818)

Known range.—Western Atlantic: Newfoundland Banks to Falkland Islands; tropical and subtropical waters worldwide except for west coast of Americas (Williams 1984).

Macrobrachium acanthurus (Wiegmann, 1836)

Known range.—Western Atlantic: Neuse River estuary, North Carolina, to Rio Grande do Sul, Brazil (Williams 1984, Ramos-Porto & Coelho 1998).

Macrobrachium carcinus (Linnaeus, 1758)

Known range.—Western Atlantic: St. Augustine, St. Johns County and Silver Glen Springs, Marion County, Florida, to Rio Grande do Sul, Brazil, including Gulf of Mexico and Caribbean Sea (Williams 1984, Ramos-Porto & Coelho 1998).

Macrobrachium ohione (Smith, 1874)

Known range.—Western Atlantic: James River, Hopewell, Virginia, to southern Georgia; coastal Alabama to Aransas Bay, Texas; Freshwater: Mississippi River and tributaries upstream to McCurtain County, Oklahoma; Fort Smith, Arkansas; St. Louis, Missouri; Washington County, Ohio (Williams 1984).

Macrobrachium olfersii (Wiegmann, 1836)

Known range.—Western Atlantic: lower Cape Fear River, North Carolina; Florida; Louisiana; Texas; Veracruz, Mexico, to Rio Grande do Sul, Brazil (Williams 1984, Ramos-Porto & Coelho 1998).

Palaemonetes (*Palaemonetes*) *intermedius* Holthuis, 1949

Known range.—Western Atlantic: Vineyard Sound, Massachusetts, to Port Aransas Texas; Bahía de la Ascensión, Quintana Roo, Mexico (Williams 1984).

Palaemonetes (*Palaemonetes*) *pugio* Holthuis, 1949

Known range.—Western Atlantic: Verte River, west of St. Modeste, Quebec, through Nova Scotia to Corpus Christi, Texas; Matamoros, Tamaulipas, to Campeche, Mexico (Williams 1984, Squires 1990, Rodríguez-Almaraz et al. 2000).

Palaemonetes (*Palaemonetes*) *vulgaris* (Say, 1818)

Known range.—Western Atlantic: southern Gulf of St. Lawrence to Cameron County, Texas; Rio Champoton and near Progreso, Yucatán, Mexico (Williams 1984, Squires 1990).

Subfamily Pontoniinae Kingsley, 1878

Remarks.—Subgeneric designations within *Periclimenes* are considered valid by Holthuis (1993).

Neopontonides beaufortensis (Borradaile, 1920)

Known range.—Western Atlantic: Beaufort, North Carolina, to Grand Isle, Louisiana; Caledonia Bay, Panama; Antigua (Williams 1984).

Periclimenaeus schmitti Holthuis, 1951

Known range.—Western Atlantic: Bogue Sound, Black Rocks off New River and Lockwoods Folly River, North Carolina; Dry Tortugas, Florida (Williams 1984).

Periclimenaeus wilsoni (Hay, 1917)

Known range.—Western Atlantic: Beaufort, North Carolina; Sapelo Island, Georgia; Loggerhead Key, near Dry Tortugas; Franklin County, Florida (Williams 1984).

★ *Periclimenes* (*Harpilius*) *americanus* (Kingsley, 1878)

Periclimenes americanus (Kingsley).—Williams, 1984:83.

Known range.—Western Atlantic: Beaufort, North Carolina, to western Gulf of Mexico, through West Indies to Aruba; Amapá to Pernambuco, Espírito Santo and São Paulo, Brazil (Williams 1984, Ramos-Porto & Coelho 1998).

★ *Periclimenes* (*Periclimenes*) *iridescens* Lebour, 1949

Periclimenes iridescens Lebour.—Williams, 1984:85.

Known range.—Western Atlantic: Bermuda; off Cape Hatteras, North Carolina; southern and northwestern Florida; Tobago; Cubagua Island, Venezuela (Williams 1984).

★ *Periclimenes* (*Periclimenes*) *longicaudatus* (Stimpson, 1860)

Periclimenes longicaudatus (Stimpson).—Williams, 1984:86.

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to southwestern Florida; West Indies to São Paulo, Brazil (Williams 1984).

★ *Periclimenes* (*Periclimenes*) *pedersoni* Chace, 1958

Periclimenes pedersoni Chace.—Williams, 1984:87.

Known range.—Western Atlantic: off Cape Lookout, North Carolina; off northwest Florida (?); Bahamas through West Indies to Bonaire; Belize (Williams 1984).

Pontonia domestica Gibbes, 1850

Known range.—Western Atlantic: Atlantic Beach near Beaufort Inlet, North Carolina, through Gulf of Mexico to South Padre Island, Texas; Bahamas; Caribbean coast of Costa Rica (Williams 1984, Strenth & Chace 1995, Vargas & Cortés 1999); Eastern Atlantic: Madeira (Williams 1984).

► *Pontonia manningi* Fransen, 2000

Remarks.—Fransen (2000:101) described this species and provided illustrations, size, color, and host information. This species is found at shallow depths to 80 m (Fransen 2000).

Known range.—Western Atlantic: North Carolina to Caribbean Sea; Gulf of Mexico;

Eastern Atlantic: Canary Islands; Cape Verde Islands (Fransen 2000).

Superfamily Alpheoidea Rafinesque, 1815

Family Alpheidae Rafinesque, 1815

► *Alpheus angulosus* McClure, 2002

Alpheus angulatus McClure, 1995.

Remarks.—McClure (1995:85) described this species and provided a diagnosis, illustrations, color, size, and habitat information. McClure (2002) provided a replacement name (*A. angulosus*) for this species because *angulatus* had previously been used by Coutière (1905) for a subspecies of *Alpheus* (*A. strenuus* var. *angulatus*) from the Indo-Pacific. Comparisons of morphological variation among species, including *A. angulosus,* of the *edwardsii* group of *Alpheus* occurring in the northern Gulf of Mexico and northwestern Atlantic were provided in McClure (1995) and McClure & Wicksten (1997).

Known range.—Western Atlantic: Beaufort, North Carolina, to Quintana Roo, Mexico, including northern Gulf of Mexico; Haiti (McClure 1995).

Alpheus armillatus H. Milne Edwards, 1837

Known range.—Western Atlantic: Bermuda; North Carolina through Gulf of Mexico and West Indies to Santa Catarina, Brazil (Williams 1984, Christoffersen 1998).

► *Alpheus estuariensis* Christoffersen, 1984

Remarks.—Christoffersen (1984:191) described this species and provided illustrations, color description, and ecological information. This species occurs from the intertidal region to depths of 22 m (Christoffersen 1984).

Known range.—Western Atlantic: east coast of Florida (near Jacksonville and Indian River region); northern Gulf of Mexico; Cuba; Dominican Republic; Trinidad; Curaçao; Ceará to Paraná, Brazil (Christoffersen 1984, 1998; McClure & Wicksten 1997). Christoffersen (1998) reported that his earlier records (Christoffersen 1984) of *A. estuariensis* in the Gulf of Mexico are actually *A. angulatus* (= *A. angulosus,* see above). However, McClure & Wicksten (1997) have reported *A. estuariensis* occurring in the northern Gulf of Mexico.

Alpheus formosus Gibbes, 1850

Known range.—Western Atlantic: Bermuda; near Beaufort, North Carolina, through Gulf of Mexico and West Indies to São Paulo, Brazil (Williams 1984, Christoffersen 1998).

Alpheus heterochaelis Say, 1818

Remarks.—McClure (1995) redescribed this species and designated a neotype to clarify taxonomic confusion surrounding this species. Comparisons of morphological variation among species, including *A. heterochaelis,* of the *edwardsii* group of *Alpheus* occurring in northern Gulf of Mexico and northwestern Atlantic were provided in McClure (1995) and McClure & Wicksten (1997).

Known range.—Western Atlantic: lower Chesapeake Bay to Aransas County, Texas; Bermuda; Cuba; Curaçao; Suriname; Pará to Paraíba, Brazil (Williams 1984, McClure 1995, Christoffersen 1998).

Alpheus normanni Kingsley, 1878

Remarks.—Based on material examined from both western Atlantic and eastern Pacific locations, Kim & Abele (1988) concluded that variation between Pacific and Atlantic forms of *A. normanni* was sufficient to recognize two species. This decision has not gained universal acceptance since *A. normanni* continues to be used for the Atlantic form. If *A. normanni* is restricted to the eastern Pacific as suggested by Kim & Abele (1988), then western Atlantic specimens would be known as *A. packardii*

Kingsley, 1880 (Christoffersen 1998). Further research is needed to resolve this taxonomic question.

Known range.—Western Atlantic: around Cape Charles, Virginia, and lower Chesapeake Bay through Gulf of Mexico and West Indies to São Paulo, Brazil; Bermuda; Eastern Pacific: Gulf of California; Panama (Williams 1984, Christoffersen 1998).

★ *Automate dolichognatha* De Man, 1888

Automate gardineri Coutière.—Williams, 1984:100.

Remarks.—Chace (1988) placed *A. gardineri* and three other nominal species in the synonymy of 'the variable and wide-ranging' *A. dolichognatha.*

Known range.—Western Atlantic: Beaufort Inlet, North Carolina; Yucatán; Virgin Islands; Barbados; Rio de Janeiro, Brazil; Indo-Pacific: Red Sea to Samoa (Williams 1984, Christoffersen 1998). Chace (1988) considered the range to be pantropical, except for the eastern Atlantic.

Automate evermanni Rathbun, 1901

Known range.—Western Atlantic: Virginia to Texas; Puerto Rico; São Paulo and Rio Grande do Sul, Brazil; Eastern Atlantic: Cape Verde Islands; Liberia to Nigeria (Williams 1984, Chace 1988, Christoffersen 1998).

Leptalpheus forceps Williams, 1965

Known range.—Western Atlantic: North Carolina to Sergipe, Brazil (Williams 1984, Christoffersen 1998).

Synalpheus fritzmuelleri Coutière, 1909

Known range.—Western Atlantic: Bermuda; Beaufort, North Carolina, to Santa Catarina, Brazil (Williams 1984, Christoffersen 1998); South Atlantic: St. Helena Island; Eastern Pacific: Baja California (Williams 1984).

Synalpheus longicarpus (Herrick, 1891)

Known range.—Western Atlantic: Beaufort, North Carolina, to west Flower Garden Reef, southeast of Galveston, Texas; Yucatán, Mexico through West Indies to Rio de Janeiro, Brazil (Williams 1984, Christoffersen 1998).

Synalpheus minus (Say, 1818)

Known range.—Western Atlantic: Bermuda; Cape Hatteras, North Carolina, to São Paulo, Brazil (Williams 1984, Christoffersen 1998).

Synalpheus townsendi Coutière, 1909

Known range.—Western Atlantic: Bermuda; Beaufort, North Carolina, to Rio de Janeiro, Brazil; Rocas Atoll, Brazil (Williams 1984, Christoffersen 1998); Eastern Pacific: Gulf of California (Williams 1984).

Family Hippolytidae Dana, 1852

▶ *Bythocaris nana* Smith, 1885

Remarks.—This species was considered extralimital by Williams (1984). Abele & Martin (1989) redescribed the species, and provided illustrations and developmental notes. *Bythocaris nana* occurs at 79–1175 m depth and is not common (Abele & Martin 1989).

Known range.—Western Atlantic: Martha's Vineyard, Massachusetts, to southern Florida; northeastern Gulf of Mexico (Abele & Martin 1989).

▶ *Caridion gordoni* (Bate, 1858)

Remarks.—Williams (1984) considered this species to be extralimital. Squires (1990) provided a description and illustrations. This species occurs at 5–421 m depth (Williams & Wigley 1977).

Known range.—Western Atlantic: southwestern Newfoundland to Chesapeake Bay; North Atlantic: Iceland; Eastern Atlantic: northern Europe to Bay of Biscay (Williams 1984, Squires 1990).

Eualus fabricii (Krøyer, 1841)

Known range.—Western Atlantic: Hudson Bay, Foxe Basin, and northwestern Greenland to Cape Cod; North Pacific: Chukchi Sea; Bering Sea to British Columbia; Western Pacific: Sea of Okhotsk to Sea of Japan (Williams 1984, Squires 1990).

Eualus gaimardii (H. Milne Edwards, 1837)

Remarks.—Squires (1990) recognized two subspecies, *E. g. gaimardii* and *E. g. belcheri,* both of which show considerable variation in diagnostic features and overlap completely in distribution. Williams (1984), however, believed that observed morphological variation was not sufficient to warrant recognition of more than one species among this material.

Known range.—Western Atlantic: Greenland and Baffin Island to Cape Cod; Eastern Atlantic: Spitsbergen to North Sea; Arctic Ocean: Point Barrow to Siberia; North Pacific: south to Sitka, Alaska (Williams 1984, Squires 1990).

Eualus pusiolus (Krøyer, 1841)

Known range.—Western Atlantic: Gulf of St. Lawrence to Cape Henry, Virginia; Northeastern Atlantic: Iceland; Murman Sea to Channel Islands, southward along Bay of Biscay to Spain; Catalonian coast of Spain; North Pacific: Chukchi and Bering seas to British Columbia and Washington; Western Pacific: Sea of Okhotsk and Sea of Japan (Williams 1984, Squires 1990).

Exhippolysmata oplophoroides (Holthuis, 1948)

Remarks.—This species occurs over a bathymetric range of 5–45 m (Rodríguez 1993, Caetano da Costa et al. 2000).

Known range.—Western Atlantic: Cape Fear, North Carolina, to Port Aransas, Texas; Guyana to northern Uruguay (Williams 1984, Caetano da Costa et al. 2000).

Hippolyte coerulescens (Fabricius, 1775)

Known range.—Tropical and subtropical Atlantic Ocean, including south of the Grand Banks in the Gulf Stream; and Sargasso Sea (Williams 1984, Squires 1990).

★ *Hippolyte obliquimanus* Dana, 1852

Hippolyte curacaoensis Schmitt.—Williams, 1984:117.

Remarks.—Udekem d'Acoz (1997) examined topotypic specimens of *Hippolyte obliquimanus* Dana and *H. exilirostratus* Dana and determined that these two nominal species are identical. He also concluded that *H. curacaoensis* Schmitt is conspecific with *H. obliquimanus.* Udekem d'Acoz (1997) redescribed *H. obliquimanus* based on this new information.

Known range.—Western Atlantic: Beaufort and Sneads Ferry, North Carolina; Puerto Rico; West Indies from Cuba to Curaçao; Venezuela to Santa Catarina, Brazil (Williams 1984, Udekem d'Acoz 1997, Christoffersen 1998).

Hippolyte pleuracanthus (Stimpson, 1871)

Known range.—Western Atlantic: Connecticut to North Carolina (Williams 1984).

Hippolyte zostericola (Smith, 1873)

Known range.—Western Atlantic: southern Massachusetts; Bermuda; North Carolina to Yucatán; Trinidad; Curaçao; Ceará, Brazil (Williams 1984, Christoffersen 1998). Christoffersen (1998) noted that previously reported occurrences of this species in Brazil may actually refer to *H. obliquimanus.*

Latreutes fucorum (Fabricius, 1798)

Known range.—Western Atlantic: Newfoundland to Brazil (Pernambuco to Bahia), including Gulf of Mexico south to Bahía de la Ascensión, Quintana Roo, Mexico; Eastern Atlantic: Azores; Cape Verde Islands

(Williams 1984, Christoffersen 1998, Rodríguez-Almaraz et al. 2000).

Latreutes parvulus (Stimpson, 1866)

Known range.—Western Atlantic: Beaufort, North Carolina, to Buenos Aires, Argentina; Eastern Atlantic: West Africa (Williams 1984, Christoffersen 1998).

Lebbeus groenlandicus (Fabricius, 1775)

Known range.—Western Atlantic: Hudson Bay to Greenland, southward to Rhode Island; North Pacific: Arctic Canada, southern Chukchi Sea through Bering Sea to Puget Sound; Western Pacific: Okhotsk Sea southward to Vladivostok (Williams 1984, Squires 1990).

★ *Lebbeus microceros* (Krøyer, 1841)

Lebbeus zebra (Leim).—Williams, 1984: 125.

Remarks.—Holthuis (1947) recognized both *L. microceros* and *L. zebra* as valid species. Couture & Trudel (1968) noted great similarity between these nominal species and commented that they might be synonymous, but rarity of material prevented an adequate evaluation of these taxa (Williams 1984). Squires (1990) placed *L. zebra* into the synonymy of *L. microceros* without comment or explanation for this action. Chace (1997) also listed *L. zebra* in the synonymy of *L. microceros.*

Known range.—Western Atlantic: Southern Greenland; Foxe Basin; Ungava Bay; Newfoundland to New Brunswick, including Gulf of St. Lawrence to southeast of Isles of Shoals; North Pacific: possibly from Bering Sea to Kamchatka; Eastern Pacific: Checleset Bay, Vancouver Island (Williams 1984, Squires 1990).

Lebbeus polaris (Sabine, 1824)

Known range.—Circumarctic; Western Atlantic: southward to Chesapeake Bay; North Pacific: Okhotsk Sea; Bering Sea to British Columbia; Eastern Atlantic: Arctic to the Hebrides (Williams 1984, Squires 1990).

Lysmata rathbunae Chace, 1970

Known range.—Western Atlantic: Bermuda; Cape Fear, North Carolina; east coast of Florida to Yucatán; Venezuela (Williams 1984).

Lysmata wurdemanni (Gibbes, 1850)

Known range.—Western Atlantic: New Jersey to Port Aransas, Texas; Suriname; French Guiana; Ceará and Bahia to Rio Grande do Sul, Brazil (Williams 1984, Christoffersen 1998).

Spirontocaris liljeborgii
(Danielssen, 1859)

Known range.—Western Atlantic: Foxe Channel and Davis Strait; Greenland, to off Delaware Bay; Northeastern Atlantic: Iceland; Spitsbergen; Murman coast to south coast of England; west and southwestern Ireland; Arctic: Alaska (Williams 1984, Squires 1990).

Spirontocaris phippsii (Krøyer, 1841)

Known range.—Circumarctic; Western Atlantic: Cornwallis Island; Hudson Bay to Martha's Vineyard; North Atlantic: Spitsbergen to southern Norway; Britain; Arctic: north of Siberia; Beaufort Sea; North Pacific: Bering Sea to Siberian east coast; Shumagin Islands, Alaska (Williams 1984, Squires 1990).

Spirontocaris spinus (Sowerby, 1805)

Known range.—Circumarctic; Western Atlantic: Hudson Bay; Foxe Basin; Greenland, southward to Massachusetts Bay; North Atlantic: Spitsbergen to northern North Sea and Irish Sea; North Pacific: Plover Bay, Siberia; Bering Sea; Shumagin Islands, Alaska; Puget Sound, Washington; Western Pacific: Okhotsk Sea; Sea of Japan (Williams 1984, Squires 1990).

Thor dobkini Chace, 1972

Known range.—Western Atlantic: off Shackleford Bank, North Carolina, to Yucatán; Louisiana; north coast of Cuba (Williams 1984).

Thor floridanus Kingsley, 1878

Known range.—Western Atlantic: Black Rocks off New River, North Carolina (?), to Yucatán (Williams 1984).

Thor manningi Chace, 1972

Known range.—Western Atlantic: Beaufort, North Carolina, to Yucatán, through West Indies to Curaçao; Brazil (Paraíba, Bahia, and São Paulo); Eastern Pacific: Islas Tres Marías, Mexico (Williams 1984, Christoffersen 1998).

Tozeuma carolinense Kingsley, 1878

Known range.—Western Atlantic: Vineyard Sound, Massachusetts, to Colón, Panama, including Gulf of Mexico; through West Indies to Curaçao; Paraíba to Alagoas and São Paulo, Brazil (Williams 1984, Christoffersen 1998).

Tozeuma serratum A. Milne-Edwards, 1881

Known range.—Western Atlantic: Nonamesset Island, Massachusetts; off Cape Hatteras and Cape Lookout, North Carolina; Cape Canaveral; extreme southern and northwestern Florida; Barbados; Colombia; off Rio de Janeiro and São Paulo, Brazil (Williams 1984, Christoffersen 1998).

▶ *Trachycaris rugosa* (Bate, 1888)

Remarks.—Based on available information, Williams (1984) presumed this species to occur beyond the southern limits of the region. However, Criales (1992) recorded *T. rugosa* from southern areas within this region. Criales (1992) provided a redescription of the species, illustrations, and commented on color, interspecific comparisons, and sexual dimorphism.

Known range.—Western Atlantic: South Carolina through the Gulf of Mexico; Caribbean Sea to Santa Marta, Colombia (Criales 1992).

Family Ogyrididae Holthuis, 1955

Ogyrides alphaerostris (Kingsley, 1880)

Known range.—Western Atlantic: Virginia to Rio Grande do Sul, Brazil, including Gulf of Mexico (Williams 1984, Christoffersen 1998).

Ogyrides hayi Williams, 1981

Known range.—Western Atlantic: Beaufort, North Carolina, to Sebastian Inlet, Florida; northwestern Florida to Mississippi; Puerto Rico; Pernambuco and São Paulo, Brazil (Williams 1984, Christoffersen 1998).

▶ Superfamily Processoidea Ortmann, 1890

Remarks.—Previously the family Processidae was placed in the superfamily Alpheoidea (Williams 1984). Chace (1992) erected the superfamily Processoidea, which consists of a single family (Processidae). Holthuis (1993) also adopted this arrangement.

Family Processidae Ortmann, 1890

Nikoides schmitti Manning & Chace, 1971

Known range.—Western Atlantic: east of Cape Lookout, North Carolina; Biscayne Bay and Dry Tortugas, Florida; Guadeloupe; the Guianas (Williams 1984).

Processa bermudensis (Rankin, 1900)

Known range.—Western Atlantic: Bermuda; Cape Hatteras, North Carolina, to northwestern Florida; Veracruz, Mexico; Cuba; Puerto Rico; Guadeloupe; Venezuela; Bahia, Rio de Janeiro and Paraná, Brazil (Williams 1984, Christoffersen 1998).

Processa fimbriata Manning & Chace, 1971

Known range.—Western Atlantic: off New River, North Carolina, to Rio de Janeiro, Brazil (Williams 1984, Christoffersen 1998).

Processa guyanae Holthuis, 1959

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to eastern Gulf of Mexico, including northern coast of Cuba; Suriname to Uruguay (Williams 1984, Christoffersen 1998).

Processa hemphilli Manning & Chace, 1971

Known range.—Western Atlantic: east of Cape Lookout and Bogue Sound, North Carolina; east coast of Florida; northwest Florida; Guadeloupe; Brazil to Buenos Aires (Williams 1984, Christoffersen 1998).

Processa profunda Manning & Chace, 1971

Known range.—Western Atlantic: southeast of Cape Hatteras, North Carolina; off South Carolina; Gulf of Mexico, off southern and western Florida; Suriname to Uruguay (Williams 1984, Christoffersen 1998).

Processa vicina Manning & Chace, 1971

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; northwest Florida; off Isla Margarita, Venezuela (Williams 1984).

Superfamily Pandaloidea Haworth, 1825

Remarks.—Christoffersen (1989) proposed a phylogeny of this taxon.

Family Pandalidae Haworth, 1825

★ *Atlantopandalus propinqvus* (G.O. Sars, 1870)

Pandalus propinquus G.O. Sars.—Williams, 1984:156.

Remarks.—In his revision of the genus *Pandalus*, Komai (1999) transferred *Pandalus propinqvus* to a monotypic genus *Atlantopandalus*; a description was provided. Additionally, Komai (1999) stated that G.O. Sars consistently spelled the name of this species as '*propinqvus*' in the original description and that this spelling should be used. This species occurs at depths of 20–2180 m (Komai 1999).

Known range.—Western Atlantic: Greenland; Davis Strait to Delaware Bay, including Gulf of St. Lawrence and Gulf of Maine; North Atlantic: Iceland; Eastern Atlantic: Norway to the British Isles; Bay of Biscay (Komai 1999).

Dichelopandalus leptocerus (Smith, 1881)

Known range.—Western Atlantic: Gulf of St. Lawrence and St. Mary's Bay, Newfoundland, to off Oregon Inlet, North Carolina; North Pacific: Shumagin Bank, Alaska (Williams 1984, Squires 1990).

▶ *Heterocarpus ensifer* A. Milne-Edwards, 1881

Remarks.—Diagnostic characters of this species were reported in Crosnier & Forest (1973), Chace (1985), and Rodríguez (1993). This species occurs on muddy bottoms usually at 200–885 m (Chace 1985), but may be found at shallower depths (140 m; Rodríguez 1993).

Known range.—Western Atlantic: North Carolina to the Guianas, including the Gulf of Mexico and Caribbean Sea; Brazil (Chace 1985, Rodríguez 1993, Ramos-Porto & Coelho 1998).

Pandalus borealis Krøyer, 1838

Remarks.—The geographic range of *Pandalus borealis* has been reported as Arctic boreal in both Atlantic and Pacific oceans (Williams 1984). Recent studies (Squires 1992, Komai 1999) have demonstrated that morphological differences between Atlantic and Pacific 'varieties' were sufficient to warrant full species rank for both. *Pandalus borealis* is restricted to the Atlantic Ocean and considered a geminate species of *P. eous* Makarov from Pacific localities (Squires 1992).

Known range.—Western Atlantic: western Greenland to Gulf of Maine; North Atlantic: Barents Sea to the North Sea (Komai 1999).

Pandalus montagui Leach, 1814

Known range.—Arctic-boreal; Western Atlantic: Greenland and Hudson Bay to Rhode Island; North Atlantic: Iceland; White Sea; Eastern Atlantic: Norway to the western Baltic; North Sea; British Isles (Williams 1984, Squires 1990).

Pantomus parvulus A. Milne-Edwards, 1883

Known range.—Western Atlantic: Cape Lookout, North Carolina, to Yucatán; Puerto Rico; St. Croix; Suriname; Uruguay (Williams 1984, Christoffersen 1989).

▶ *Plesionika edwardsii* (Brandt, 1851)

Remarks.—Chan & Yu (1991) provided a diagnosis, color description, and interspecific comparisons. This species occurs on muddy bottoms at depths of 50–690 m (Rodríguez 1993), commonly at 200–400 m (Chan & Yu 1991).

Known range.—Western Atlantic: Virginia to Gulf of Mexico; Eastern Atlantic: Mediterranean to Angola; Indo-Pacific (Chan & Yu 1991).

▶ *Plesionika martia* (A. Milne-Edwards, 1883)

Remarks.—Williams (1984) considered this species to be extralimital. This species occurs at 165–2100 m depth (Williams & Wigley 1977).

Known range.—Western Atlantic: south of Nantucket, Massachusetts, to Brazil; Bermuda; Eastern Atlantic: southwest Ireland; Bay of Biscay to southern Africa; Mediterranean Sea; Central Pacific: Hawaii; Indo-Pacific: East Africa to Japan, including Gulf of Aden; New Zealand; southeastern Australia (Williams & Wigley 1977).

▶ *Plesionika tenuipes* (Smith, 1881)

Remarks.—Williams (1984) considered this species to be extralimital. This species occurs at 159–476 m depth (Williams 1984).

Known range.—Western Atlantic: Rhode Island to southern Florida; Gulf of Mexico (Williams 1984).

▶ ★ *Plesionika willisi* (L. H. Pequegnat, 1970)

Parapandalus willisi L. H. Pequegnat.—Williams, 1984:484.

Remarks.—Williams (1984) considered this species to be extralimital. Chace (1985) placed *Parapandalus* into the synonymy of *Plesionika.* This species occurs at 150–500 m depth (Williams & Wigley 1977).

Known range.—Western Atlantic: south of Martha's Vineyard, Massachusetts; Gulf of Mexico to French Guiana (Williams & Wigley 1977).

Superfamily Crangonoidea Haworth, 1825

Family Crangonidae Haworth, 1825

Argis dentata (Rathbun, 1902)

Remarks.—Komai (1997) evaluated the systematics of this species and several congeners to clarify their taxonomic status. In this study, he also provided a detailed description, illustrations, color, size and comparative information for *A. dentata.*

Known range.—Arctic-boreal; Western North Atlantic: northwest Greenland; Hudson Bay; Canadian Arctic islands to Nova Scotia; North Pacific: Bering Sea to Sitka, Alaska; southeast coast of Kamchatka; northern Okhotsk Sea (Komai 1997).

★ *Crangon* (*Crangon*) *septemspinosa* Say, 1818

Crangon septemspinosa Say.—Williams, 1984:159.

Remarks.—Subgeneric designation considered valid by Holthuis (1993).

Known range.—Primarily subarctic-boreal; Western Atlantic: northern Gulf of St. Lawrence to east Florida (Williams 1984, Squires 1990). Squires (1990) restricted the geographic range to the north Atlantic.

★ *Philocheras gorei* (Dardeau, 1980)

Pontophilus gorei Dardeau.—Williams, 1984:161.

Remarks.—Chace (1984) provided morphological evidence for recognizing *Philocheras* as a valid genus and removed it from the synonymy of *Pontophilus.* Christoffersen's (1988) phylogenetic analysis supported this arrangement. Bathymetric range was reported as 59–194 m (Christoffersen 1998).

Known range.—Western Atlantic: central Georgia; central eastern Florida; Gulf of Mexico (southwestern Florida, Cape San Blas and Padre Island, Texas); Rio de Janeiro, Brazil; Uruguay (Dardeau & Heard 1983, Williams 1984, Christoffersen 1988).

Pontophilus brevirostris Smith, 1881

Known range.—Western Atlantic: Gulf of Maine to eastern Gulf of Mexico, off Dry Tortugas, Florida; Cuba (Williams 1984).

Pontophilus norvegicus (M. Sars, 1861)

Known range.—Western Atlantic: Greenland to Maryland; North Atlantic: Iceland; Spitsbergen; Murman coast; Eastern Atlantic: northwestern Europe, including British Isles to Bay of Biscay; and Balearic Islands (Williams 1984, Squires 1990).

Sabinea sarsii Smith, 1879

Known range.—Western Atlantic: Davis Strait to southeast of Nantucket, Massachusetts; North Atlantic: Iceland; Eastern Atlantic: northern Europe (Williams 1984, Squires 1990).

Sabinea septemcarinata (Sabine, 1824)

Known range.—Western Atlantic: Hudson Bay and Greenland to Massachusetts Bay; Arctic-North Atlantic: Iceland (except south coast), Kara, White and Barents seas; Wrangel Island; Eastern Atlantic: north of Faroes; Norway (north of 67°N); British Isles; North Pacific: Arctic Canada and Alaska to Point Barrow and Chukchi Sea (Williams 1984, Squires 1990).

Sclerocrangon boreas (Phipps, 1774)

Known range.—Western Atlantic: Hudson Bay; east and west Greenland south to Cape Cod; Arctic-North Atlantic: Iceland; Spitsbergen; Kara and White seas; Franz Joseph Land; Novaya Zemlya; Eastern Atlantic: Faroes; Norway (north of approximately 67°N); Arctic-North Pacific: Arctic Canada, north coast of Alaska; Chukchi Sea south to British Columbia (Williams 1984, Squires 1990).

Infraorder Astacidea Latreille, 1802
Superfamily Nephropoidea Dana, 1852
Family Nephropidae Dana, 1852
Subfamily Nephropinae Dana, 1852
Homarus americanus H. Milne Edwards, 1837

Known range.—Western Atlantic: Newfoundland to Cape Hatteras, North Carolina; occasionally Wilmington, North Carolina and south Florida (Williams 1984, Cofer-Shabica & Nielsen 1988, Holthuis 1991). Williams (1984) noted that this species is occasionally found as far south as Wilmington, North Carolina. One specimen of *H. americanus,* however, was collected off southern Florida (Miami Beach, 252 m; Cofer-Shabica & Nielsen 1988), suggesting that the range of this species occasionally extends further south, especially in deeper waters.

► Subfamily Thymopinae Holthuis, 1974
► *Nephropsis aculeata* Smith, 1881

Remarks.—Species diagnosis provided in Hothuis (1991). This species occurs on mud or fine sand sediments at 137–824 m, but usually between 200–600 m (Holthuis 1991).

Known range.—Western Atlantic: Massachusetts to French Guiana, including Gulf of Mexico and Caribbean Sea; Bermuda (Holthuis 1991).

★ Infraorder Thalassinidea Latreille, 1831

Remarks.—Thalassinidea was considered a Section under the infraorder Anomura in Williams (1984:180). Poore (1994) proposed a phylogeny of the infraorder and provided a new classification, diagnoses, and keys to families and currently recognized genera.

Superfamily Callianassoidea Dana, 1852
Family Callianassidae Dana, 1852

Remarks.—Manning & Felder (1991) restricted this family as a result of their revision of the American Callianassidae. In a phylogenetic analysis of generic relationships within the family based on 93 adult morphological characters, Tudge et al. (2000) determined that the Callianassidae comprised a monophyletic group. Sakai (1999) presented very different conclusions regarding the composition of, and generic relationships within, the Callianassidae. Sakai's work, however, was not conducted within a phylogenetic framework and is widely regarded as controversial. More research is needed to resolve the composition and relationships of genera in this and related families and subfamilies.

Subfamily Callianassinae Dana, 1852

Remarks.—Tudge et al. (2000) conducted a phylogenetic analysis of relationships within the family Callianassidae based on adult morphological characters and they determined that the subfamily Callianassinae was a monophyletic group.

★ *Biffarius biformis* (Biffar, 1971)

Callianassa biformis Biffar.—Williams, 1984:182.

Remarks.—In a recent revision of the American Callianassidae, Manning & Felder (1991) concluded that *Callianassa* was a composite of numerous genera. Manning & Felder (1991) described the genus *Biffarius* and provided a diagnosis, illustrations, and comparative information regarding the genera within the subfamily Callianassinae.

Known range.—Western Atlantic: Bass River, Yarmouth, Nova Scotia; Nantucket Sound, Massachusetts; Chesapeake Bay (?); North Inlet, South Carolina, to McIntosh County, Georgia; Franklin County, northwest Florida (Williams 1984).

★ *Gilvossius setimanus* (De Kay, 1844)

Callianassa atlantica Rathbun.—Williams, 1984:180.

Remarks.—Manning (1987) addressed the status of *Gonodactylus setimanus* DeKay. He determined this species was valid as *Callianassa setimanus* (DeKay) and that it was the senior synonym of *Callianassa atlantica* Rathbun. Members of *Callianassa sensu stricto,* as restricted by Manning & Felder (1991), are not represented in the American fauna. The genus *Gilvossius* was described (Manning & Felder, 1992) with *Gonodactylus setimanus* DeKay (= *Callianassa atlantica* Rathbun) as the type species.

Known range.—Western Atlantic: Bass River, Nova Scotia, to Georgia; Franklin County, Florida (Williams 1984).

▶ *Necallianassa berylae* Heard & Manning, 1998

Remarks.—Heard & Manning (1998: 883–884) described this genus and species and provided illustrations and diagnostic comparisons with eastern Atlantic congeners. *Necallianassa berylae* occurs at depths of 35–75 m (Heard & Manning 1998).

Known range.—Western Atlantic: South Carolina and Georgia (Heard & Manning 1998).

Subfamily Callichirinae Manning & Felder, 1991

Remarks.—Tudge et al. (2000) conducted a phylogenetic analysis of relationships within the family Callianassidae utilizing adult morphological characters. They determined that the subfamily Callichirinae was a paraphyletic group and that more research is needed to resolve relationships within this group.

★ *Callichirus major* (Say, 1818)

Callianassa major Say.—Williams, 1984: 183.

Remarks.—Manning & Felder (1986) redefined *Callichirus* to remove the ambiguity surrounding previous concepts of this genus.

Known range.—Western Atlantic: Beaufort Inlet, North Carolina, to Cape Canaveral, Florida; Grand Terre Island to Timbalier Island, Louisiana; Sergipe to Santa Catarina, Brazil (Williams 1984, Rodrigues & Shimizu 1998).

Family Laomediidae Borradaile, 1903

Naushonia crangonoides Kingsley, 1897

Known range.—Western Atlantic: Bass River, Yarmouth, Nova Scotia; Vineyard Sound and Elizabeth Islands, Massachusetts, to Bogue Sound, North Carolina (Williams 1984).

Family Upogebiidae Borradaile, 1903

Upogebia affinis (Say, 1818)

Remarks.—Williams (1993) provided an improved diagnosis and detailed description of this species and noted that its southern limits of distribution are in Texas. Specimens identified as *U. affinis* from more southern locations (West Indies to São Paulo, Brazil) are actually *Upogebia paraffinis* Williams, 1993.

Known range.—Western Atlantic: Massachusetts to southern Texas (Williams 1993).

Superfamily Axioidea Huxley, 1879

Family Axiidae Huxley, 1879

► *Axius armatus* Smith, 1881

Remarks.—Kensley (2001) redescribed this species, provided illustrations, and compared *A. armatus* to its sympatric congener, *A. serratus.* Although Sakai & de Saint Laurent (1989) questioned the generic placement of this species, Kensley (2001) provided morphological evidence supporting placement of this species in the genus *Axius.* This apparently rare species occurs at depths of 108–260 m (Kensley 2001).

Known range.—Western Atlantic: Massachusetts to South Carolina (Kensley 2001).

Axius serratus Stimpson, 1852

Remarks.—Kensley (2001) redescribed, illustrated, and compared this species to its Atlantic congeners. This species occurs at depths of 19–220 m (Kensley 2001), which represents an increase in the maximum reported depth of occurrence.

Known range.—Western Atlantic: Nova Scotia to Maryland (Kensley 2001).

★ *Calaxius jenneri* (Williams, 1974)

Axiopsis jenneri (Williams).—Williams, 1984:185.

Remarks.—Sakai & de Saint Laurent (1989) described the genus *Calaxius* in their revision of the family Axiidae.

Known range.—Western Atlantic: Cape Lookout, North Carolina (Williams 1984).

► Family Calocarididae Ortmann, 1891

Remarks.—Kensley (1989) reinstated the Calocarididae Ortmann, which contained only *Calocaris,* and then expanded the family with the addition of several genera.

Calocaris templemani Squires, 1965

Known range.—Western Atlantic: Newfoundland to the Gulf of Maine; Cape Lookout, North Carolina (Williams 1984, Kensley 1989, Sakai & de Saint Laurent 1989, Squires 1990). The southernmost locality reported for this species is southeast of Cape Lookout, North Carolina (Williams 1984). This appears to be the only recorded occurrence of *C. templemani* this far south.

Infraorder Palinura Latreille, 1802
Superfamily Palinuroidea Latreille, 1802
Family Palinuridae Latreille, 1802
Panulirus argus (Latreille, 1804)

Remarks.—Based on mtDNA samples from individuals collected from nine locations between Bermuda and Venezuela, Silberman et al. (1994) hypothesized that *Panulirus argus* was genetically homogenous throughout the tropical western Atlantic and Caribbean. However, three individuals with distinctly different mtDNA haplotypes, collected off Miami, Florida, were identified (Silberman et al. 1994). Sarver et al. (1998) compared mtDNA sequences between western Atlantic-Caribbean populations and Brazilian lobsters and found sufficient differences to suggest that *P. argus* is a complex of two species or subspecies. In addition to genetic differences, characteristic color patterns were also identified distinguishing the Brazilian *P. argus* from the Caribbean form (Sarver et al. 1998). They recommended provisional recognition of two subspecies until formal taxonomic revision could be completed: *Panulirus argus argus* representing populations from Bermuda to Venezuela and *Panulirus argus westonii* representing populations from Brazil. Sarver et al. (2000) re-examined the genetically distinct individuals of Silberman et al. (1994) and determined that these unusual individuals were the provisionally recognized Brazilian form of *P. argus* (*P. argus westonii*). However, until formal revision is conducted, the taxonomic status of these subspecies remains uncertain.

Known range.—Western Atlantic: Bermuda; North Carolina to Rio de Janeiro, Brazil, including Gulf of Mexico and Caribbean Sea (Williams 1984, Holthuis 1991).

Family Scyllaridae Latreille, 1825
Subfamily Arctidinae Holthuis, 1985
▶ *Scyllarides aequinoctialis* (Lund, 1793)

Remarks.—This species was originally considered to occur outside the region, and therefore was not included in Williams (1984). Lyons (1970) provided a detailed description. *Scyllarides aequinoctialis* occurs on sandy or rocky bottoms at depths of 0–180 m, usually 1–64 m (Lyons 1970, Holthuis 1991).

Known range.—Western Atlantic: Bermuda; South Carolina to southern Brazil, including the Gulf of Mexico, Caribbean Sea, and West Indies (Holthuis 1991).

Scyllarides nodifer (Stimpson, 1866)

Known range.—Western Atlantic: Bermuda; Cape Lookout, North Carolina, to Yucatán, including Gulf of Mexico (Williams 1984, Holthuis 1991).

Subfamily Scyllarinae Latreille, 1825
Scyllarus americanus (Smith, 1869)

Known range.—Western Atlantic: Bogue Inlet, North Carolina, to Campeche Banks, Mexico; Venezuela (Williams 1984).

Scyllarus chacei Holthuis, 1960

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to Bahia, Brazil, including Gulf of Mexico, West Indies, and Caribbean Sea (Williams 1984, Coelho & Ramos-Porto 1998b).

Scyllarus depressus (Smith, 1881)

Known range.—Western Atlantic: Martha's Vineyard, Massachusetts; Cape Hatteras, North Carolina, to São Paulo, Brazil, including Gulf of Mexico and West Indies (Williams 1984).

Infraorder Anomura MacLeay, 1838
Superfamily Galatheoidea Samouelle, 1819
Family Galatheidae Samouelle, 1819
Galathea rostrata A. Milne-Edwards, 1880

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to southern Florida; northwestern Florida to Mississippi River delta; off Cape Catoche, Yucatán (Williams 1984).

▶ *Munida forceps* A. Milne-Edwards, 1880

Remarks.—Williams (1984) did not include this species in his study because the known geographic range and depth of occurrence were outside the region. This species is now known from off southern New England and Virginia within the region. *Munida forceps* occurs at 80–337 m (Williams 1988, Melo-Filho & Melo 1992). Melo-Filho & Melo (1992) provided a description, illustrations, and measurements; Williams (1988) provided a color description and figure of male carapace.

Known range.—Western Atlantic: Veatch and Lydonia Canyons, off southern New England (Williams 1988); Virginia; Florida; Gulf of Mexico; Antilles; Guianas; Brazil (Melo-Filho & Melo 1992).

Munida iris iris A. Milne-Edwards, 1880

Known range.—Western Atlantic: off Nova Scotia through southeastern Gulf of Mexico to near Cozumel Island, Yucatán; through Caribbean islands to Rio Grande do Sul, Brazil (Williams 1984, Squires 1990, Melo-Filho 1998).

Munida irrasa A. Milne-Edwards, 1880

Known range.—Western Atlantic: off Bermuda; off Cape Lookout, North Carolina, through eastern Gulf of Mexico; Caribbean Sea to Uruguay (Williams 1984).

Munida longipes A. Milne-Edwards, 1880

Known range.—Western Atlantic: Baltimore Canyon, off the coast of Maryland (Williams 1988) southward through Gulf of Mexico to Belize; through West Indies to Curaçao (Williams 1984); São Paulo to Rio Grande do Sul, Brazil (Melo-Filho 1998).

Munida pusilla Benedict, 1902

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to Straits of Florida, through eastern Gulf of Mexico to Yucatán; Colombia; Trinidad (Williams 1984); Amapá, Brazil (Melo-Filho 1998).

Munida valida Smith, 1883

Known range.—Western Atlantic: off Nova Scotia to Rio Grande do Sul, Brazil, including Gulf of Mexico and Caribbean (Williams 1984, Squires 1990, Melo-Filho & Melo 1992, Melo-Filho 1998).

Family Porcellanidae Haworth, 1825
Euceramus praelongus Stimpson, 1860

Known range.—Western Atlantic: Delaware Bay to Aransas area, Texas (Williams 1984).

Megalobrachium soriatum (Say, 1818)

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to Port Aransas, Texas; West Indies to Barbados; Contoy Island, Mexico; Bahia Caledonia and Galeta Island, Panama (Williams 1984); Ceará to São Paulo, Brazil (Veloso 1998).

Pachycheles pilosus (H. Milne Edwards, 1837)

Known range.—Western Atlantic: Charleston, South Carolina; Key West to Sarasota Bay, Florida; through West Indies to Tobago and Aruba (Williams 1984).

Pachycheles rugimanus A. Milne-Edwards, 1880

Known range.—Western Atlantic: Cape Lookout, North Carolina, through Florida to St. Thomas, U.S. Virgin Islands; Contoy Island, Mexico (Williams 1984); Amapá to Pará (Veloso 1998) and Pernambuco, Brazil (Williams 1984).

▶ *Petrolisthes armatus* (Gibbes, 1850)

Remarks.—This species was recently reported in the region (Knott et al. 2000). Although Knott et al. (2000) reported the presence of this crab as an introduction, the occurrence of *P. armatus* in Georgia and South Carolina possibly represents a northern range extension because the original description by Gibbes (1850) listed the locality of specimens examined as "Florida." This species is the dominant decapod crustacean on rocky substrates in Georgia and is well established on rocky rubble, oyster reefs, and other shallow subtidal and intertidal habitats throughout Georgia and South Carolina (Knott et al. 2000).

Known range.—Western Atlantic: Bermuda; South Carolina southward through the Gulf of Mexico; Bahamas; West Indies and Caribbean; northern South America to Santa Catarina, Brazil; Central Atlantic: Ascension Island; Eastern Atlantic: tropical West Africa; Eastern Pacific: Gulf of California to Peru (Veloso 1998, Knott et al. 2000).

Petrolisthes galathinus (Bosc, 1802)

Known range.—Western Atlantic: Cape Hatteras, North Carolina, through Gulf of Mexico and Caribbean Sea to Rio Grande do Sul, Brazil; Eastern Pacific: Isla San Lucas, Costa Rica, to off La Libertad, Ecuador (Williams 1984, Veloso 1998).

Polyonyx gibbesi Haig, 1956

Known range.—Western Atlantic: Woods Hole, Massachusetts, to Uruguay (Williams 1984).

Porcellana sayana (Leach, 1820)

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to Rio Grande do Sul, Brazil, including Gulf of Mexico and Caribbean Sea (Williams 1984, Veloso 1998).

Porcellana sigsbeiana A. Milne-Edwards, 1880

Known range.—Western Atlantic: off Martha's Vineyard, Massachusetts, to southwestern Caribbean Sea off Colombia; West Indies to Virgin Islands (Williams 1984); Pará and Maranhão, Brazil (Veloso 1998).

Superfamily Hippoidea Latreille, 1825

Family Albuneidae Stimpson, 1858

Albunea gibbesii Stimpson, 1859

Known range.—Western Atlantic: Bermuda; east of Cape Lookout, North Carolina, to Texas, through West Indies to São Paulo, Brazil (Williams 1984, Calado 1998).

Albunea paretii Guérin-Méneville, 1853

Known range.—Western Atlantic: Beaufort Inlet, North Carolina, to Corpus Christi, Texas, through West Indies to Rio Grande do Sul, Brazil (Williams 1984, Calado 1998); Eastern Atlantic: Cape Verde Islands; Senegal to Ghana (Williams 1984).

Lepidopa websteri Benedict, 1903

Known range.—Western Atlantic: mouth of Chesapeake Bay; Drum Inlet, North Carolina, to east central Florida; Tampa Bay, Florida; Petit Bois Island, Mississippi (Williams 1984, Manning 1988).

Family Hippidae Latreille, 1825

Emerita benedicti Schmitt, 1935

Known range.—Western Atlantic: Charleston County, South Carolina, to Veracruz, Mexico (Williams 1984).

Emerita talpoida (Say, 1817)

Known range.—Western Atlantic: Harwich, Massachusetts, to Horn Island, Mississippi; Progreso, Yucatán, Mexico (Williams 1984).

Superfamily Coenobitoidea Dana, 1851

Remarks.—Williams (1984) recognized two superfamilies (Coenobitoidea and Paguroidea) for hermit crabs. McLaughlin (1983) had recommended that the superfamily Coenobitoidea be suppressed and that a single superfamily of hermit crabs should be recognized. Martin & Davis (2001) accepted the arrangement proposed by McLaughlin (1983). However, McLaughlin & Lemaitre (2001a) recently provided evidence to support reinstatement of the Coenobitoidea. Based on their results, two distinct superfamilies should be recognized with respect to hermit crab higher classification.

Family Diogenidae Ortmann, 1892

Cancellus ornatus Benedict, 1901

Known range.—Western Atlantic: Cape Fear, North Carolina, through eastern Gulf of Mexico; Greater and Lesser Antilles, to Bahia, Brazil (Williams 1984, Rieger 1998).

Clibanarius vittatus (Bosc, 1802)

Known range.—Western Atlantic: Potomac River, Gunston, Virginia, to Santa Catarina, Brazil, including the Gulf of Mexico (Williams 1984).

Dardanus fucosus Biffar & Provenzano, 1972

Known range.—Western Atlantic: near Cape Hatteras, North Carolina, to Pará, Brazil (Williams 1984, Rieger 1998).

Dardanus insignis (de Saussure, 1858)

Known range.—Western Atlantic: off Oregon Inlet, North Carolina, to Port Aransas, Texas; through West Indies to Argentina (Williams 1984, Rieger 1998).

Paguristes hummi Wass, 1955

Known range.—Western Atlantic: Newport River, North Carolina, to off Sapelo Island, Georgia; southwestern Florida, including Tampa Bay, to off Isles Dernieres, Louisiana; Caribbean coast of Colombia (Williams 1984, Campos & Sánchez 1995, Strasser & Price 1999).

Paguristes lymani A. Milne-Edwards & Bouvier, 1893

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; Florida Keys to Swan Island, off Honduras; through West Indies to Guyana (Williams 1984).

Paguristes moorei Benedict, 1901

Known range.—Western Atlantic: off Cape Lookout, North Carolina; Florida Straits; Puerto Rico (Williams 1984).

Paguristes sericeus A. Milne-Edwards, 1880

Known range.—Western Atlantic: off Cape Lookout, North Carolina; West Flower Garden Bank, northwestern Gulf of Mexico, to Virgin Islands (Williams 1984).

Paguristes spinipes A. Milne-Edwards, 1880

Known range.—Western Atlantic: Gulf Stream south of Cape Lookout, North Carolina; off Cape Canaveral to Florida Straits; Sarasota, Florida; Barbados to Pernambuco and Alagoas, Brazil (Williams 1984, Rieger 1998).

Paguristes tortugae Schmitt, 1933

Known range.—Western Atlantic: reefs off Beaufort, North Carolina, to southern and southwestern Florida; Gulf of Mexico;

through West Indies to São Paulo, Brazil (Williams 1984, Rieger 1998).

Paguristes triangulatus A. Milne-Edwards & Bouvier, 1893

Known range.—Western Atlantic: off Oregon Inlet, North Carolina, to Tortugas, Florida; Barbados; Trinidad (Williams 1984).

Petrochirus diogenes (Linnaeus, 1758)

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to Uruguay, including Gulf of Mexico and West Indies (Williams 1984, Rieger 1998).

Superfamily Paguroidea Latreille, 1802
Family Lithodidae Samouelle, 1819
Lithodes maja (Linnaeus, 1758)

Known range.—Western Atlantic: West Greenland to Baltimore Canyon, off the coast of Maryland; North Atlantic: East Greenland; Iceland; Northeastern Atlantic: Spitsbergen to the British Isles; the Netherlands (Williams 1984, 1988; Squires 1990).

Family Paguridae Latreille, 1802
► *Anisopagurus hopkinsi* Lemaitre & McLaughlin, 1996

Remarks.—Lemaitre & McLaughlin (1996:101) described and illustrated this species and discussed congeneric affinities. This species occurs at depths of 91–165 m (Lemaitre & McLaughlin 1996).

Known range.—Western Atlantic: off Georgia; Gulf of Mexico (Lemaitre & McLaughlin 1996).

► *Catapagurus sharreri*
A. Milne-Edwards, 1880

Remarks.—Williams (1984) considered this species to be extralimital. Asakura (2001) rediagnosed this genus and species. This species occurs at 60–882 m depth (Williams & Wigley 1977) on sediments consisting of sand, mud and shell fragments (Rieger 1998).

Known range.—Western Atlantic: 40°N, southward to Rio de Janeiro, Brazil, including the Caribbean Sea (Williams & Wigley 1977).

★ *Goreopagurus piercei* (Wass, 1963)

Pagurus piercei Wass.—Williams, 1984: 218.

Remarks.—McLaughlin (1988) examined a large sample of *P. piercei* and observed several characters that excluded this species from the genus *Pagurus.* A new genus (*Goreopagurus*) was erected and described (McLaughlin 1988) and *G. piercei* was rediagnosed and illustrated. Discovery of an additional species belonging to this genus required McLaughlin & Haig (1995) to emend and expand the original generic diagnosis.

Known range.—Western Atlantic: Mid-Atlantic Bight, off eastern United States, to southeastern Florida; northern Gulf of Mexico (McLaughlin 1988).

► ★ *Hemipagurus gracilis* Smith, 1881

Catapagurus gracilis (Smith).—Williams, 1984:484.

Remarks.—Asakura (2001) removed *Hemipagurus* from the synonymy of *Catapagurus,* rediagnosed *Hemipagurus,* and redescribed *H. gracilis,* the type species. Williams (1984) considered this species to be extralimital. This species occurs at 73–418 m depth (Williams & Wigley 1977).

Known range.—Western Atlantic: Massachusetts to Barbados (Williams & Wigley 1977).

► *Iridopagurus reticulatus* García-Gómez, 1983

Remarks.—García-Gómez (1983:37) described this species and provided a species diagnosis, color description, and behavioral observations. This species occurs at depths of 1–38 m (García-Gómez 1983).

Known range.—Western Atlantic: North Carolina to Florida; Bahamas; Jamaica; Dominican Republic; U.S. Virgin Islands; Leeward Islands; Bonaire; Curaçao; Belize; Colombia; Venezuela; Suriname; French Guiana (García-Gómez 1983).

★ *Manucomplanus ungulatus* (Studer, 1883)

Manucomplanus corallinus (Benedict).—Williams, 1984:224.

Remarks.—Lemaitre & McLaughlin (1996) determined that the range of variation of specimens of the nominal species *M. corallinus* and *M. ungulatus* was such that the two taxa could not be separated. Consequently, they placed *M. corallinus* in the synonymy of *M. ungulatus.* The authors provided a species diagnosis and illustrations.

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to Florida; Gulf of Mexico; Straits of Florida; Bahamas; Eastern Atlantic: South and West Africa (Williams 1984, Lemaitre & McLaughlin 1996).

Pagurus acadianus Benedict, 1901

Known range.—Western Atlantic: Straits of Belle Island and Notre Dame Bay, Newfoundland; Gulf of St. Lawrence to mouth of Chesapeake Bay (Williams 1984, Squires 1990).

Pagurus annulipes (Stimpson, 1860)

Remarks.—Lemaitre et al. (1982) reported the depth distribution for this species as subtidal to 90 m, which represented an increase in the maximum reported depth of occurrence.

Known range.—Western Atlantic: Vineyard Sound, Massachusetts, to south central Florida (Williams 1984, Lemaitre et al. 1982).

Pagurus arcuatus Squires, 1964

Known range.—Western Atlantic: Greenland to off Virginia Capes (Williams 1984).

► *Pagurus brevidactylus* (Stimpson, 1859)

Remarks.—Lemaitre et al. (1982) provided a species diagnosis and commented on interspecific comparisons. This species occurs from the intertidal to 50 m (Lemaitre et al. 1982).

Known range.—Western Atlantic: Bermuda; northeastern Florida; Bahamas to Brazil; Gulf of Mexico; Caribbean (Lemaitre et al. 1982).

Pagurus carolinensis McLaughlin, 1975

Remarks.—Lemaitre et al. (1982) provided species diagnosis and interspecific comparisons.

Known range.—Western Atlantic: North Carolina to southeastern Florida (Lemaitre et al. 1982); Tampa Bay, Florida (Strasser & Price 1999).

Pagurus defensus (Benedict, 1892)

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to Georgia; Dry Tortugas, Florida, to Alabama (Williams 1984).

Pagurus impressus (Benedict, 1892)

Known range.—Western Atlantic: off Diamond Shoals, North Carolina, to near Cape Canaveral, Florida; Florida Bay (near Flamingo), north to Pensacola, Florida; Port Aransas, Texas (Williams 1984).

Pagurus longicarpus Say, 1817

Known range.—Western Atlantic: Minas Basin and Chignecto Bay to Hutchinson Island, Florida; southwestern Florida to Texas (Williams 1984, Squires 1990).

► *Pagurus maclaughlinae* García-Gómez, 1982

Remarks.—García-Gómez (1982:647) recognized and described this species. Lemaitre et al. (1982) reported this species in the region and provided a species diagnosis. *Pagurus maclaughlinae* occurs from the subtidal to 5 m (García-Gómez 1982).

Known range.—Western Atlantic: Wassaw, Georgia, to Florida; Gulf of Mexico; Caribbean (Lemaitre et al. 1982).

Pagurus politus (Smith, 1882)

Known range.—Western Atlantic: Nova Scotia to off Dry Tortugas, Florida (Williams 1984, Squires 1990).

Pagurus pollicaris Say, 1817

Known range.—Western Atlantic: Grand Manan, New Brunswick, to northeastern Florida; Key West, Florida, to Texas (Williams 1984).

Pagurus pubescens Krøyer, 1838

Known range.—Western Atlantic: West Greenland; Foxe Basin; Hudson Bay to Cape Hatteras, North Carolina; Arctic-North Atlantic: East Greenland; Iceland; Spitsbergen; Barents Sea; Novaya Zemlya; Eastern Atlantic: Faroes and the British Isles (Williams 1984, Squires 1990).

★ *Pagurus stimpsoni* (A. Milne-Edwards & Bouvier, 1893)

Pagurus hendersoni Wass.—Williams, 1984:214.

Remarks.—Lemaitre et al. (1982), in comparing type material of *P. hendersoni* with specimens of *P. stimpsoni,* determined that the two species were conspecific, and placed *P. hendersoni* in the synonymy of *P. stimpsoni. Pagurus stimpsoni* occurs from the subtidal purportedly to 512 m (Wass 1963), usually from the subtidal to 73 m. Depths of occurrence reported for types of *P. hendersoni* (228 and 347–512 m) by Wass are problematic according to Lemaitre et al. (1982) who were unable to verify the accuracy of these collection data.

Known range.—Western Atlantic: North Carolina to Florida; Gulf of Mexico; Caribbean coast of South America (Lemaitre et al. 1982).

Phimochirus holthuisi (Provenzano, 1961)

Remarks.—McLaughlin (1981) reported the bathymetric range for this species as 1–210 m.

Known range.—Western Atlantic: North Carolina to Florida; Straits of Florida and Bahama Islands; Gulf of Mexico from Florida to Texas; Caribbean and northern South America from Colombia to Bahia, Brazil (McLaughlin 1981, Williams 1984, Rieger 1998).

Pylopagurus discoidalis (A. Milne-Edwards, 1880)

Remarks.—McLaughlin & Lemaitre (2001b) rediagnosed the genus *Pylopagurus* and diagnosed, illustrated, and discussed morphological variation of all species within this genus.

Known range.—Western Atlantic: North Carolina to central Brazil, including Gulf of Mexico and Caribbean (Williams 1984, McLaughlin & Lemaitre 2001b).

Rhodochirus rosaceus (A. Milne-Edwards & Bouvier, 1893)

Known range.—Western Atlantic: south of Cape Lookout, North Carolina, to Key West, Florida; northwestern Gulf of Mexico; Grenada; Suriname; São Paulo and Rio Grande do Sul, Brazil (McLaughlin 1981, Williams 1984, Rieger 1998).

Tomopaguropsis problematica (A. Milne-Edwards & Bouvier, 1893)

Known range.—Western Atlantic: northeast of Cape Lookout, North Carolina; southern Florida and Bahamas; Barbados; off Honduras (Williams 1984).

▶ *Tomopagurus cokeri* (Hay, 1917)

Remarks.—McLaughlin (1981) redescribed the genus and provided a species diagnosis and illustrations. This species occurs at 44–302 m (McLaughlin 1981).

Known range.—Western Atlantic: south of Cape Lookout, North Carolina; off northeastern Florida; Gulf of Mexico; Caribbean; off French Guiana (McLaughlin 1981).

▶ *Tomopagurus wassi* McLaughlin, 1981

Remarks.—McLaughlin (1981) redescribed the genus, described this species, and provided illustrations and comparative information. This species occurs at 75–360 m (McLaughlin 1981).

Known range.—Western Atlantic: southeastern United States; Straits of Florida; Gulf of Mexico; Caribbean to northern Brazil (McLaughlin 1981).

▶ Family Parapaguridae Smith, 1882
▶ *Parapagurus pilosimanus* Smith, 1879

Remarks.—Lemaitre (1989) provided a description, illustrations, and information on symbiotic associations and affinities. This species occurs at 102–3864 m, but is most frequently found in depths of 400–1400 m (Lemaitre 1989).

Known range.—North Atlantic: southwest of Iceland and the Faroe Islands to west of Ireland; Western Atlantic: Nova Scotia to Guyana; Eastern Atlantic: Bay of Biscay to Gulf of Guinea; South Atlantic: Tristan da Cunha (Lemaitre 1989).

▶ *Sympagurus pictus* Smith, 1883

Remarks.—Lemaitre (1989) provided a description, illustrations, and information on symbiotic associations and affinities. This species occurs at 180–2322 m, but is most frequently found at depths of 200 to 800 m (Lemaitre 1989).

Known range.—Western Atlantic: off Long Island, New York to off French Guiana (Lemaitre 1989).

Infraorder Brachyura Latreille, 1802
Superfamily Dromioidea De Haan, 1833
Family Dromiidae De Hann, 1833
★ *Cryptodromiopsis antillensis*
(Stimpson, 1858)

Dromidia antillensis Stimpson.—Williams, 1984:255.

Remarks.—McLay (1993) redefined the genera within the family Dromiidae. As a result, *Dromidia antillensis* was reassigned to the genus *Cryptodromiopsis.*

Known range.—Western Atlantic: Bermuda; off Cape Hatteras, North Carolina, to Rio Grande do Sul, Brazil, including Gulf of Mexico and Caribbean Sea; Central Atlantic: Saint Helena (Williams 1984, Melo et al. 1998).

▶ *Dromia erythropus*
(George Edwards, 1771)

Remarks.—Previously, the geographic range of this species was considered to be outside the region, however, Williams (unpublished data) records this species from off North Carolina. *Dromia erythropus* inhabits various types of sediments from the intertidal to 360 m (Laughlin et al. 1982, Melo et al. 1998) and is usually found with sponges and ascidians on its carapace (Melo et al. 1998).

Known range.—Western Atlantic: Bermuda; Florida to São Paulo, Brazil (Laughlin et al. 1982, Melo et al. 1998). Williams (unpublished) noted a specimen "Taken off North Carolina (33°48′06″N, 76°34′24″W), 105 m, 14 May 1981 (USNM 202800)."

Hypoconcha arcuata Stimpson, 1858

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to west Florida; St. Thomas, U.S. Virgin Islands; Suriname to São Paulo, Brazil (Williams 1984, Melo et al. 1998).

★ *Hypoconcha parasitica*
(Linnaeus, 1763)

Hypoconcha sabulosa (Herbst).—Williams, 1984:258.

Remarks.—Holthuis and Manning (1987) concluded that *Hypoconcha parasitica* was the oldest available name for the species formerly known as *H. sabulosa.*

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, through Gulf of Mexico to São Paulo, Brazil (Williams 1984, Melo et al. 1998).

Hypoconcha spinosissima Rathbun, 1933

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to Gulf of Mexico, off Mississippi River delta; Yucatán; Jamaica (Williams 1984).

Superfamily Homoloidea De Haan, 1839

Family Homolidae De Haan, 1839

▶ *Homola minima* Guinot & Richer de Forges, 1995

Homola barbata (Fabricius).—Williams, 1984:261 (in part).

Remarks.—Guinot & Richer de Forges (1995:326) described this species, provided photographs, and discussed congeneric comparisons. *Homola minima* occurs at depths of 55–690 m (Guinot & Richer de Forges 1995, Martin & Zimmerman 2001). *Homola barbata,* formerly considered to be a wide-ranging species (Williams 1984), is now known to occur only in the Mediterranean Sea and also possibly in the adjoining eastern Atlantic (Guinot & Richer de Forges 1995).

Known range.—Western Atlantic: Martha's Vineyard, Massachusetts, to Rio Grande do Sul, Brazil; Bahamas (Guinot & Richer de Forges 1995, Martin & Zimmerman 2001).

Family Latreilliidae Stimpson, 1858

Latreillia manningi Williams, 1982

Known range.—Western Atlantic: Nantucket Shoals, off Massachusetts, to off Havana, Cuba; Venezuela; Central Atlantic: Ascension Island (Williams 1984).

Superfamily Raninoidea De Haan, 1841

Family Raninidae De Haan, 1841

Remarks.—Guinot (1993) subdivided the family Raninidae into six subfamilies: Ranininae De Haan, 1841, Notopodinae Serène & Umali, 1972, Symethinae Goeke, 1981, Raninoidinae Lörenthey & Beurlen, 1929, Lyreidinae Guinot, 1993, and Cyrtorhinae Guinot, 1993. Three subfamilies (Ranininae, Notopodinae, and Symethinae) were recognized in Williams (1984).

★ Subfamily Lyreidinae Guinot, 1993

▶ *Lysirude nitidus* (A. Milne-Edwards, 1880)

Remarks.—Diagnostic characteristics and congeneric comparisons are provided in Goeke (1980, 1985) and Tucker (1998). This species is found on soft mud bottoms at depths of 119–823 m (Powers 1977, as *Lyreidus bairdii*).

Known range.—Western Atlantic: Massachusetts; Gulf of Mexico; Greater Antilles to Venezuela; Suriname (Goeke 1980).

★ Subfamily Notopodinae Serène & Umali, 1972

Remarks.—Placement of *Ranilia* in subfamily Notopodinae was supported by Tucker's (1998) phylogenetic study.

Ranilia constricta (A. Milne-Edwards, 1880)

Known range.—Western Atlantic: southeast of Cape Fear, North Carolina; Palm Beach, Florida, to Florida Straits and Yucatán Channel; Cuba; off Barbados (Williams 1984); Amapá, Rio de Janeiro to Rio Grande do Sul, Brazil (Melo et al. 1998); Central Atlantic: Ascension Island; Eastern Atlantic: Senegal to Congo; Annobon Island (Williams 1984).

Ranilia muricata H. Milne Edwards, 1837

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to northwestern Gulf of Mexico; Colombia (Williams 1984); Pernambuco, Brazil (Melo et al. 1998).

★ Subfamily Raninoidinae Lörenthey & Beurlen, 1929

Remarks.—Placement of *Raninoides* in subfamily Raninoidinae was supported by Tucker's (1998) phylogenetic study.

Raninoides loevis (Latreille, 1825)

Remarks.—This species was listed under subfamily Ranininae in Williams (1984).

Known range.—Western Atlantic: south of Cape Hatteras, North Carolina, to São Paulo, Brazil, including Gulf of Mexico, southern Caribbean Sea and Leeward Islands (Williams 1984, Melo et al. 1998).

★ Family Symethidae Goeke, 1981

Remarks.—This taxon was previously considered a subfamily of the Raninidae (e.g., Williams 1984, Guinot 1993). Tucker (1998) considered the subfamily Symethinae sufficiently distinct to warrant elevation of the subfamily to the rank of family.

Symethis variolosa (Fabricius, 1793)

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina, through western Gulf of Mexico to São Paulo, Brazil, and Fernando de Noronha (Williams 1984, Melo et al. 1998).

★ Superfamily Cyclodorippoidea Ortmann, 1892

Remarks.—Tavares (1991a) proposed the use of the superfamilial name Cyclodorippoidea to replace Tymoloidea. Martin & Davis (2001) accepted this arrangement.

★ Family Cyclodorippidae Ortmann, 1892

Family Tymolidae.—Williams, 1984:259.

Remarks.—Family Tymolidae is placed in the synonymy of Cyclodorippidae (Tavares 1991a, 1993, 1996). Tavares (1996) conducted a revision of the family Cyclodorippidae.

Clythrocerus granulatus (Rathbun, 1898)

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; Honduras; southern Florida, through Antilles, to Venezuela and Trinidad (Williams 1984), and southward to Rio Grande do Sul, Brazil (Melo et al. 1998).

▶ *Clythrocerus nitidus* (A. Milne-Edwards, 1880)

Remarks.—Tavares (1996) included a description and illustrations, and discussed morphological variation for this species. This species occurs at 12–531 m (Tavares 1996).

Known range.—Western Atlantic: South Carolina; Florida; Barbados; Grenada (Tavares 1996).

★ *Deilocerus perpusillus* (Rathbun, 1901)

Clythrocerus perpusillus Rathbun.—Williams, 1984:260.

Remarks.—As a result of his review of the New World cyclodorippoid crabs, Tavares (1993) identified and described four new genera, including *Deilocerus. Clythrocerus perpusillus* was designated the type species of this new genus.

Known range.—Western Atlantic: North Carolina to Georgia; Bahama Banks; Gulf of Mexico; Puerto Rico; Barbados; Amapá to Rio Grande do Sul, Brazil (Williams 1984, Tavares 1996, Melo et al. 1998).

Superfamily Dorippoidea MacLeay, 1838
Family Dorippidae MacLeay, 1838
Subfamily Ethusinae Guinot, 1977
★ *Ethusa americana* A. Milne-Edwards, 1880

Ethusa mascarone americana A. Milne-Edwards.—Williams, 1984:269.

Remarks.—Hendrickx (1989) elevated

the subspecies *E. m. americana* to full species status. *Ethusa americana* occurs only in the western Atlantic; references of this species at eastern Pacific localities refer to *E. panamensis* Finnegan. *Ethusa mascarone* (Herbst) occurs in the Mediterranean (Manning & Holthuis 1981).

Known range.—Western Atlantic: south of Cape Lookout, North Carolina, to Gulf of Mexico and West Indies; Maranhão to Rio de Janeiro, Brazil (Williams 1984, Melo et al. 1998).

Ethusa microphthalma Smith, 1881

Known range.—Western Atlantic: off Martha's Vineyard, Massachusetts, to Cuba; throughout Gulf of Mexico (Williams 1984); São Paulo, Brazil (Melo et al. 1998).

Ethusa tenuipes Rathbun, 1897

Known range.—Western Atlantic: off Cape Lookout, North Carolina; East Florida to Gulf of Mexico, east of Mississippi River delta; Cuba (Williams 1984); Rio de Janeiro to São Paulo, Brazil (Melo et al. 1998).

Superfamily Calappoidea H. Milne Edwards, 1837

Family Calappidae H. Milne Edwards, 1837

Remarks.—Bellwood (1996) evaluated phylogenetic relationships of four subfamilies within the Calappidae (Calappinae, Matutinae, Orithyiinae, and Hepatinae) using cladistic analysis. She rejected the monophyly of an expanded Calappidae, but demonstrated support for the monophyly of each component taxon and proposed elevating the four subfamilies to family status. Additionally, Bellwood (1996) reassigned these families to different superfamilies, with Calappidae and Hepatidae remaining in the superfamily Calappoidea, Matutidae placed in the superfamily Leucosioidea, and Orithyiidae placed in the superfamily Dorippoidea. Based on fossil evidence (carapace morphology), Schweitzer and Feldmann (2000) supported the conclusions of Bellwood (1996).

Acanthocarpus alexandri Stimpson, 1871

Known range.—Western Atlantic: Georges Bank, off Massachusetts, to west coast of Florida; Puerto Rico to Grenadines; Rio de Janeiro (Williams 1984) to Rio Grande do Sul, Brazil (Melo et al. 1998).

Calappa flammea (Herbst, 1794)

Known range.—Western Atlantic: Woods Hole region, Massachusetts, to Florida Keys; Gulf coast of United States and Mexico; Bahamas; Bermuda (Williams 1984).

Calappa ocellata Holthuis, 1958

Known range.—Western Atlantic: Bermuda; Cape Hatteras, North Carolina, to Rio de Janeiro, Brazil (Williams 1984).

Calappa sulcata Rathbun, 1898

Remarks.—This species occurs on sand, mud, and calcareous algal bottoms from shallow depths to 200 m (Melo et al. 1998).

Known range.—Western Atlantic: Cape Hatteras, North Carolina, through Gulf of Mexico to Paraná, Brazil (Williams 1984, Melo et al. 1998).

★ *Calappa tortugae* Rathbun, 1933

Calappa angusta A. Milne-Edwards.—Williams, 1984:273 (in part).

Remarks.—Williams & Child (1989) determined that "*Calappa angusta,*" as previously understood, was poorly defined and actually comprised a complex of species. The next available name for species of *Calappa* in the western Atlantic, *Calappa saussurei tortugae* Rathbun, was removed from synonymy and elevated to full species rank (Williams & Child 1989). Species diagnosis, illustrations and measurements were provided in Williams & Child (1989). This species occurs at 13–238 m (Williams & Child 1989).

Known range.—Western Atlantic: North Carolina to off Venezuela, including Gulf of Mexico, Caribbean, and Leeward Islands (Williams & Child 1989).

★ *Cryptosoma balguerii*
(Desbonne, 1867)

Cycloes bairdii (Stimpson).—Williams, 1984:278.

Remarks.—Galil & Clark (1996) reported that populations of *C. bairdii* occurred exclusively in the eastern Pacific (Baja California to Costa Rica); previous records of *C. bairdii* from Costa Rica to Ecuador were actually those of a new *Cryptosoma* species, whereas records reported as *C. bairdii* from Atlantic localities pertained to *C. balguerii* (a nominal species previously considered to be a subjective synonym of *Cycloes bairdii*). *Cryptosoma balguerii* occurs in shallow waters to 230 m (Galil & Clark 1996).

Known range.—Western Atlantic: North Carolina and Bermuda to Espirito Santo, Brazil (Galil & Clark 1996).

▶ ★ *Cyclozodion angustum*
(A. Milne-Edwards, 1880)

Calappa angusta A. Milne-Edwards.—Williams, 1984:273 (in part).

Remarks.—Williams & Child (1989) concluded that *Calappa angusta,* as described by A. Milne-Edwards, was generically misplaced. They described the genus *Cyclozodion,* of which *C. angustum* (A. Milne-Edwards) is the type species, and provided illustrations, measurements, and comparative information. This species occurs at 95–421 m (Williams & Child 1989).

Known range.—Western Atlantic: off Cape Canaveral, Florida, to Isla Providencia, Colombia; Guyana (Williams & Child 1989).

▶ *Cyclozodion tuberatum* Williams &
Child, 1989

Remarks.—Williams & Child (1989:112) described this species and provided illustrations, measurements and color description. This species occurs at 31–188 m depth, rarely to 640 m (Williams & Child 1989).

Known range.—Western Atlantic: off Cape Lookout, North Carolina, through Bahamas; eastern Gulf of Mexico; and Suriname (Williams & Child 1989).

★ Family Hepatidae Stimpson, 1871

Remarks.—Species in the genera *Hepatus* and *Osachila* were previously assigned to the subfamily Matutinae (Williams 1984). Based on results of a phylogenetic study by Bellwood (1996) and corroborating fossil evidence (carapace morphology) of Schweitzer & Feldmann (2000), these genera are now placed in the family Hepatidae.

Hepatus epheliticus (Linnaeus, 1763)

Known range.—Western Atlantic: Chesapeake Bay to western Gulf of Campeche, Mexico; Cuba; Jamaica; Dominican Republic (Williams 1984).

Hepatus pudibundus (Herbst, 1785)

Known range.—Western Atlantic: Georgia to Rio Grande do Sul, Brazil (Williams 1984, Melo et al. 1998).

Osachila semilevis Rathbun, 1916

Known range.—Western Atlantic: off Beaufort, North Carolina, to northwest Florida (Williams 1984).

Osachila tuberosa Stimpson, 1871

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to northwest Florida and Yucatán Channel (Williams 1984); Rio de Janeiro and Rio Grande do Sul, Brazil (Melo et al. 1998).

Superfamily Leucosioidea Samouelle,
1819
Family Leucosiidae Samouelle, 1819

Remarks.—Leucosiidae was previously assigned to the superfamily Calappoidea

(Williams 1984). Based on results of a phylogenetic study of the Calappidae, Bellwood (1996) placed the family Leucosiidae in the superfamily Leucosioidea.

Subfamily Ebaliinae Stimpson, 1871

Ebalia cariosa (Stimpson, 1860)

Known range.—Western Atlantic: Bogue Sound near Beaufort, North Carolina, to west Florida; western Gulf of Mexico; Jamaica; northeastern South America to São Paulo, Brazil (Williams 1984).

Ebalia stimpsonii A. Milne-Edwards, 1880

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; west Florida to Barbados (Williams 1984); Amapá to São Paulo, Brazil (Melo et al. 1998).

Speloeophorus nodosus (Bell, 1855)

Known range.—Western Atlantic: Florida; West Indies (Williams 1984); Maranhão to Rio de Janeiro, Brazil (Melo et al. 1998).

Speloeophorus pontifer (Stimpson, 1871)

Known range.—Western Atlantic: southeast of Cape Lookout and off Beaufort, North Carolina, to west Florida; West Indies to Barbados (Williams 1984).

Subfamily Iliinae Stimpson, 1871

Myropsis quinquespinosa Stimpson, 1871

Known range.—Western Atlantic: south of Martha's Vineyard, Massachusetts, to Suriname, including Gulf of Mexico and Caribbean Sea (Williams 1984).

Persephona mediterranea (Herbst, 1794)

Known range.—Western Atlantic: New Jersey to Rio Grande do Sul, Brazil, including Gulf of Mexico and Caribbean Sea (Williams 1984, Melo et al. 1998).

Subfamily Leucosiinae Samouelle, 1819

★ *Acanthilia intermedia* (Miers, 1886)

Iliacantha intermedia Miers.—Williams, 1984:290.

Remarks.—Galil (2000) removed *I. intermedia* from the genus *Iliacantha* and placed it in the newly erected genus *Acanthilia* Galil; generic description and species redescription are provided. This species occurs at depths of 10–329 m.

Known range.—Western Atlantic: North Carolina to Brazil (Galil 2000).

Callidactylus asper Stimpson, 1871

Known range.—Western Atlantic: south of Cape Lookout, North Carolina, through southeastern Gulf of Mexico to Panama, and southeastward to Alagoas, Brazil (Williams 1984).

Iliacantha subglobosa Stimpson, 1871

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to northwest Florida; through eastern Gulf of Mexico and Caribbean Sea, south to Alagoas, Brazil (Williams 1984).

Superfamily Majoidea Samouelle, 1819

Remarks.—Recent investigations of interrelationships within the Majoidea include those of Drach & Guinot (1983), Griffin & Tranter (1986), Clark & Webber (1991), Guinot & Richer de Forges (1997), Guinot & Bouchard (1998), and Pohle & Marques (2000). Although all subfamilies within the superfamily have not been considered in a phylogenetic framework, previously recognized subfamilies within the family Majidae have been elevated to the level of family (Hendrickx 1995). Martin & Davis (2001) also adopted this arrangement. However, results of a recent phylogenetic analysis based on larval characters (Pohle & Marques 2000) supported monophyly only of the Oregoniidae, Majidae and Inachidae.

★ Family Epialtidae MacLeay, 1838

Remarks.—All species listed below were previously placed in subfamily Epialtinae of the Majidae in Williams (1984).

Epialtus dilatatus A. Milne-Edwards, 1878

Known range.—Western Atlantic: off Beaufort Inlet and New River, North Carolina; southwest Florida; Yucatán; Bahamas to St. Thomas (Williams 1984).

Sphenocarcinus corrosus
A. Milne-Edwards, 1875

Remarks.—Tavares (1991b) provided a generic revision and diagnosis.

Known range.—Western Atlantic: off Cape Lookout, North Carolina; Gulf of Mexico to Barbados (Williams 1984).

★ Family Inachidae MacLeay, 1838

Remarks.—Elevation of subfamily Inachinae to family level was supported by the cladistic analysis of Clark & Webber (1991). Other morphological evidence (Guinot & Bouchard 1998) supported this conclusion. All species of the genera *Anomalothir, Metoporhaphis, Podochela,* and *Stenorhynchus* (listed below) were previously placed in subfamily Inachinae of the Majidae in Williams (1984). The genus *Rochinia* was previously placed in the subfamily Pisinae of the Majidae (Williams 1984, Griffin & Tranter 1986). Cladistic relationships hypothesized by Clark & Webber (1991) indicated that *Rochinia* should be placed in the Inachidae. Tavares (1991b) conducted a generic revision of *Rochinia.*

Anomalothir furcillatus (Stimpson, 1871)

Known range.—Western Atlantic: off Cape Lookout, North Carolina, through eastern Gulf of Mexico; West Indies to Grenada (Williams 1984).

Metoporhaphis calcarata (Say, 1818)

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to Rio de Janeiro, Brazil, including Gulf of Mexico and Caribbean Sea (Williams 1984, Melo 1998).

Podochela gracilipes Stimpson, 1871

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to Rio Grande do Sul, including Gulf of Mexico and Caribbean Sea (Williams 1984, Melo 1998).

Podochela riisei Stimpson, 1860

Known range.—Western Atlantic: Bermuda; North Carolina to Campeche, Mexico; Antilles; Rio de Janeiro, Brazil (Williams 1984, Melo 1998).

Podochela sidneyi Rathbun, 1924

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to Veracruz, Mexico; northwestern Cuba; Yucatán Channel (Williams 1984).

Rochinia crassa
(A. Milne-Edwards, 1879)

Known range.—Western Atlantic: Nantucket Shoals, Massachusetts, to Gulf of Mexico, off southern Texas; northern Cuba; west of Cabo de la Vela, Colombia; off French Guiana (Williams 1984). Recently, a male measuring 89.2 mm carapace width and 89.5 mm carapace length was caught off Lunenburg, Nova Scotia, at 243 m (Moriyasu et al. 2001). This first recorded occurrence of this species in Canadian waters constitutes a northern range extension from the previous northernmost occurrence on Nantucket Shoals, Massachusetts (Williams 1984). Moriyasu et al. (2001) considered this as a stray occurrence of this species in Canadian waters.

Rochinia tanneri (Smith, 1883)

Known range.—Western Atlantic: off Martha's Vineyard, Massachusetts, to Straits of Florida (Williams 1984).

Rochinia umbonata (Stimpson, 1871)

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina, through eastern and northern Gulf of Mexico to northeast of Nicaragua; through West Indies to St. Vincent (Williams 1984).

Stenorhynchus seticornis (Herbst, 1788)

Remarks.—Goeke (1989) determined that two co-occurring species were confused under the name *S. seticornis.* He restricted the specific description of *S. seticornis,* redescribed the species, and selected a neotype. This species occurs at 1–366 m (Goeke 1989).

Known range.—Western Atlantic: Bermuda; Cape Fear, North Carolina, to Rio Grande do Sul, Brazil, including Gulf of Mexico, Antilles, and northern South America (Williams 1984, Goeke 1989, Melo 1998).

► *Stenorhynchus yangi* Goeke, 1989

Remarks.—Goeke (1989:631) described this species and provided a diagnosis, illustrations, color description, and discussed morphological variation. This species occurs at 31–365 m (Goeke 1989).

Known range.—Western Atlantic: off Martha's Vineyard, Massachusetts, to Suriname, including Gulf of Mexico (Goeke 1989).

★ Family Inachoididae Dana, 1851

Remarks.—Drach & Guinot (1983) proposed elevating the Inachoidinae to family level. This decision was corroborated with morphological evidence (Guinot & Richer de Forges 1997). The genera included within this family are based on the recommendation of Guinot & Richer de Forges (1997). All species listed below were previously placed in the subfamily Inachinae of the Majidae in Williams (1984).

Aepinus septemspinosus (A. Milne-Edwards, 1879)

Known range.—Western Atlantic: south of Cape Lookout, North Carolina; southwest of Cape San Blas, Florida; Bahama Banks to São Paulo, Brazil, and Fernando de Noronha Archipelago and Rocas Atoll, Brazil (Williams 1984, Melo 1998).

Anasimus latus Rathbun, 1894

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to Amapá, Brazil, including Gulf of Mexico and Antilles (Williams 1984, Melo 1998).

Arachnopsis filipes Stimpson, 1871

Known range.—Western Atlantic: southeast of Cape Hatteras, North Carolina; Gulf of Mexico, off northwest Florida, through Antilles to Rio Grande do Norte, Brazil (Williams 1984, Melo 1998).

Batrachonotus fragosus Stimpson, 1871

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to southern and western Florida; West Indies to Barbados (Williams 1984).

Collodes robustus Smith, 1883

Known range.—Western Atlantic: Cape Cod, Massachusetts, to southeast of Cape Lookout, North Carolina (Williams 1984).

Collodes trispinosus Stimpson, 1871

Known range.—Western Atlantic: near Cape Hatteras, North Carolina, to southern and western Florida (Williams 1984); Amapá, Rio de Janeiro, and São Paulo, Brazil (Melo 1998).

Euprognatha rastellifera Stimpson, 1871

Known range.—Western Atlantic: off Georges Bank to Uruguay, including Antilles (Williams 1984, Melo 1998 as *E. acuta*).

Inachoides forceps A. Milne-Edwards, 1879

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; west coast of Florida to Rio de Janeiro, Brazil, including Antilles; the Guianas (Williams 1984, Melo 1998).

▶ *Pyromaia arachna* Rathbun, 1924

Remarks.—Lemaitre et al. (2001) provided information on distinguishing characteristics and congeneric comparisons. This species occurs on mud, mud-sand, and mud-shell sediments at 183–324 m depth (Powers 1977).

Known range.—Western Atlantic: South Carolina to Gulf of Mexico (Powers 1977, Lemaitre et al. 2001).

Pyromaia cuspidata Stimpson, 1871

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to west Florida; Cuba; Yucatán Channel to Nicaragua (Williams 1984).

★ Family Mithracidae Balss, 1929

Remarks.—All species of *Hemus, Macrocoeloma, Microphrys, Mithrax, Mithraculus,* and *Stenocionops* (listed below) were previously placed in the subfamily Mithracinae of the Majidae in Williams (1984). Based on results of his investigation of western Atlantic *Mithrax* crabs, Wagner (1990) considered the morphological evidence sufficient to warrant recognition of distinct genera instead of two subgenera within *Mithrax*; *Mithraculus* was elevated to full generic status.

Hemus cristulipes A. Milne-Edwards, 1875

Known range.—Western Atlantic: off Cape Lookout, North Carolina; South Carolina; northwest Gulf of Mexico and Yucatán, through West Indies to Rio de Janeiro, Brazil, and Fernando de Noronha Archipelago (Williams 1984, Melo 1998).

Macrocoeloma camptocerum (Stimpson, 1871)

Known range.—Western Atlantic: Beaufort Harbor, North Carolina; around southern Florida to Alligator Harbor, Florida (Williams 1984); Amapá to Maranhão, Brazil (Melo 1998).

Macrocoeloma eutheca (Stimpson, 1871)

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; off northwest Florida through Bahama Banks and West Indies; Central America; Maranhão to Espírito Santo, Brazil (Williams 1984, Melo 1998).

Macrocoeloma trispinosum (Latreille, 1825)
Macrocoeloma trispinosum, variety of Rathbun, 1925
Macrocoeloma trispinosum nodipes (Desbonne, 1867)

Remarks.—Williams (1984:328) listed these nominal taxa together in one species account. No further investigation of these taxa has been conducted, and further revision is needed. Until further results are available, these taxa are considered as they were in Williams (1984).

Known range (for *M. trispinosum* (Latreille, 1825).—Western Atlantic: Beaufort, North Carolina, to Alligator Harbor, Florida; Yucatán; West Indies to São Paulo, Brazil, and Fernando de Noronha Archipelago (Williams 1984, Melo 1998).

Microphrys antillensis Rathbun, 1920

Known range.—Western Atlantic: Cape Hatteras to Cape Fear, North Carolina; Antilles; Paraíba to Rio de Janeiro, Brazil (Williams 1984, Melo 1998).

Microphrys bicornutus (Latreille, 1825)

Known range.—Western Atlantic: Bermuda; near Beaufort, North Carolina, through Gulf of Mexico to Rio Grande do Sul, Brazil; Fernando de Noronha Archipelago, Brazil (Williams 1984, Melo 1998).

★ *Mithraculus forceps*
(A. Milne-Edwards, 1875)

Mithrax (*Mithraculus*) *forceps* (Milne Edwards).—Williams, 1984:337.

Known range.—Western Atlantic: Bermuda; Cape Hatteras, North Carolina, through Gulf of Mexico and Antilles to São Paulo, Brazil; Fernando de Noronha Archipelago and Rocas Atoll, Brazil (Williams 1984, Wagner 1990, Melo 1998).

★ *Mithrax cornutus* de Saussure, 1857

Mithrax (*Mithrax*) *acuticornis* Stimpson.—Williams, 1984:332.

Remarks.—Wagner (1990) determined that *M. cornutus* and *M. acuticornis* were conspecific. *Mithrax cornutus* was originally regarded as extralimital by Williams (1984:484). This species occurs between 20–458 m (Wagner 1990).

Known range.—Western Atlantic: Bermuda; off Cape Lookout, North Carolina; east and west coasts of Florida, through Gulf of Mexico, Yucatán Channel, and West Indies to Rio de Janeiro, Brazil (Williams 1984, Wagner 1990, Melo 1998).

★ *Mithrax hispidus* (Herbst, 1790)

Mithrax (*Mithrax*) *hispidus* (Herbst).—Williams, 1984:333.
Mithrax (*Mithrax*) *pleuracanthus* Stimpson.—Williams, 1984:334.

Remarks.—Wagner (1990) placed *M. pleuracanthus* in the synonymy of *M. hispidus.*

Known range.—Western Atlantic: Delaware Bay; Bermuda; Beaufort, North Carolina; Charleston, South Carolina; Georgia to Pensacola, Florida; northwestern Gulf of Mexico to Yucatán Channel; Bahamas and Florida Keys through West Indies; Colombia to São Paulo, Brazil (Williams 1984, Wagner 1990, Melo 1998).

★ *Mithrax spinosissimus* (Lamarck, 1818)

Mithrax (*Mithrax*) *spinosissimus* (Lamarck).—Williams, 1984:335.

Known range.—Western Atlantic: North (?) and South Carolina to Nicaragua, through West Indies to Barbados; Venezuela (Williams 1984, Wagner 1990).

★ *Mithrax verrucosus* H. Milne Edwards, 1832

Mithrax (*Mithrax*) *verrucosus* H. Milne Edwards.—Williams, 1984:336.

Known range.—Western Atlantic: Charleston, South Carolina; Florida; Campeche Banks; Curaçao; Venezuela; West Indies to Fernando de Noronha Archipelago and Rocas Atoll, Brazil (Williams 1984, Wagner 1990, Melo 1998).

Stenocionops furcata coelata
(A. Milne-Edwards, 1878)

Known range.—Western Atlantic: Beaufort, North Carolina, to northwest Florida and Alabama; Yucatán Channel; West Indies to Barbados (Williams 1984).

► *Stenocionops furcata furcata*
(Olivier, 1791)

Remarks.—This subspecies was only referenced in the remarks section of *S. f. coelata* in Williams (1984). It is unclear why *S. f. furcata* was not given a full account since its geographic range and depth distribution (shallow water to 64 m) were clearly within the limits of coverage. Much confusion surrounds identification of members of this species group, and more research is needed (D. Felder, pers. comm.). Until such time, both subspecies are considered valid as in Williams (1984).

Known range.—Western Atlantic: Georgia to Rio Grande do Sul, Brazil, including Antilles and Colombia (Williams 1984, Melo 1998).

Stenocionops spinimana (Rathbun, 1892)

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to Florida Straits; Gulf of Mexico, off Mobile Bay, Alabama, and east of Chandeleur Island, off Mississippi (Williams 1984); São Paulo, Brazil (Melo 1998).

► *Stenocionops spinosissima* (de Saussure, 1857)

Remarks.—This species was considered extralimital by Williams (unpublished), but reported occurrence off North Carolina (Powers 1977) indicated that this species should be included. This species occurs at depths of 46–480 m on mud and sand sediments (Powers 1977, Melo 1998), with its center of distribution in the Gulf of Mexico at 110–183 m (Powers 1977).

Known range.—Western Atlantic: off North Carolina; south and southwest Florida; off Texas and east coast of Mexico; north coast of Cuba; Haiti; Guadeloupe; Dominica; Rio Grande do Norte to Rio Grande do Sul, Brazil; Fernando de Noronha Archipelago, Brazil (Powers 1977, Melo 1998).

★ Family Oregoniidae Garth, 1958

Remarks.—Family level status was supported by a cladistic analysis (Clark & Webber 1991) and morphological evidence (Guinot & Bouchard 1998). In their classification, Martin & Davis (2001) recognized this taxon at the subfamily level. All species listed below were previously placed in the subfamily Oregoniinae of the Majidae in Williams (1984).

Chionoecetes opilio opilio (O. Fabricius, 1788)

Known range.—Western Atlantic: Greenland south to St. Lawrence estuary and Gulf of Maine; Arctic-North Pacific: Point Barrow, Alaska, and northeastern Siberia through Bering Strait to Alaskan Peninsula and Aleutian chain; Eastern Pacific: Kamchatka; Okhotsk Sea southward to Japan (Williams 1984).

Hyas araneus (Linnaeus, 1758)

Known range.—Western Atlantic: West Greenland to Rhode Island; Arctic-North Atlantic: between Greenland and Iceland; Spitsbergen; Kara Sea; Eastern Atlantic: through British Isles and northwest France (Williams 1984, Squires 1990).

Hyas coarctatus coarctatus Leach, 1815

Known range.—Western Atlantic: Hudson Bay and Greenland to North Carolina; Arctic-Eastern Atlantic: Murman Sea to Iceland and the British Isles (Williams 1984, Squires 1990).

★ Family Pisidae Dana, 1851

Remarks.—The following six species (listed below) were previously placed in the subfamily Pisinae of the Majidae in Williams (1984).

Coelocerus spinosus A. Milne-Edwards, 1875

Known range.—Western Atlantic: off Cape Fear, North Carolina, to Cape Canaveral, Florida; west Florida to east of Mississippi River delta (Williams 1984).

Libinia dubia H. Milne Edwards, 1834

Known range.—Western Atlantic: Cape Cod, Massachusetts, to southern Texas; Bahamas; Cuba (Williams 1984).

Libinia emarginata Leach, 1815

Known range.—Western Atlantic: Prince Edward Island and Nova Scotia to western Gulf of Mexico (Williams 1984, Squires 1990).

Nibilia antilocapra (Stimpson, 1871)

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to Gulf of Mexico just east of Mississippi River delta; Gulf of Campeche; Antilles; off Guyana; Rio Grande do Norte and Rio Grande do Sul, Brazil (Williams 1984, Melo 1998).

Pelia mutica (Gibbes, 1850)

Known range.—Western Atlantic: Buzzards Bay and Vineyard Sound, Massachusetts, to Texas; Cuba; Puerto Rico; St. Thomas, U.S. Virgin Islands (Williams 1984).

★ Family Tychidae Dana, 1851

Remarks.—All species listed below were previously placed in the subfamily Tychinae of the Majidae in Williams (1984).

Pitho lherminieri (Schramm, 1867)

Known range.—Western Atlantic: off Beaufort Inlet, North Carolina, to west Florida; Veracruz, Mexico; West Indies to São Paulo, Brazil (Williams 1984).

Tyche emarginata White, 1847

Known range.—Western Atlantic: off Beaufort Inlet, North Carolina, through Bahamas to west coast of Florida (Williams 1984); Antilles; Rio Grande do Norte, Brazil (Melo 1998).

Superfamily Parthenopoidea MacLeay, 1838

Family Parthenopidae MacLeay, 1838

Subfamily Parthenopinae MacLeay, 1838

Remarks.—Ng & Rodríguez (1986) did not recognize subgenera within the genus *Parthenope*; *Platylambrus* was assigned full generic status.

★ *Celatopesia concava* (Stimpson, 1871)

Cryptopodia concava Stimpson.—Williams, 1984:346.

Remarks.—Chiong & Ng (1998) determined that the American species of the genus *Cryptopodia,* including *C. concava,* differed markedly in carapace appearance from that of the Indo-West Pacific species. *Celatopesia* was described, and the American species formerly included in *Cryptopodia* were referred to the new genus (Chiong & Ng 1998). Generic comparisons, species redescription and illustrations were also provided (Chiong & Ng 1998).

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; east central Florida; south of Cape San Blas, Florida, to St. Thomas, U.S. Virgin Islands; through Antilles; Maranhão to Rio de Janeiro, Brazil (Williams 1984, Melo 1998).

Heterocrypta granulata (Gibbes, 1850)

Known range.—Western Atlantic: from Nantucket Sound, Massachusetts, around peninsular Florida to southern Texas; through West Indies to Trinidad; Ceará to Paraná, Brazil (Williams 1984, Melo 1998).

Mesorhoea sexspinosa Stimpson, 1871

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; off northwest Florida to Flanagan Passage, Virgin Islands (Williams 1984).

★ *Parthenope agona* (Stimpson, 1871)

Parthenope (*Parthenope*) *agona* (Stimpson).—Williams, 1984:342.

Known range.—Western Atlantic: off Cape Hatteras and Cape Lookout, North Carolina; east central Florida; Gulf of Mexico (Pensacola, Florida to near Ft. Myers, Florida), through Florida Straits, West Indies and Caribbean Sea to Paraná, Brazil (Williams 1984, Melo 1998).

★ *Platylambrus fraterculus* (Stimpson, 1871)

Parthenope (*Platylambrus*) *fraterculus* (Stimpson).—Williams, 1984:343.

Known range.—Western Atlantic: off Cape Fear, North Carolina; east central Florida southward; Gulf of Mexico (off Cape San Blas, Florida) to Florida Straits; off Cape Catoche, Yucatán, Mexico; through West Indies to Rio Grande do Sul, Brazil (Williams 1984, Melo 1998).

★ *Platylambrus granulata* (Kingsley, 1879)

Parthenope (*Platylambrus*) *granulata* (Kingsley).—Williams, 1984:344.

Known range.—Western Atlantic: Bermuda; off Cape Hatteras, North Carolina, southward around Florida into Gulf of Mexico to Louisiana; Bahía Honda, Cuba (?); St. Thomas, U.S. Virgin Islands (Williams 1984).

★ *Platylambrus pourtalesii* (Stimpson, 1871)

Parthenope (*Platylambrus*) *pourtalesii* (Stimpson).—Williams, 1984:345.

Known range.—Western Atlantic: off Martha's Vineyard, Massachusetts; New Jersey to southern Florida; Gulf of Mexico through West Indies to Grenada (Williams 1984, Abele & Kim 1986).

Solenolambrus tenellus Stimpson, 1871

Known range.—Western Atlantic: off Cape Lookout, North Carolina; east central Florida southward, including the Florida Keys, into eastern Gulf of Mexico to near Cape St. George, Florida; Bahamas; Barbados (Williams 1984, Abele & Kim 1986).

Solenolambrus typicus Stimpson, 1871

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; western Gulf of Mexico off Corpus Christi, Texas, and north of Yucatán; Nicaragua Shelf; southern Florida through West Indies to Suriname and Rio de Janeiro, Brazil (Williams 1984, Melo 1998).

Superfamily Cancroidea Latreille, 1802
Family Cancridae Latreille, 1802

Remarks.—Based on fossil evidence (primarily characters of the carapace and chelipeds) Nations (1975) recognized four subgenera (*Glebocarcinus* Nations, 1975, *Romaleon* Gistl, 1848, *Metacarcinus* A. Milne-Edwards, 1862, *Cancer,* sensu stricto Linnaeus, 1758) within the genus *Cancer.* Williams (1984) adopted this classification. Schweitzer & Feldmann (2000) re-evaluated the Cancridae and elevated the subgenera of Nations (1975) to full generic status, again basing their conclusions only on fossil evidence. This classification has not gained acceptance with researchers working on extant species. Until more thorough investigation, incorporating a broader range of characters, is conducted, the classification of Williams (1984) will be followed. Williams & Wahle (1992) summarized and illustrated the differences between juvenile *Cancer borealis* and *C. irroratus.*

Cancer (*Metacarcinus*) *borealis* Stimpson, 1859

Known range.—Western Atlantic: Nova Scotia to south of Dry Tortugas, Florida (Williams 1984).

Cancer (*Cancer*) *irroratus* Say, 1817

Known range.—Western Atlantic: Labrador to off Miami, Florida (Williams 1984).

Superfamily Portunoidea Rafinesque, 1815
Family Geryonidae Colosi, 1923
► ★ *Chaceon quinquedens* (Smith, 1879)

Geryon quinquedens Smith.—Williams, 1984:485.

Remarks.—Williams (1984) considered this species to be extralimital. Manning & Holthuis (1989) described the new genus *Chaceon* for 21 species including *C. quinquedens.* This species occurs at 40–2155 m depth, but is usually found at the shelf edge or on the continental slope (Wigley et al. 1975, Williams 1984).

Known range.—Western Atlantic: Nova Scotia southward to Gulf of Mexico; Cuba; Brazil and Argentina (Wigley et al. 1975, Williams & Wigley 1977, Williams 1984).

Family Portunidae Rafinesque, 1815

Subfamily Carcininae Alcock, 1899

Carcinus maenas (Linnaeus, 1758)

Remarks.—Behrens Yamada & Hauck (2001) provided extensive information on distinguishing characteristics of this species and evaluated the usefulness of these characters in making field identifications.

Known range.—Western Atlantic (introduced): Northumberland Strait and Cape Breton to Virginia; Eastern Atlantic: Iceland; Norway, including southwestern and rarely southern Baltic Sea, through North Sea and British Isles to Mauritania; northwest Africa; also introduced to South Africa; Madagascar; Red Sea; Myanmar; India; Ceylon; Japan; Australia; Tasmania (Williams 1984, Squires 1990, Behrens Yamada & Hauck 2001); multiple eastern Pacific localities, including sites in California, Oregon, Washington, and Vancouver Island, British Colombia (Cohen et al. 1995, Grosholz & Ruiz 1996, Behrens Yamada et al. 2000).

Subfamily Polybiinae Ortmann, 1893

► *Bathynectes longispina* Stimpson, 1871

Remarks.—Williams (1984) considered this species to be extralimital. This species has been captured and observed recently at depths somewhat shallower (124–152 m; V. Guida, pers. comm.) than previously reported (100–1455 m, commonly >200 m; Williams & Wigley 1977). Manning & Holthuis (1981) reported that western Atlantic specimens identified as *B. superbus* (Costa, 1853) are actually *B. longispina.*

Known range.—Western Atlantic: Martha's Vineyard, Massachusetts, to off Mississippi River delta southward to Goajara Peninsula, Colombia; Bermuda (Williams 1984).

Ovalipes ocellatus (Herbst, 1799)

Known range.—Western Atlantic: Northumberland Strait, Prince Edward Island, to Georgia (Williams 1984).

Ovalipes stephensoni Williams, 1976

Known range.—Western Atlantic: southern New Jersey to Biscayne Bay, Florida (Williams 1984, Stehlik et al. 1991).

Subfamily Portuninae Rafinesque, 1815

Arenaeus cribrarius (Lamarck, 1818)

Remarks.—Juveniles of this species were collected at 6–10 m on sand and mud-sand sediments (Scelzo 2001).

Known range.—Western Atlantic: Vineyard Sound, Massachusetts, to Mar del Plata, Argentina (Williams 1984, Scelzo 2001).

Callinectes bocourti A. Milne-Edwards, 1879

Known range.—Western Atlantic: occasionally North Carolina, Florida, and Mississippi; otherwise Jamaica; Belize to Santa Catarina, Brazil, including Antilles and northern coast of South America (Williams 1984, Melo 1998).

Callinectes danae Smith, 1869

Known range.—Western Atlantic: Bermuda; New Hanover County, North Carolina (near Cape Fear); southern Florida; eastern side of Yucatán Peninsula to Rio Grande do Sul, Brazil, including Antilles and northern coast of South America (Williams 1984, Melo 1998).

Callinectes exasperatus (Gerstaecker, 1856)

Known range.—Western Atlantic: Bermuda; Duval County, east of Jacksonville, Florida, to Santa Catarina, Brazil, including Antilles and Venezuela; extreme southern Texas; Veracruz, Mexico (Williams 1984, Melo 1998).

Callinectes larvatus Ordway, 1863

Known range.—Western Atlantic: Bermuda; Beaufort, North Carolina, through Caribbean Sea to São Paulo, Brazil, including Antilles (Williams 1984, Melo 1998).

Callinectes ornatus Ordway, 1863

Known range.—Western Atlantic: Virginia through southern Florida; Bermuda; northwestern Yucatán to Rio Grande do Sul, Brazil, including Antilles (Williams 1984, Melo 1998).

Callinectes sapidus Rathbun, 1896

Known range.—Western Atlantic: Cape Cod, Massachusetts, to northern Argentina, including Bermuda, Antilles, Central America, and Venezuela (occasionally north of Cape Cod to Maine and Nova Scotia, in favorably warm periods); Eastern Atlantic: Øresund, Denmark; the Netherlands and adjacent North Sea; northwest and southwest France; Mediterranean Sea, including northern Adriatic, Aegean, and western Black seas; Eastern Pacific: Japan (Williams 1984, Squires 1990, Melo 1998).

Callinectes similis Williams, 1966

Known range.—Western Atlantic: off Delaware Bay to Key West, Florida; northwestern Florida around Gulf of Mexico to off Campeche, Yucatán; Isla de Providencia, Colombia (Williams 1984).

Cronius ruber (Lamarck, 1818)

Known range.—Western Atlantic: Little Egg Inlet, New Jersey; Rehoboth Bay, Delaware; Virginia; South Carolina to Rio Grande do Sul, Brazil, including Central America, Antilles, and northern South America; Eastern Atlantic: West Africa from Mauritania to Angola; Cape Verde, Principe, São Tome and Annobon islands; Eastern Pacific: Baja California to Peru; Clipperton Island; Galápagos Islands (Williams 1984, Melo 1998).

Portunus anceps (de Saussure, 1858)

Known range.—Western Atlantic: Bermuda; Cape Hatteras, North Carolina, to Rio de Janeiro, Brazil, including Antilles (Williams 1984, Melo 1998).

Portunus depressifrons (Stimpson, 1859)

Known range.—Western Atlantic: Bermuda; Fort Macon, North Carolina, through northwest Florida to Gulf of Campeche and Caribbean Sea (Williams 1984).

Portunus floridanus Rathbun, 1930

Known range.—Western Atlantic: east of Cape Lookout, North Carolina, to Nicaragua; through West Indies and northern South America to Suriname (Williams 1984).

Portunus gibbesii (Stimpson, 1859)

Known range.—Western Atlantic: southern Massachusetts through Gulf of Mexico along coast to French Guiana (Williams 1984); Bahia, Brazil (Melo 1998).

Portunus ordwayi (Stimpson, 1860)

Known range.—Western Atlantic: Vineyard Sound, Massachusetts; Bermuda; North Carolina through Gulf of Mexico, West Indies and Caribbean Sea to Rio Grande do Sul, Brazil; Fernando de Noronha, Brazil (Williams 1984, Melo 1998).

Portunus sayi (Gibbes, 1850)

Known range.—Western Atlantic: off the Grand Banks through Gulf of Mexico to the Guianas; Bermuda; Eastern Atlantic: Canary Islands; Morocco (Williams 1984, Squires 1990).

Portunus spinicarpus (Stimpson, 1871)

Known range.—Western Atlantic: off Oregon Inlet, North Carolina, to Santa Catarina, Brazil, including Antilles and northern South America (Williams 1984, Melo 1998).

Portunus spinimanus Latreille, 1819

Known range.—Western Atlantic: New Jersey to Rio Grande do Sul, Brazil, including Gulf of Mexico, West Indies and northern South America; Bermuda (Williams 1984, Melo 1998).

Superfamily Xanthoidea MacLeay, 1838

Remarks.—Guinot (1978) concluded that Xanthidae actually represented eight different families (Carpiliidae Ortmann, 1893, Menippidae Ortmann, 1893, Platyxanthidae Guinot, 1977, Xanthidae McLeay, 1838, Panopeidae Ortmann, 1893, Pilumnidae Samouelle, 1819, Trapeziidae Miers, 1886, and Geryonidae Colosi, 1924) which should be recognized under the superfamily Xanthoidea. Williams (1984) elected not to adopt this classification. Instead, he placed the majority of xanthid taxa (exclusive of the Goneplacidae) under the single family Xanthidae. In the intervening years, Guinot's classification, with minor modification, has gained acceptance by the majority of crustacean researchers (Schubart, Neigel, & Felder 2000, Martin & Davis 2001).

Family Goneplacidae MacLeay, 1838

Remarks.—The Goneplacidae has long been recognized as containing heterogenous groups of genera (Hendrickx 1998, and references therein). Because revisionary studies of the Goneplacidae are still in progress, formal subdivision into subfamilies is not attempted here. Furthermore, after further revision of this family, it is likely that new families will be added and subfamilies elevated to full family status (Guinot 1978, Williams 1984, Sternberg, pers. comm.).

Euryplax nitida Stimpson, 1859

Known range.—Western Atlantic: Bermuda; off Beaufort, North Carolina, to Heald Bank, Texas; Antilles to Santa Catarina, Brazil (Williams 1984, Melo 1998).

Frevillea hirsuta (Borradaile, 1916)

Known range.—Western Atlantic: North Carolina to Rio Grande do Sul, Brazil (Williams 1984, Melo 1998).

Goneplax sigsbei
(A. Milne-Edwards, 1880)

Known range.—Western Atlantic: east of Cape Fear, North Carolina; Grenada (Williams 1984).

Speocarcinus carolinensis Stimpson, 1859

Known range.—Western Atlantic: south of Cape Hatteras, North Carolina, to Rio Grande do Sul, Brazil, including West Indies (Williams 1984, Melo 1998).

★ Family Menippidae Ortmann, 1893

Remarks.—Williams (1984) listed these taxa under the family Xanthidae.

Eriphia gonagra (Fabricius, 1781)

Known range.—Western Atlantic: Bermuda; North Carolina to Patagonia, including Central America, Antilles, and northern South America (Williams 1984, Melo 1998).

Menippe mercenaria (Say, 1818)

Remarks.—Williams & Felder (1986) recognized two morphologically distinct populations of stone crab in the Gulf of Mexico and determined that these populations represented distinct species. Range of *Menippe mercenaria* was restricted; *M. adina* Williams & Felder, which ranges from northwestern Florida around the Gulf of Mexico to Tamaulipas State, Mexico, was described (Williams & Felder 1986).

Known range.—Western Atlantic: Cape Lookout, North Carolina, through peninsular Florida; Bahamas and Greater Antilles to Yucatán Peninsula, Mexico; and Belize (Williams & Felder 1986).

★ Family Panopeidae Ortmann, 1893

Remarks.—Williams (1984) listed these taxa under the family Xanthidae. Genera included in this family were based on the conclusions of Guinot (1978) and subsequent acceptance of generic placements by

Martin & Abele (1986). Schubart, Neigel, & Felder (2000) presented a molecular phylogeny of western Atlantic Panopeidae.

★ *Dyspanopeus sayi* (Smith, 1869)

Neopanope sayi (Smith).—Williams, 1984: 409.

Remarks.—Martin & Abele (1986) described the new genus *Dyspanopeus* for *D. sayi* (occurring in the western Atlantic) and *D. texanus* (occurring in the Gulf of Mexico).

Known range.—Western Atlantic: southern Gulf of St. Lawrence to Florida Keys; Eastern Atlantic (introduced): Bristol Channel, United Kingdom (Williams 1984, Squires 1990).

Eurypanopeus abbreviatus
(Stimpson, 1860)

Known range.—Western Atlantic: South Carolina to Rio Grande do Sul, Brazil, including Gulf of Mexico, Antilles, and northern South America (Williams 1984, Melo 1998).

Eurypanopeus depressus (Smith, 1869)

Known range.—Western Atlantic: Massachusetts Bay through Florida to southern Texas; Dutch West Indies; Uruguay; Bermuda (Williams 1984).

Eurytium limosum (Say, 1818)

Known range.—Western Atlantic: Bermuda; South Carolina; Louisiana to Santa Catarina, Brazil, including West Indies and Caribbean Sea (Williams 1984, Melo 1998).

Glyptoplax smithii A. Milne-Edwards,
1880

Remarks.—This species previously was placed in the family Goneplacidae (Williams 1984). Guinot (1978) transferred this species to the Panopeidae; Martin & Abele (1986) adopted this arrangement.

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to Gulf of Mexico and Yucatán Channel (Williams 1984).

Hexapanopeus angustifrons
(Benedict & Rathbun, 1891)

Known range.—Western Atlantic: Vineyard Sound, Massachusetts, to Port Aransas, Texas; West Indies; Pernambuco to Santa Catarina, Brazil (Williams 1984, Melo 1998).

Hexapanopeus paulensis Rathbun, 1930

Known range.—Western Atlantic: South Carolina to Uruguay, including Gulf of Mexico (Williams 1984).

Panopeus herbstii H. Milne Edwards,
1834

Remarks.—Williams (1983) examined the *Panopeus herbstii* species complex and determined that ‘forms’ previously recognized by Rathbun (1930) were sufficiently different and represented distinct species. As a result, *P. herbstii* was better defined, and its range determined to be the shallow intertidal and subtidal waters of the eastern United States.

Known range.—Western Atlantic: Boston Harbor, Massachusetts, to Indian River County, Florida (Williams 1983).

► *Panopeus obesus* Smith, 1869

Remarks.—This species was recognized previously as a form of *Panopeus herbstii* (Rathbun 1930). Williams (1983) rediagnosed this form and elevated it to full species rank; diagnosis, measurements, and color description of this species were also provided. *Panopeus obesus* is found in marsh edge, and shallow intertidal and subtidal waters of the Carolinian province.

Known range.—Western Atlantic: Beaufort, North Carolina, to northeastern Florida; Sarasota County, Florida, to Louisiana; Texas; northern Mexico (Williams 1983).

Panopeus occidentalis de Saussure, 1857

Known range.—Western Atlantic: Bermuda; North Carolina to Santa Catarina, Brazil, including Central America, Antilles and northern South America (Williams 1984, Melo 1998).

Panoplax depressa Stimpson, 1871

Remarks.—This species was placed previously in the family Goneplacidae (Williams 1984). Guinot (1978) transferred this species to the Panopeidae; Martin & Abele (1986) adopted this arrangement.

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; off Jacksonville and Cape San Blas, Florida; through Antilles; Amapá to Pernambuco, Brazil (Williams 1984, Melo 1998).

Rhithropanopeus harrisii (Gould, 1841)

Known range.—Western Atlantic: southwestern Gulf of St. Lawrence to Veracruz, Mexico; Eastern Atlantic (introduced): parts of Europe; Eastern Pacific (introduced): west coast of United States (Williams 1984, Squires 1990).

★ Family Pilumnidae Samouelle, 1819

Remarks.—Williams (1984) listed these taxa under the family Xanthidae.

Lobopilumnus agassizii (Stimpson, 1871)

Known range.—Western Atlantic: Bermuda; North Carolina; eastern Gulf of Mexico; Yucatán; Cuba; Venezuela; Trinidad (Williams 1984).

Pilumnus dasypodus Kingsley, 1879

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to Santa Catarina, Brazil, including Gulf of Mexico, Caribbean Sea, and West Indies (Williams 1984, Melo 1998).

Pilumnus floridanus Stimpson, 1871

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to Bahia, Brazil, including Gulf of Mexico, Yucatán Channel, Central America, Venezuela, and West Indies (Williams 1984, Melo 1998).

Pilumnus lacteus Stimpson, 1871

Known range.—Western Atlantic: near Beaufort, North Carolina, to Florida; Cuba (Williams 1984).

Pilumnus pannosus Rathbun, 1896

Known range.—Western Atlantic: Bogue Sound, off Beaufort, North Carolina, to Port Aransas, Texas; West Indies to Virgin Islands (Williams 1984).

Pilumnus sayi Rathbun, 1897

Known range.—Western Atlantic: North Carolina to Curaçao, including Gulf of Mexico and West Indies (Williams 1984).

★ Family Pseudorhombilidae Alcock, 1900

Remarks.—This taxon was previously considered a subfamily (Pseudorhombilinae) within the Goneplacidae (Williams 1984). Hendrickx (1998) proposed the family designation to accommodate six genera.

Nanoplax xanthiformis
(A. Milne-Edwards, 1881)

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to Rio de Janeiro, Brazil, including Gulf of Mexico, Yucatán, West Indies, and northern South America (Williams 1984, Melo 1998).

★ Family Trapeziidae Miers, 1886

Remarks.—Williams (1984) listed this taxon under the family Xanthidae.

Domecia acanthophora acanthophora (Desbonne & Schramm, 1867)

Known range.—Western Atlantic: Bermuda; Cape Lookout Shoals, North Carolina; northwestern Gulf of Mexico to Alagoas, Brazil, including West Indies and Caribbean Sea (Williams 1984, Melo 1998).

Family Xanthidae MacLeay, 1838

Allactaea lithostrota Williams, 1974

Known range.—Western Atlantic: Bermuda; off Cape Lookout, North Carolina; Florida Straits; off Cape Catoche, Yucatán; off Venezuela and Suriname (Williams 1984); Antilles; off Rio de Janeiro to Rio Grande do Sul, Brazil (Melo 1998).

Carpoporus papulosus Stimpson, 1871

Known range.—Western Atlantic: between Cape Hatteras and Cape Lookout, North Carolina; Gulf of Mexico, off Mobile Bay southeastward; Cape Catoche, Yucatán (Williams 1984).

Glyptoxanthus erosus (Stimpson, 1859)

Known range.—Western Atlantic: Cape Lookout, North Carolina, southward around Florida into Gulf of Mexico to off Grand Isle, Louisiana; Yucatán; West Indies to Guadeloupe (Williams 1984).

Melybia thalamita Stimpson, 1871

Known range.—Western Atlantic: off Cape Lookout, North Carolina, southwest of Mississippi River delta to São Paulo, Brazil, including West Indies and northern South America (Williams 1984, Melo 1998).

Micropanope nuttingi (Rathbun, 1898)

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to São Paulo, Brazil, including Gulf of Mexico and West Indies (Williams 1984, Melo 1998).

Micropanope sculptipes Stimpson, 1871

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina, to Port Aransas, Texas; West Indies to Barbados; Amapá to Rio de Janeiro, Brazil (Williams 1984, Melo 1998).

Micropanope urinator (A. Milne-Edwards, 1881)

Known range.—Western Atlantic: off Cape Hatteras and Cape Lookout, North Carolina; Florida Keys to St. Croix (Williams 1984); Antilles; Pará to Maranhão, Brazil (Melo 1998).

Paractaea rufopunctata nodosa (Stimpson, 1860)

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; off Mississippi River delta, through West Indies to Uruguay; Central Atlantic: Ascension Island (Williams 1984, Melo 1998).

Pseudomedaeus agassizii (A. Milne-Edwards, 1880)

Known range.—Western Atlantic: Cape Hatteras, North Carolina, to southern Texas (Williams 1984).

Pseudomedaeus distinctus (Rathbun, 1898)

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, through Straits of Florida to northwest of Dry Tortugas; Puerto Rico; Barbados (Williams 1984).

Tetraxanthus rathbunae Chace, 1939

Known range.—Western Atlantic: off Cape Lookout, North Carolina, to Rio Grande do Sul, Brazil, including Gulf of Mexico and Antilles (Williams 1984, Melo 1998).

Superfamily Pinnotheroidea De Haan, 1833

Family Pinnotheridae De Haan, 1833

Remarks.—Marques & Pohle (1995) conducted a phylogenetic analysis of this family using larval characters and demonstrated that several taxa are paraphyletic taxa and that further analysis will be needed to resolve relationships within this family.

Subfamily Pinnotherinae De Haan, 1833

Remarks.—Griffith (1987) presented a hypothesis of phylogenetic relationships within the genus *Dissodactylus* based on adult morphology. Marques & Pohle (1995) conducted a phylogenetic analysis of members of this genus using larval characters and produced results that only partially corroborated the relationships proposed by Griffith (1987). In a separate analysis, both data sets (adult morphology and larval morphology) were combined (Marques & Pohle 1995). Results of this analysis provided a more robust hypothesis of relationships than when either character set was analyzed independently.

Dissodactylus crinitichelis Moreira, 1901

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; off northwest Florida; Caribbean Sea and South America to Rio de la Plata, Argentina (Williams 1984).

Dissodactylus mellitae (Rathbun, 1900)

Known range.—Western Atlantic: western Vineyard Sound, Massachusetts, to Charleston, South Carolina; Hutchinson Island, east Florida; western Florida; off Galveston, Texas (Williams 1984).

★ *Gemmotheres chamae* (Roberts, 1975)

Pinnotheres chamae Roberts.—Williams, 1984:440.

Remarks.—Campos (1996) described the new genus *Gemmotheres* for *P. chamae*; illustrations were also provided.

Known range.—Western Atlantic: North Carolina coast (Williams 1984, Campos 1996).

▶ *Parapinnixa beaufortensis* Rathbun, 1918

Remarks.—Williams (1984) considered this species to be extralimital.

Known range.—Western Atlantic: off Beaufort, North Carolina (Williams 1984).

Parapinnixa bouvieri Rathbun, 1918

Known range.—Western Atlantic: off Charleston, South Carolina; south of Dry Tortugas, Florida; off Cape Catoche, Yucatán; Puerto Rico; Amapá, Brazil (Williams 1984, Melo 1998).

Parapinnixa hendersoni Rathbun, 1918

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; off Tampa Bay, Florida, through West Indies to Curaçao; Venezuela; Maranhão to Espírito Santo, Brazil (Williams 1984, Melo 1998).

Pinnaxodes floridensis Wells and Wells, 1961

Known range.—Western Atlantic: off North Carolina to Georgia; northwest Florida (Williams 1984).

★ *Tumidotheres maculatus* (Say, 1818)

Pinnotheres maculatus Say.—Williams, 1984:441.

Remarks.—Campos (1989) described the new genus *Tumidotheres* and discussed generic relationships and life history traits.

Known range.—Western Atlantic: off Martha's Vineyard, Massachusetts, to Golfo San Matías, Argentina (Williams 1984).

★ *Zaops ostreum* (Say, 1817)

Pinnotheres ostreum Say.—Williams, 1984: 444.

Remarks.—Manning (1993) concluded that *Zaops* Rathbun, 1900 should be removed from the synonymy of *Pinnotheres* and recognized as a distinct genus. Additionally, other pinnotherid genera formerly placed in the synonymy of *Pinnotheres* were diagnosed, figured and differentiated from *Pinnotheres* sensu Manning (1993).

Known range.—Western Atlantic: Salem, Massachusetts, to Santa Catarina, Brazil (Williams 1984).

Subfamily Pinnothereliinae Alcock, 1900

★ *Austinixa cristata* (Rathbun, 1900)

Pinnixa cristata Rathbun.—Williams, 1984:453.

Remarks.—Heard & Manning (1997) recognized and described the new genus *Austinixa* for *Pinnixa cristata* and six other species formerly assigned to *Pinnixa.*

Known range.—Western Atlantic: Beaufort, North Carolina, to Miami, Florida; northern and southwestern Gulf of Mexico (Manning & Felder 1989); Central America; Brazil (Melo 1998).

Pinnixa chaetopterana Stimpson, 1860

Known range.—Western Atlantic: Wellfleet, Massachusetts, to Rio Grande do Sul, Brazil (Williams 1984).

Pinnixa cylindrica (Say, 1818)

Known range.—Western Atlantic: North Falmouth, Massachusetts, to Pensacola, Florida, including Dry Tortugas (Williams 1984).

Pinnixa floridana Rathbun, 1918

Known range.—Western Atlantic: southeast of Cape Lookout, North Carolina; Hutchinson Island, east Florida; west coast of Florida (Williams 1984).

Pinnixa lunzi Glassell, 1937

Known range.—Western Atlantic: off the eastern shore of Virginia; North and South Carolina; Georgia; off Mississippi River delta; Seven and One-Half Fathom Reef, off Texas (Williams 1984).

Pinnixa retinens Rathbun, 1918

Known range.—Western Atlantic: Delaware Bay; Chesapeake Bay; Little River Inlet, South Carolina; Alligator Harbor, Florida; Aransas area of Texas coast (Williams 1984).

Pinnixa sayana Stimpson, 1860

Known range.—Western Atlantic: Vineyard Sound, Massachusetts, to Beaufort, North Carolina; Hutchinson Island, east central Florida; Sarasota Bay, Florida to Grand Isle, Louisiana; Amapá to Rio Grande do Sul, Brazil (Williams 1984, Melo 1998).

Superfamily Ocypodoidea Rafinesque, 1815

Family Ocypodidae Rafinesque, 1815

Subfamily Ocypodinae Rafinesque, 1815

Remarks.—Rosenberg (2001) conducted a phylogenetic analysis of the genus *Uca* using 236 discrete morphological characters. Although many scientists ignore subgeneric designations, Rosenberg (2001) considered subgenera within *Uca* to be valid. The three species of *Uca* occurring in the region are considered to be members of the subgenus *Minuca* (Rosenberg 2001).

Ocypode quadrata (Fabricius, 1787)

Known range.—Western Atlantic: Block Island, Rhode Island, to Rio Grande do Sul, Brazil; Fernando de Noronha Archipelago, Brazil; Bermuda (Williams 1984, Melo 1998).

Uca minax (LeConte, 1855)

Remarks.—Felder & Staton (1994) analyzed electrophoretic allozyme assays and observed slight differentiation between Gulf of Mexico and Atlantic populations.

Known range.—Western Atlantic: Buzzards Bay, Cape Cod, Massachusetts, to Daytona Beach, Florida; Yankeetown, northwest Florida, to Matagorda Bay, Texas (Williams 1984, Barnwell & Thurman 1984).

Uca pugilator (Bosc, 1802)

Known range.—Western Atlantic: Cape Cod, Massachusetts, southward around the tip of peninsular Florida and westward to Pensacola Beach, Florida; possible rare occurrences in Bahamas and western Gulf of Mexico (Barnwell & Thurman 1984).

Uca pugnax (Smith, 1870)

Known range.—Western Atlantic: Provincetown, Massachusetts, to Daytona Beach, Florida (Williams 1984, Barnwell & Thurman 1984).

Family Palicidae Bouvier, 1898

Palicus alternatus Rathbun, 1897

Known range.—Western Atlantic: Cape Hatteras to southeast of Cape Fear, North Carolina; Gulf of Mexico along west coast of Florida from Cape San Blas to Key West (Williams 1984).

Palicus faxoni Rathbun, 1897

Known range.—Western Atlantic: off Cape Hatteras, North Carolina, to near Cape Canaveral, Florida; off Yucatán, Mexico, near Quita Sueño Banks; southwest of St. Christopher; Rio Grande do Norte to Rio de Janeiro, Brazil (Williams 1984, Melo 1998).

► *Palicus gracilis* (Smith, 1883)

Remarks.—Williams (1984) considered this species to be extralimital. This species occurs at 183–512 m (Williams & Wigley 1977).

Known range.—Western Atlantic: Martha's Vineyard, Massachusetts, to Curaçao, including Gulf of Mexico (Williams & Wigley 1977).

Palicus sica (A. Milne-Edwards, 1880)

Known range.—Western Atlantic: off Charleston, South Carolina, to Cape Canaveral, Florida; west coast of Florida to Rio Grande do Sul, Brazil, including West Indies (Williams 1984, Melo 1998).

Superfamily Grapsoidea MacLeay, 1838

Family Grapsidae MacLeay, 1838

Remarks.—Previously, family Grapsidae was considered to be comprised of four subfamilies. Based on a cladistic study by Sternberg & Cumberlidge (1998) the Grapsidae were redefined and restricted to include all genera previously placed in the subfamily Grapsinae. Molecular data also supported elevation of grapsid subfamilies to full family status (Schubart, Cuesta, Diesel, & Felder 2000).

Pachygrapsus transversus (Gibbes, 1850)

Known range.—Western Atlantic: Bermuda; Cape Lookout, North Carolina, to Montevideo, Uruguay; Eastern Atlantic: Mediterranean Sea to northern Angola; Eastern Pacific: California to Peru; Galápagos Islands (Williams 1984).

Planes minutus (Linnaeus, 1758)

Known range.—Western Atlantic: off the Grand Banks of Newfoundland south to 11°N, exclusive of Gulf of Mexico; Eastern Atlantic: southern North Sea south to 11°N, including Mediterranean Sea (Williams 1984, Squires 1990).

★ Family Plagusiidae Dana, 1851

Remarks.—This taxon was previously considered a subfamily of the Grapsidae (e.g., Williams 1984, Guinot & Bouchard 1998). Based on results of a cladistic study, Sternberg & Cumberlidge (1998) concluded that the two genera (*Percnon* and *Plagusia*) placed in the subfamily Plagusiinae formed a monophyletic taxon; subfamily Plagusiinae was redefined and elevated to family status (Plagusiidae). Based on results of a molecular phylogeny, however, Schubart, Cuesta, Diesel, & Felder (2000) questioned taxonomic placement of *Percnon* in this family. Sternberg & Cumberlidge (1998) had placed *Euchirograpsus* in the Varuninae. However, based on morphological and molecular evidence (Schubart, Cuesta, Diesel, & Felder 2000), *Euchirograpsus* belongs in the Plagusiidae.

Euchirograpsus americanus
A. Milne-Edwards, 1880

Remarks.—This species was previously considered a member of the Varuninae (Williams 1984). Based on molecular evidence and larval morphology, Schubart, Cuesta, Diesel, & Felder (2000) proposed inclusion of this species in the family Plagusiidae.

Known range.—Western Atlantic: Oceanographer Canyon, edge of Georges Bank; off Oregon Inlet, North Carolina; Florida to Venezuela, including West Indies; Rio Grande do Sul, Brazil (Williams 1984, 1988; Melo 1998).

Percnon gibbesi
(H. Milne Edwards, 1853)

Remarks.—Based on molecular evidence, Schubart, Cuesta, Diesel, & Felder (2000) suggested that this species does not belong in the family Plagusiidae. Those authors reported that the taxonomic position of *Percnon gibbesi* was uncertain and required further investigation. Until more definitive results are available, placement of this species will remain in the Plagusiidae.

Known range.—Western Atlantic: Bermuda; Fort Macon, North Carolina; southern Florida and Bahamas to Fernando de Noronha Archipelago, Brazil, including Antilles; Eastern Atlantic: Azores to Angola; Mediterranean Sea (Pipitone et al. 2001); Eastern Pacific: Cape San Lucas, lower California, to Chile; Galápagos Islands (Williams 1984, Melo 1998).

Plagusia depressa (Fabricius, 1775)

Known range.—Western Atlantic: Bermuda; Beaufort, North Carolina, to Bahia, Brazil, including Gulf of Mexico and West Indies; Fernando de Noronha Archipelago, Rocas Atoll, Saint Paul Rocks, and Trindade Island, Brazil; Eastern Atlantic: Azores; Madeira; Morocco to northern Angola; Central Atlantic: St. Helena Island (Williams 1984, Melo 1998).

★ Family Sesarmidae Dana, 1851

Remarks.—This taxon was previously considered a subfamily of the Grapsidae (e.g., Williams 1984, Guinot & Bouchard 1998). Based on results of a cladistic study, Sternberg & Cumberlidge (1998) concluded that taxa previously included in the subfamily Sesarminae formed a polyphyletic group. However, one clade comprising the majority of *Sesarma*-like genera, including *Sesarma* and *Armases,* was redefined as the family Sesarmidae (Sternberg & Cumberlidge 1998).

★ *Armases cinereum* (Bosc, 1802)

Sesarma (*Chiromantes*) *cinereum* (Bosc).—Williams, 1984:465.

Remarks.—Abele (1992) described the new genus *Armases* for American species of *Sesarma* assigned to the subgenus *Chiromantes*; generic diagnosis, species description, and illustrations are provided. The phylogeny of *Armases* proposed by Niem (1996) supported establishment of *Armases* Abele, 1992.

Known range.—Western Atlantic: Magothy River, Chesapeake Bay, Maryland, to Palm Beach, east Florida; Collier County, west Florida, to Veracruz, Mexico (Williams 1984).

★ *Sesarma reticulatum* (Say, 1817)

Sesarma (*Sesarma*) *reticulatum* (Say).—Williams, 1984:466.

Remarks.—Subgenera were not recognized within the genus *Sesarma* by Abele (1992). Based on electrophoretic results, Felder & Staton (1994) concluded that allozyme divergence between Gulf of Mexico and Atlantic populations was comparable to levels previously reported for speciated populations, suggesting that *Sesarma reticulatum* represented a species complex.

Known range.—Western Atlantic: Woods Hole, Massachusetts, to Volusia County, east Florida; Sarasota, west Florida, to Barra del Tordo, Tamaulipas, Mexico (Williams 1984, Felder & Staton 1994).

★ Family Varunidae H. Milne Edwards, 1853

Remarks.—This taxon was previously considered a subfamily of the Grapsidae (e.g., Williams 1984, Guinot & Bouchard 1998). Cladistic analysis revealed that the Varuninae is an artificial group in need of re-examination (Sternberg & Cumberlidge 1998). It is possible that this group, presently recognized at the family level (Schubart, Cuesta, Diesel, & Felder 2000, Martin & Davis 2001) may prove to represent several different families (Sternberg & Cumberlidge 1998). Molecular data also support this conclusion (Schubart, Cuesta, Diesel, & Felder 2000).

► *Hemigrapsus sanguineus* (De Haan, 1853)

Remarks.—The Asian shore crab was most likely introduced in the western Atlantic via ballast water discharged sometime in the early 1980's (McDermott 1998). The crab was first discovered in 1988 in southern New Jersey (Williams & McDermott 1990). *Hemigrapsus sanguineus* was the most abundant brachyuran at the intertidal monitoring site in southern New Jersey, some areas of Long Island Sound (McDermott 1998) and Narragansett Bay, RI (pers. obs.). McDermott (1998) reported this crab occurring in the upper to middle intertidal zone of New Jersey, whereas others (Lohrer & Whitlatch 1997, Ledesma & O'Connor 2001) observed higher abundances in the middle and lower intertidal zone of sampling locations in eastern Long Island Sound and southeastern New England. Crab abundance increased with increased rock cover (Ledesma & O'Connor 2001).

Known range.—Western Atlantic: Appledore Island, Isles of Shoals, Maine (J. Morin, pers. comm.) and New Hampshire (McDermott 2000) to Oregon Inlet, North Carolina (McDermott 1998); Eastern Atlantic: Le Havre, France; "Oosterschelde", Netherlands (Breton et al. 2002); Western Pacific: Sakhalin, Korea; north China to Hong Kong; all coasts of Japan from Hokkaido to Okinawa (Williams & McDermott 1990).

Discussion

The decapod crustacean assemblage occurring in shallow waters (≤190 m) of the temperate eastern United States from Maine to Cape Canaveral, Florida, totals 391 species. This assemblage includes 122 shrimp species (28 penaeids, 2 stenopodids, and 92 carideans), 10 thalassinideans, 8 lobsters, 61 anomurans, and 190 brachyurans. By comparison, the previous comprehensive review of this assemblage by Williams (1984) recognized 103 species of shrimps (21 penaeids, 2 stenopodids, and 80 carideans), 8 thalassinideans (including callianassids, upogebiids and axiids), 6 lobsters, 51 anomurans, and 174 brachyurans (total decapods = 342).

Since publication of Williams (1984), 51 species are new to this checklist. Thirteen species (Table 1) previously considered extralimital by Williams (1984:484) because their centers of distribution or abundance occur beyond the boundaries of the region are now incorporated into the updated checklist because their geographic and bathymetric ranges are within the limits set for the region under consideration. An additional 16 species (Table 1), most likely excluded (i.e., not even considered as ex-

Table 1.—Western Atlantic decapod Crustacea occurring in regions that were considered 'extralimital' or excluded from consideration by Williams (1984) because their geographic or bathymetric range centered beyond the boundaries of regions of consideration.

'Extralimital'	Excluded
Pleoticus robustus	*Aristaeomorpha foliacea*
Bythocaris nana	*Hadropenaeus affinis*
Caridion gordoni	*Hadropenaeus modestus*
Plesionika martia	*Penaeopsis serrata*
Plesionika tenuipes	*Lucifer typus*
Plesionika willisi	*Heterocarpus ensifer*
Catapagurus sharreri	*Plesionika edwardsii*
Hemipagurus gracilis	*Nephropsis aculeata*
Mithrax cornutus	*Tomopagurus cokeri*
Bathynectes longispina	*Parapagurus pilosimanus*
Chaceon quinquedens	*Sympagurus pictus*
Parapinnixa beaufortensis	*Munida forceps*
Palicus gracilis	*Lysirude nitidus*
	Cyclozodion angustum
	Pyromaia arachna
	Stenocionops furcata furcata

tralimital) from consideration by Williams because their bathymetric distributions were centered beyond 190 m or their geographic distributions were centered south of Cape Canaveral, Florida, are included in the present checklist for this same reason. Twelve species, discovered and described during the past 20 years, were also added to the regional assemblage (Table 2). Four species (*Trachycaris rugosa, Axius armatus, Pagurus brevidactylus, Panopeus obesus*) were added through a refined understanding of the systematics of species complexes with improved recognition and delineation of component species. One nonindigenous species (*Hemigrapsus sanguineus*) was introduced and has become established in the region. An additional five species (*Parapenaeus americanus, Scyllarides aequinoctialis, Petrolisthes armatus, Dromia erythropus, Clythrocerus nitidus*) have also become part of the regional assemblage through northward extension of their geographic ranges.

Six species have been removed from Williams (1984) checklist (Table 3). Four species (*Pontonia margarita, Anisopagurus pygmaeus, Iridopagurus caribbensis,* and *Hyas coarctatus alutaceus*) once thought to be members of this assemblage (Williams 1984) are removed from the checklist because recent revisions and investigations involving these species (García-Gómez 1983, Lemaitre & McLaughlin 1996, Fransen 2000) clearly indicate that they do not occur in the region. One eastern Pacific species (*Notolopas lamellatus*) was erroneously reported from the region by Rathbun (Williams 1984). Additionally, *Leptochela bermudensis* was previously included in the checklist because it was considered as likely to occur in the region by Williams (1984). Since this species has never actually been recorded from the region, it has been removed from the checklist.

Better understanding of species concepts and interspecific variation has necessitated placement of some nominal species previously considered part of this regional assemblage into synonymy. For decapod crustaceans of the eastern United States, eleven nominal species (Table 4) have been re-evaluated and determined not to represent distinct species. Additionally, one family and one genus have also been placed into synonymy (Table 4).

A significant proportion of systematic research on western Atlantic decapod crusta-

Table 2.—Summary of more recently described western Atlantic decapod Crustacea not previously listed in Williams (1984).

Family	Genus and species	Year of description	Geographic range	Depth of occurrence
Disciadidae	*Discias vernbergi*	1987	Georgia–west Florida	54–74 m
Palaemonidae	*Pontonia manningi*	2000	North Carolina–Gulf of Mexico, Caribbean Sea, eastern Atlantic	shallow–80 m
Alpheidae	*Alpheus angulosus*	2002	North Carolina–Gulf of Mexico, Mexico, Haiti	intertidal, shallow
Alpheidae	*Alpheus estuariensis*	1984	Florida, Gulf of Mexico, Caribbean Sea, Brazil	intertidal–22 m
Callianassidae	*Necallianassa berylae*	1998	South Carolina–Georgia	35–75 m
Paguridae	*Anisopagurus hopkinsi*	1996	Georgia–Gulf of Mexico	91–165 m
Paguridae	*Iridopagurus reticulatus*	1983	North Carolina–Florida, Bahamas, Greater and Lesser Antilles, northern South America	1–38 m
Paguridae	*Pagurus maclaughlinae*	1982	Georgia–Florida, Gulf of Mexico, Caribbean	1–5 m
Paguridae	*Tomopagurus wassi*	1981	Southeastern United States, Florida Straits, Gulf of Mexico, Caribbean–northern Brazil	75–360 m
Homolidae	*Homola minima*	1995	Massachussetts–Brazil	55–690 m
Calappidae	*Cyclozodion tuberatum*	1988	North Carolina–Bahamas–eastern Gulf of Mexico, Suriname	31–188 m
Inachidae	*Stenorhynchus yangi*	1989	Massachussetts–Gulf of Mexico–Suriname	31–365 m

Table 3.—Summary of western Atlantic decapod crustacean species previously (Williams 1984) considered to be part of the fauna off the eastern United States but now known not to occur in the region. These species were removed from the checklist.

Species	Range	Reason for removal from checklist
Leptochela bermudensis Gurney, 1939	Bermuda, Puerto Rico through the Lesser Antilles	Previously considered likely to occur in the region (Williams 1984), but has never been reported.
Pontonia margarita Smith, 1869	Eastern Pacific	Formerly thought to be a widespread species; with resolution of species complex now known to occur only in the Pacific Ocean (Fransen 2000).
Anisopagurus pygmaeus (Bouvier, 1918)	Florida Keys, Cuba to Curaçao	Resolution of species systematics indicated geographic range occurs beyond limits of region (Lemaitre & McLaughlin 1996).
Iridopagurus caribbensis (A. Milne-Edwards & Bouvier, 1893)	Miami, Florida to Colombia	Resolution of species systematics indicated geographic range occurs beyond limits of region (García-Gómez 1983).
Hyas coarctatus alutaceus Brandt, 1851	Eastern Pacific	Resolution of species systematics indicated geographic range occurs beyond limits of region (Squires 1990).
Notolopas lamellatus Stimpson, 1871	Eastern Pacific	Erroneously reported from the region (Williams 1984).

Table 4.—Summary of nominal taxa of western Atlantic decapod crustaceans placed in synonymy since publication of Williams (1984).

Nominal taxa appearing in Williams (1984)		Senior synonym
Automate gardineri	=	*Automate dolichognatha*
Hippolyte curacaoensis	=	*Hippolyte obliquimanus*
Lebbeus zebra	=	*Lebbeus microceros*
Callianassa atlantica	=	*Gilvossius setimanus*
Manucomplanus corallinus	=	*Manucomplanus ungulatus*
Pagurus hendersoni	=	*Pagurus stimpsoni*
Hypoconcha sabulosa	=	*Hypoconcha parasitica*
Homola barbata (in part)	=	*Homola minima*
Cycloes bairdii	=	*Cryptosoma balguerii*
Mithrax pleuracanthus	=	*Mithrax hispidus*
Mithrax acuticornis	=	*Mithrax cornutus*
Family Tymolidae	=	Family Cyclodorippidae
Genus *Parapandalus*	=	Genus *Plesionika*

ceans is being conducted on higher-level relationships. Better understanding of relationships based on identification of monophyletic groups has required reorganization of taxa at higher levels (e.g., within superfamilies, families, and genera) as well as elevating subfamilies and subgenera to family and generic levels, respectively. In the nearly 20-year period since Williams (1984), one new superfamily (Processoidea) and one new family (Anchistioididae) are recognized in the infraorder Caridea, and two subgenera have been elevated to genera (*Farfantepenaeus* and *Litopenaeus*) in the family Penaeidae, for shrimps occurring in the region. Thalassinideans, previously placed in the section Thalassinidea within infraorder Anomura, are now recognized at the level of infraorder. Within brachyuran taxa, three new subfamilies within the Raninidae are now recognized, 17 former subfamilies (seven in Majidae, four in Xanthidae, three in Grapsidae, one each in Raninidae, Calappidae, and Goneplacidae) have been elevated to family, two subgenera elevated to genus (*Mithraculus* in family Majidae and *Platylambrus* in family Parthenopidae), and one subspecies (of *Ethusa*) elevated to species. Considerable changes in generic concepts involving western Atlantic decapod crustaceans have also necessitated the recognition and redefinition of genera to accommodate western Atlantic decapod species. Fifteen new genera have been described since publication of Williams' (1984) monograph, including one genus each in the Penaeidae, Pandalidae, Axiidae, and Paguridae, two in Callianassidae, and nine brachyuran genera placed in seven different families (Table 5). Twenty-one species of decapods occurring in the region have been reassigned to genera other than those listed in Williams (1984).

Knowledge concerning well-known faunas, such as that of the decapod crustaceans of the western Atlantic, is not static, and new discoveries, additional collecting, and better understanding of systematic relationships will continue to improve our understanding of regional biodiversity. New evidence from adult morphology, fossils, larval development, and molecular genetics has led to the reinterpretation of classical views of decapod crustacean relationships. Hypotheses of phylogenetic relationships are being proposed at a relatively fast rate compared with previous time periods and the taxonomic status of species continues to be re-evaluated. Information gained from these systematic studies will undoubtedly result in better understanding of the species, provide refined hypotheses of relationships among these taxa, and subsequently will continue to improve our knowledge regard-

Table 5.—Summary of western Atlantic decapod crustacean species assigned to new genera or reassigned to established genera since publication of Williams (1984).

Species name as appears in Williams (1984)	Species name as appears in present compilation	Newly-described genus? (Y/N)
Hymenopenaeus robustus	*Pleoticus robustus*	N
Trachypenaeus constrictus	*Rimapenaeus constrictus*	Y
Pandalus propinquus	*Atlantopandalus propinqvus*	Y
Parapandalus willisi	*Plesionika willisi*	N
Pontophilus gorei	*Philocheras gorei*	N
Callianassa biformis	*Biffarius biformis*	Y
Callianassa atlantica	*Gilvossius setimanus*	Y
Callianassa major	*Callichirus major*	N
Axiopsis jenneri	*Calaxius jenneri*	Y
Pagurus piercei	*Goreopagurus piercei*	Y
Dromidia antillensis	*Cryptodromiopsis antillensis*	N
Clythrocerus perpusillus	*Deilocerus perpusillus*	Y
Iliacantha intermedia	*Acanthilia intermedia*	Y
Cryptopodia concava	*Celatopesia concava*	Y
Geryon quinquedens	*Chaceon quinquedens*	Y
Neopanope sayi	*Dyspanopeus sayi*	Y
Pinnotheres chamae	*Gemmotheres chamae*	Y
Pinnotheres maculatus	*Tumidotheres maculatus*	Y
Pinnotheres ostreum	*Zaops ostreum*	N
Pinnixa cristata	*Austinixa cristata*	Y
Sesarma cinereum	*Armases cinereum*	Y

ing the marine decapod crustacean assemblage of the eastern United States.

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Literature Cited

Abele, L. G. 1992. A review of the grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae) in America, with the description of a new genus.—Smithsonian Contributions to Zoology 527:1–60.

———, & W. Kim. 1986. An illustrated guide to the marine decapod crustaceans of Florida.—Technical Series of the State of Florida Department of Environmental Regulation, Vol. 8, Part 1 & 2:1–760.

———, & J. W. Martin. 1989. American species of the deep-sea shrimp genus *Bythocaris* (Crustacea, Decapoda, Hippolytidae).—Bulletin of Marine Science 45:26–51.

Asakura, A. 2001. A revision of the hermit crabs of the genera *Catapagurus* A. Milne-Edwards and *Hemipagurus* Smith from the Indo-West Pacific (Crustacea: Decapoda: Anomura: Paguridae).—Invertebrate Taxonomy 15:823–891.

Baldwin, J. D., A. L. Bass, B. W. Bowen, & W. H. Clark, Jr. 1998. Molecular phylogeny and biogeography of the marine shrimp *Penaeus*.—Molecular Phylogenetics and Evolution 10: 399–407.

Barnwell, F. H., & C. L. Thurman, II. 1984. Taxonomy and biogeography of the fiddler crabs (Ocypodidae: Genus *Uca*) of the Atlantic and Gulf coasts of eastern North America.—Zoological Journal of the Linnean Society 81:23–87.

Behrens Yamada, S., & L. Hauck. 2001. Field identification of the European green crab species: *Carcinus maenas* and *Carcinus aestuarii.*—Journal of Shellfish Research 20:905–912.

———, C. Hunt, & N. Richmond. 2000. The arrival of the European green crab, *Carcinus maenas,* in Oregon estuaries. Pp. 94–99 *in* J. Pederson, ed., Marine bioinvasions: Proceedings of the First National Conference, January 24–27, 1999. MIT, MIT Sea Grant College Program, Massachusetts.

Bellwood, O. 1996. A phylogenetic study of the Calappidae H. Milne Edwards 1837 (Crustacea: Brachyura) with a reappraisal of the status of the family.—Zoological Journal of the Linnean Society 118:165–193.

Boothe, B. B., Jr., & R. W. Heard. 1987. *Discias vernbergi,* new species, a caridean shrimp (Crustacea: Decapoda: Bresiliidae) from the northwestern Atlantic.—Proceedings of the Biological Society of Washington 100:506–514.

Bowman, T. E., & J. C. McCain. 1967. Distribution of the planktonic shrimp, *Lucifer,* in the western North Atlantic.—Bulletin of Marine Science 17: 660–671.

Breton, G., M. Faasse, P. Noël, & T. Vincent. 2002. A new alien crab in Europe: *Hemigrapsus sanguineus* (Decapoda: Brachyura: Grapsidae).—Journal of Crustacean Biology 22:184–189.

Caetano da Costa, R., A. Fransozo, F. L. M. Mantelatto, & R. H. Castro. 2000. Occurrence of shrimp species (Crustacea: Decapoda: Natantia: Penaeidea and Caridea) in Ubatuba Bay, Ubatuba, SP, Brazil.—Proceedings of the Biological Society of Washington 113:776–781.

Calado, T. C. dos S. 1998. Malacostraca—Eucarida. Hippoidea. Pp. 407–411 *in* P. S. Young, ed., Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Campos C., N. H., & H. Sánchez M. 1995. Los cangrejos ermitaños del género *Paguristes* Dana (Anomura: Diogenidae) de la costa norte colombiana, con la descripción de dos nuevas especies.—Caldasia 17:569–585.

Campos, E. 1989. *Tumidotheres,* a new genus for *Pinnotheres margarita* Smith, 1869, and *Pinnotheres maculatus* Say, 1818 (Brachyura: Pinnotheridae).—Journal of Crustacean Biology 9:672–679.

———. 1996. Partial revision of pinnotherid crab genera with a two-segmented palp on the third maxilliped (Decapoda: Brachyura).—Journal of Crustacean Biology 16:556–563.

Chace, F. A., Jr. 1984. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907–1910, Part 2: Families Glyphocrangonidae and Crangonidae.—Smithsonian Contributions to Zoology 397:1–63.

———. 1985. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907–1910, Part 3: Families Thalassocarididae and Pandalidae.—Smithsonian Contributions to Zoology 411:1–143.

———. 1988. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907–1910, Part 5: Family Alpheidae.—Smithsonian Contributions to Zoology 466:1–99.

———. 1992. On the classification of the Caridea (Decapoda).—Crustaceana 63:70–80.

———. 1997. The caridean shrimps (Crustacea: Decapoda) of the *Albatross* Philippine Expedition, 1907–1910, Part 7: Families Atyidae, Eugonatonotidae, Rhynchocinetidae, Bathypalaemonellidae, Processidae, and Hippolytidae.—Smithsonian Contributions to Zoology 587:1–106.

Chan, T-Y, & H-P Yu. 1991. Two similar species: *Plesionika edwardsii* (Brandt, 1851) and *Plesionika crosnieri,* new species (Crustacea: Decapoda: Pandalidae).—Proceedings of the Biological Society of Washington 104:545–555.

Chiong, W. L., & P. K. L. Ng. 1998. A revision of the buckler crabs of the genus *Cryptopodia* H. Milne Edwards, 1834 (Crustacea: Decapoda: Brachyura: Parthenopidae).—The Raffles Bulletin of Zoology 46:157–216.

Christoffersen, M. L. 1984. The western Atlantic snapping shrimps related to *Alpheus heterochaelis* Say (Crustacea, Caridea), with the description of a new species.—Papéis Avulsos de Zoologia 35:189–208.

———. 1988. Genealogy and phylogenetic classification of the world Crangonidae (Crustacea, Caridea), with a new species and new records for the south western Atlantic.—Revista Nordestina de Biologia 6:43–59.

———. 1989. Phylogeny and classification of the Pandaloidea (Crustacea, Caridea).—Cladistics 5: 259–274.

———. 1998. Malacostraca. Eucarida. Caridea. Crangonoidea and Alpheoidea (except Glyphocrangonidae and Crangonidae). Pp. 351–372 *in* P. S. Young, ed., Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Clark, P. F., & W. R. Webber. 1991. A redescription of *Macrocheira kaempferi* (Temminck, 1836) zoeas with a discussion of the classification of the Majoidea Samouelle, 1819 (Crustacea: Brachyura).—Journal of Natural History 25:1259–1279.

Coelho, P. A., & M. Ramos-Porto. 1998a. Malacostraca. Eucarida. Stenopodidea. Pp. 323–324 *in* P. S. Young, ed., Catalogue of Crustacea of Brazil.

Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

———, & ———. 1998b. Malacostraca–Eucarida. Palinuridea. Pp. 387–392 *in* P. S. Young, ed., Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Cofer-Shabica, S. V., & R. B. Nielsen, Jr. 1988. First record of an American lobster, *Homarus americanus,* from off southern Florida.—Bulletin of Marine Science 43:315–317.

Cohen, A. N., J. T. Carlton, & M. C. Fountain. 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas* in San Francisco Bay, California.—Marine Biology 122: 225–237.

Coutière, H. 1905. Les Alpheidae. Pp. 852–921, figs. 127–139, pls. 70–87 *in* J. S. Gardiner, ed., The fauna and geography of the Maldive and Laccadive Archipelagoes, vol. 2, part 4, Cambridge University Press, Cambridge, England.

Couture, R., & P. Trudel. 1968. Les crevettes des eaux côtières du Québec, Taxonomie et distribution.—Le Naturaliste Canadien 95:857–885.

Criales, M. M. 1992. Redescription of the hippolytid shrimp *Trachycaris rugosa* (Bate) (Crustacea: Decapoda: Caridea) from the western Atlantic, with notes on sexual dimorphism.—Proceedings of the Biological Society of Washington 105:562–570.

———, & R. Lemaitre. 1997. Discovery and morphological variation of the caridean shrimp *Discias atlanticus* Gurney, 1939 (Crustacea: Decapoda: Bresiliidae) associated with the polychaete worm *Chaetopterus variopedatus* (Renier, 1804).—Caribbean Journal of Science 33:246–250.

Crosnier, A., & J. Forest. 1973. Les crevettes profondes de l'Atlantique oriental tropical.—Faune Tropicale 19:1–409.

Dall, W., B. J. Hill, P. C. Rothlisberg, & D. J. Sharples. 1990. The biology of the Penaeidae.—Advances in Marine Biology 27:1–489.

Dardeau, M. R., & R. W. Heard, Jr. 1983. Crangonid shrimps (Crustacea: Caridea), with a description of a new species of *Pontocaris.*—Memoirs of the Hourglass Cruises 6(2):1–39.

D'Incao, F. 1998. Malacostraca. Eucarida. Dendrobranchiata. Pp. 311–321 *in* P. S. Young, ed., Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Drach, P., & D. Guinot. 1983. Les Inachoididae Dana, famille de Majoidea caractérisée par des connexions morphologiques d'un type nouveau entre carapace, pleurites, sternites, pléon.—Comptes rendus hebdomadaires des Séances de l'Académie des Sciences 297:37–42.

Engle, V. D., & J. K. Summers. 1999. Latitudinal gradients in benthic community composition in Western Atlantic estuaries.—Journal of Biogeography 26:1007–1023.

Felder, D. L., & J. L. Staton. 1994. Genetic differentiation in trans-Floridian species complexes of *Sesarma* and *Uca* (Decapoda: Brachyura).—Journal of Crustacean Biology 14:191–209.

Fransen, C. H. J. M. 2000. *Pontonia manningi,* new species, a bivalve-associated shrimp from the tropical and subtropical Atlantic (Decapoda: Pontoniinae).—Journal of Crustacean Biology 20 (Special no. 2):101–108.

Galil, B. S. 2000. *Acanthilia,* a new genus of leucosioid crabs (Crustacea: Brachyura) from the Atlantic coast of the Americas.—Proceedings of the Biological Society of Washington 113:426–430.

———, & P. F. Clark. 1996. A revision of *Cryptosoma* Brullé, 1837 and *Cycloes* de Haan, 1837 (Crustacea: Brachyura: Calappidae).—Zoological Journal of the Linnean Society 117:175–204.

García-Gómez, J. 1982. The *Provenzanoi* group of hermit crabs (Crustacea, Decapoda, Paguridae) in the western Atlantic. Part 1. *Pagurus maclaughlinae,* a new species.—Bulletin of Marine Science 32:647–655.

———. 1983. Revision of *Iridopagurus* (Crustacea: Decapoda: Paguridae) with descriptions of new species from American waters.—Bulletin of Marine Science 33:10–54.

Gibbes, L. R. 1850. On the carcinological collections of the United States, and an enumeration of the most remarkable, and descriptions of new species.—Proceedings of the American Association for Advancement of Science 3:167–201.

Goeke, G. D. 1980. Range extensions of six western Atlantic frog crabs (Brachyura: Gymnopleura: Raninidae) with notes on the taxonomic status of *Lyreidus bairdii.*—Proceedings of the Biological Society of Washington 93:145–152.

———. 1985. Decapod Crustacea: Raninidae.—Mémoire du Muséum National de l'Histoire Naturelle (Séries A, Zoologie) 133:205–228.

———. 1989. *Stenorhynchus yangi,* a new western Atlantic species of arrow crab (Crustacea: Brachyura, Majidae) and a redescription of *S. seticornis* (Herbst, 1788).—Proceedings of the Biological Society of Washington 102:620–636.

Griffin, D. J. G., & H. A. Tranter. 1986. The Decapoda Brachyura of the Siboga Expedition. Part VIII. Majidae. Siboga-Expedition Monograph 39 (C4), 148:1–335.

Griffith, H. 1987. Phylogenetic relationships and evolution in the genus *Dissodactylus* Smith, 1870 (Crustacea: Brachyura: Pinnotheridae).—Canadian Journal of Zoology 65:2292–2310.

Grosholz, E. D., & G. M. Ruiz. 1996. Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*.—Biological Conservation 78:59–66.

Guinot, D. 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyoures.—Bulletin Biologique de la France et de la Belgique 112:211–292.

———. 1993. Données nouvelles sur les Raninoidea de Haan, 1841 (Crustacea Decapoda Brachyura Podotremata).—Comptes-rendus hebdomadaires des Séances de l'Académie des Sciences (Paris), Series III 316:1324–1331.

———, & J.-M. Bouchard. 1998. Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura).—Zoosystema 20:613–694.

———, & B. Richer de Forges. 1995. Crustacea Decapoda Brachyura: révision de la famille des Homolidae de Haan, 1839.—Mémoires du Muséum National d'Histoire Naturelle 163:283–517.

———, & ———. 1997. Affinités entre les Hymenosomatidae MacLeay, 1838 et les Inachoididae Dana, 1851 (Crustacea, Decapoda, Brachyura).—Zoosystema 19:453–502.

Gusmão, J., C. Lazoski, & A. M. Solé-Cava. 2000. A new species of *Penaeus* (Crustacea: Penaeidae) revealed by allozyme and cytochrome oxidase 1 analysis.—Marine Biology 137:435–446.

Heard, R. W., & R. B. Manning. 1997. *Austinixa,* a new genus of pinnotherid crab (Crustacea: Decapoda: Brachyura), with the description of *A. hardyi,* a new species from Tobago, West Indies.—Proceedings of the Biological Society of Washington 110:393–398.

———, and ———. 1998. A new genus and species of ghost shrimp (Crustacea: Decapoda: Callianassidae) from the Atlantic Ocean.—Proceedings of the Biological Society of Washington 111:883–888.

Hendrickx, M. E. 1989. Notes on the genus *Ethusa* Roux, 1828, and description of *Ethusa steyaerti* n. sp. (Crustacea, Decapoda, Dorippidae), from the continental shelf of the Gulf of California, Mexico.—Bulletin du Muséum National d'Histoire Naturelle, Paris, 4^{e} séries, 11, Section A, n^{os} 2:407–423.

———. 1995. Checklist of brachyuran crabs (Crustacea: Decapoda) from the eastern tropical Pacific.—Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 65:125–150.

———. 1998. A new genus and species of "goneplacid-like" brachyuran crab (Crustacea: Decapoda) from the Gulf of California, Mexico, and a proposal for the use of the family Pseudorhombilidae Alcock, 1900.—Proceedings of the Biological Society of Washington 111:634–644.

Holthuis, L. B. 1947. The Decapoda of the Siboga-Expedition. Part IX. The Hippolytidae and Rhynchocinetidae collected by the Siboga and Snellius Expeditions with remarks on other species.—Siboga-Expeditie, Mongraphie 39a^{8}, 100 p.

———. 1991. FAO species catalogue. Volume 13. Marine lobsters of the world.—FAO Fisheries Synopsis No. 125, Volume 13:1–292.

———. 1993. The recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda) with an appendix on the order Amphionidacea. Nationaal Natuurhistorisch Museum, Leiden. 328 pp.

———, & R. B. Manning. 1987. *Hypoconcha parasitica* (Linnaeus, 1763), a senior synonym of *Hypoconcha sabulosa* (Herbst, 1799) (Crustacea: Decapoda: Brachyura).—Proceedings of the Biological Society of Washington 100:1018–1022.

Kensley, B. 1983. New records of bresiliid shrimp from Australia, South Africa, Caribbean, and Gulf of Mexico (Decapoda: Natantia: Caridea).—Smithsonian Contributions to Zoology 394:1–31.

———. 1989. New genera in the thalassinidean families Calocarididae and Axiidae (Crustacea: Decapoda).—Proceedings of the Biological Society of Washington 102:960–967.

———. 2001. Two sympatric species of *Axius* from the North-West Atlantic (Decapoda, Thalassinidea, Axiidae).—Crustaceana 74:951–962.

Kim, W., & L. Abele. 1988. The snapping shrimp genus *Alpheus* from the eastern Pacific (Decapoda: Caridea: Alpheidae).—Smithsonian Contributions to Zoology 454:1–119.

Knott, D., C. Boyko, & A. Harvey. 2000. Introduction of the green porcelain crab, *Petrolisthes armatus* (Gibbes, 1850) into the South Atlantic Bight. P. 404 (Abstract only) *in* J. Pederson, ed., Marine bioinvasions: Proceedings of the First National Conference. MIT, Massachusetts.

Komai, T. 1997. Revision of *Argis dentata* and related species (Decapoda: Caridea: Crangonidae), with description of a new species from the Okhotsk Sea.—Journal of Crustacean Biology 17:135–161.

———. 1999. A revision of the genus *Pandalus* (Crustacea: Decapoda: Caridea: Pandalidae).—Journal of Natural History 33:1265–1372.

Laughlin, R. A., P. J. Rodríguez, & J. A. Marval. 1982. The complete larval development of the sponge crab *Dromia erythropus* (George Edwards, 1771) (Brachyura: Dromiidae) from the Archipiélago de los Roques, Venezuela.—Journal of Crustacean Biology 2:342–359.

Ledesma, M. E., & N. J. O'Connor. 2001. Habitat and diet of the non-native crab *Hemigrapsus sanguineus* in southeastern New England.—Northeastern Naturalist 8:63–78.

Lemaitre, R. 1989. Revision of the genus *Parapagurus*

(Anomura: Paguroidea: Parapaguridae), including redescriptions of the western Atlantic species.—Zoologische Verhandelingen, Leiden 253:1–106.

———, N. H. Campos, & A. Bermúdez. 2001. A new species of *Pyromaia* from the Caribbean Sea, with a redescription of *P. propinqua* Chace, 1940 (Decapoda: Brachyura: Majoidea: Inachoididae).—Journal of Crustacean Biology 21: 760–773.

———, & P. A. McLaughlin. 1996. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species. Part V. *Anisopagurus* McLaughlin, *Manucomplanus* McLaughlin, and *Protoniopagurus* new genus.—Bulletin of Marine Science 59:89–141.

———, ———, & J. García-Gómez. 1982. The *Provenzanoi* group of hermit crabs (Crustacea, Decapoda, Paguridae) in the western Atlantic. Part IV. A review of the group with notes on variations and abnormalities.—Bulletin of Marine Science 32:670–701.

Lohrer, A. M., & R. B. Whitlatch. 1997. Ecological studies on the recently introduced Japanese shore crab (*Hemigrapsus sanguineus*), in eastern Long Island Sound. Pp. 49–60 *in* N. C. Balcom, ed., Proceedings of the Second Northeast Conference on Nonindigenous Aquatic Nuisance Species. Connecticut Sea Grant College Program, Connecticut.

Lyons, W. 1970. Scyllarid lobsters (Crustacea, Decapoda).—Memoirs of the Hourglass Cruises 1(4):1–74.

Maggioni, R., A. D. Rogers, N. Maclean, & F. D'Incao. 2001. Molecular phylogeny of western Atlantic *Farfantepenaeus* and *Litopenaeus* shrimp based on mitochondrial 16S partial sequences.—Molecular Phylogenetics and Evolution 18:66–73.

Manning, R. B. 1987. Notes on western Atlantic Callianassidae (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 100:386–401.

———. 1988. Notes on albuneid crabs (Crustacea: Decapoda: Albuneidae) from the central east coast of Florida.—Proceedings of the Biological Society of Washington 101:626–632.

———. 1993. Three genera removed from the synonymy of *Pinnotheres* Bosc, 1802 (Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 106:523–531.

———, & D. L. Felder. 1986. The status of the callianassid genus *Callichirus* Stimpson, 1866 (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 99:437–443.

———, & ———. 1989. The *Pinnixa cristata* complex in the western Atlantic, with a description of two new species (Crustacea: Decapoda: Pinnotheridae).—Smithsonian Contributions to Zoology 473:1–26.

———, & ———. 1991. Revision of the American Callianassidae (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 104:764–792.

———, & ———. 1992 [1991]. *Gilvossius*, a new genus of callianassid shrimp from the eastern United States (Crustacea: Decapoda: Thalassinidea).—Bulletin of Marine Science 49:558–561.

———, & L. B. Holthuis. 1981. West African brachyuran crabs (Crustacea: Decapoda).—Smithsonian Contributions to Zoology 306:1–379.

———, & ———. 1989. Two new genera and nine new species of geryonid crabs (Crustacea: Decapoda: Geryonidae).—Proceedings of the Biological Society of Washington 102:50–77.

Maris, R. C. 1986. Larvae of *Xiphopenaeus kroyeri* (Heller, 1862) (Crustacea: Decapoda: Penaeidae) from offshore waters of Virginia, U.S.A.—Proceedings of the Biological Society of Washington 99:602–603.

Marques, F., & G. Pohle. 1995. Phylogenetic analysis of the Pinnotheridae (Crustacea, Brachyura) based on larval morphology, with emphasis on the *Dissodactylus* species complex.—Zoologica Scripta 24:347–364.

Martin, J. W., & L. G. Abele. 1986. Notes on male pleopod morphology in the brachyuran crab family Panopeidae Ortmann, 1893, *sensu* Guinot (1978) (Decapoda).—Crustaceana 50:182–198.

———, & G. E. Davis. 2001. An updated classification of the Recent Crustacea.—Natural History Museum of Los Angeles County, Science Series 39:1–124.

———, & T. L. Zimmerman. 2001. Notes on three western Atlantic deep-sea crabs (Decapoda, Brachyura).—Crustaceana 74:411–414.

McClure, M. R. 1995. *Alpheus angulatus*, a new species of snapping shrimp from the Gulf of Mexico and northwestern Atlantic, with a redescription of *A. heterochaelis* Say, 1818 (Decapoda: Caridea: Alpheidae).—Proceedings of the Biological Society of Washington 108:84–97.

———. 2002. Revised nomenclature of *Alpheus angulatus* McClure, 1995 (Decapoda: Caridea: Alpheidae).—Proceedings of the Biological Society of Washington 115:368–370.

———, & M. K. Wicksten. 1997. Morphological variation of species of the *edwardsii* group of *Alpheus* in the northern Gulf of Mexico and northwestern Atlantic (Decapoda: Caridea: Alpheidae).—Journal of Crustacean Biology 17:480–487.

McDermott, J. J. 1998. The western Pacific brachyuran

(*Hemigrapsus sanguineus*: Grapsidae), in its new habitat along the Atlantic coast of the United States: geographic distribution and ecology.—ICES Journal of Marine Science 55:289–298.

———. 2000. Natural history and biology of the Asian shore crab *Hemigrapsus sanguineus* in the western Atlantic: a review, with new information. Pp. 193–199 *in* J. Pederson, ed., Marine bioinvasions: Proceedings of the First National Conference, January 24–27, 1999. MIT, MIT Sea Grant College Program, Massachusetts.

McLaughlin, P. A. 1981. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species. Part I. Ten new genera of the Paguridae and a redescription of *Tomopagurus* A. Milne Edwards and Bouvier.—Bulletin of Marine Science 31:1–30.

———. 1983. Hermit crabs–are they really polyphyletic?—Journal of Crustacean Biology 3:608–621.

———. 1988. The rediscovery of *Ceratopagurus* Yokoya and a new genus for *Pagurus piercei* Wass (Decapoda, Paguroidea, Paguridae).—Crustaceana 55:257–267.

———, & J. Haig. 1995. A new species of *Goreopagurus* McLaughlin (Decapoda: Anomura: Paguridae) from the Pacific, and a comparison with its Atlantic counterpart.—Proceedings of the Biological Society of Washington 108:68–75.

———, & R. Lemaitre. 2001a. A new family for a new genus and new species of hermit crab of the superfamily Paguroidea (Decapoda: Anomura) and its phylogenetic implications.—Journal of Crustacean Biology 21:1062–1076.

———, & ———. 2001b. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with descriptions of new genera and species. Part VI. *Pylopagurus* A. Milne-Edwards & Bouvier, 1891, *Haigia* McLaughlin, 1981, and *Pylopaguridium*, a new genus.—Proceedings of the Biological Society of Washington 114:444–483.

McLay, C. L. 1993. Crustacea Decapoda: The sponge crabs (Dromiidae) of New Caledonia and the Philippines with a review of the genera.—Mémoires du Muséum National d'Histoire Naturelle 156:111–251.

Melo, G. A. S. 1998. Malacostraca-Eucarida. Brachyura. Oxyrhyncha and Brachyrhyncha. Pp. 455–515 *in* P. S. Young, ed., Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

———, M. F. A. Torres, & O. Campos, Jr. 1998. Malacostraca-Eucarida. Brachyura. Dromiacea and Oxystomata. Pp. 439–454 *in* P. S. Young, ed., Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Melo-Filho, G. A. S. 1998. Malacostraca-Eucarida. Chyrostilidae and Galatheidae. Pp. 393–397 *in* P. S. Young, ed., Catalogue of Crustacea of Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

———, & G. A. S. Melo. 1992. Reexamination of the material of *Munida* Leach (Crustacea: Anomura: Galatheidae) collected by the *H.M.S. Challenger* (1872–1876) along the Brazilian coast.—Proceedings of the Biological Society of Washington 105:760–774.

Moriyasu, M., H. J. Squires, R. Campbell, & K. Benhalima. 2001. Northern range extensions for two decapod crustaceans, the inflated spiny crab *Rochinia crassa* (A. Milne-Edwards, 1879) and the purplehead gamba prawn *Aristeus antillensis* A. Milne-Edwards & Bouvier, 1909, in the northwestern Atlantic.—Crustaceana 74:255–260.

Nations, J. D. 1975. The genus *Cancer* (Crustacea: Brachyura): systematics, biogeography and fossil record.—Natural History Museum of Los Angeles County Science Bulletin 23:1–104.

Ng, P. K. L., & G. Rodríguez. 1986. New records of *Mimilambrus wileyi* Williams, 1979 (Crustacea: Decapoda: Brachyura), with notes on the systematics of the Mimilambridae Williams, 1979, and Parthenopidae MacLeay, 1838, sensu Guinot, 1978.—Proceedings of the Biological Society of Washington 99:88–99.

Niem, V. H. 1996. Phylogenetic relationships among American species of *Sesarma* (subgenus *Armases*) (Brachyura, Grapsidae).—Crustaceana 69:330–348.

Pérez Farfante, I. 1977a. American solenocerid shrimps of the genera *Hymenopenaeus, Haliporoides, Pleoticus, Hadropenaeus* new genus, and *Mesopenaeus* new genus.—Fishery Bulletin 75:261–346.

———. 1977b. Range extensions of the shrimps *Solenocera necopina* Burkenroad and *Parapenaeus americanus* Rathbun (Crustacea, Decapoda, Penaeoidea).—Proceedings of the Biological Society of Washington 90:597–599.

———. 1980. Revision of the penaeid shrimp genus *Penaeopsis* (Crustacea: Decapoda).—Fishery Bulletin 77:721–763.

———. 1988. Illustrated key to penaeoid shrimps of commerce in the Americas.—NOAA Technical Report, National Marine Fisheries Service, 64: 1–32.

———, & B. F. Kensley. 1997. Penaeoid and sergestoid shrimps and prawns of the world. Keys and diagnoses for the families and genera.—Mémoires du Muséum National d'Histoire Naturelle 175:1–233.

Pipitone, C., F. Badalamenti, & A. Sparrow. 2001. Contribution to the knowledge of *Percnon gibbesi* (Decapoda, Grapsidae), an exotic species spreading rapidly in Sicilian waters.—Crustaceana 74:1009–1017.

Pohle, G., & F. Marques. 2000. Larval stages of *Paradasygyius depressus* (Bell, 1835) (Crustacea: Decapoda: Brachyura: Majidae) and a phylogenetic analysis for 21 genera of Majidae.—Proceedings of the Biological Society of Washington 113:739–760.

Poore, G. C. B. 1994. A phylogeny of the families of Thalassinidea (Crustacea: Decapoda) with keys to families and genera.—Memoirs of the Museum of Victoria 54:79–120.

Powers, L. W. 1977. A catalogue & bibliography to the crabs (Brachyura) of the Gulf of Mexico.—Contributions in Marine Science 20 (supplement):1–190.

Ramos-Porto, M., & P. A. Coelho. 1998. Malacostraca. Eucarida. Caridea (Alpheoidea excluded). Pp. 325–350 *in* P. S. Young, ed., Catalogue of Crustacea in Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Rathbun, M. J. 1925. The spider crabs of America.—United States National Museum Bulletin 129: 1–613.

———. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae.—United States National Museum Bulletin 152:1–609.

Rieger, P. J. 1998. Malacostraca–Eucarida. Paguroidea. Pp. 413–429 *in* P. S. Young, ed., Catalogue of Crustacea in Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Rodrigues, S. de A., & R. M. Shimizu. 1998. Malacostraca–Eucarida. Thalassinidea. Pp. 379–385 *in* P. S. Young, ed., Catalogue of Crustacea in Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Rodríguez, B. 1993. Shrimps. Pp. 107–131 *in* K. Carpenter, W. Fischer, and L. Garibaldi, eds., Field guide to the commercial marine and brackish-water resources of the northern coast of South America. FAO, Rome.

Rodríguez-Almaraz, G., A. Leija-Tristán, & R. Mendoza. 2000. Records of caridean shrimps (Crustacea: Decapoda) from the coasts of the Mexican Pacific Ocean, Gulf of Mexico and Mexican Caribbean.—Bulletin of Marine Science 67: 857–867.

Rosenberg, M. S. 2001. The systematics and taxonomy of fiddler crabs: A phylogeny of the genus *Uca*.—Journal of Crustacean Biology 21:839–869.

Sakai, K. 1999. Synopsis of the family Callianassidae, with keys to subfamilies, genera and species, and the description of new taxa (Crustacea: Decapoda: Thalassinidea).—Zoologische Verhandelingen, Leiden 326:1–152.

———, & M. de Saint Laurent. 1989. A check list of Axiidae (Decapoda, Crustacea, Thalassinidea, Anomura), with remarks and in addition descriptions of one new subfamily, eleven new genera and two new species.—Naturalists 3:1–104.

Sarver, S. K., D. W. Freshwater, & P. J. Walsh. 2000. The occurrence of the provisional Brazilian subspecies of spiny lobster (*Panulirus argus westonii*) in Florida waters.—Fishery Bulletin 98: 870–873.

———, J. D. Silberman, & P. J. Walsh. 1998. Mitochondrial DNA sequence evidence supporting recognition of two subspecies or species of the Florida spiny lobster *Panulirus argus*.—Journal of Crustacean Biology 18:177–186.

Scelzo, M. A. 2001. First record of the portunid crab *Arenaeus cribrarius* (Lamarck, 1818) (Crustacea: Brachyura: Portunidae) in marine waters of Argentina.—Proceedings of the Biological Society of Washington 114:605–610.

Schubart, C. D., J. A. Cuesta, R. Diesel, & D. L. Felder. 2000. Molecular phylogeny, taxonomy, and evolution of nonmarine lineages within the American grapsoid crabs (Crustacea: Brachyura).—Molecular Phylogenetics and Evolution 15:179–190.

———, J. E. Neigel, & D. L. Felder. 2000. Molecular phylogeny of mud crabs (Brachyura: Panopeidae) from the northwestern Atlantic and the role of morphological stasis and convergence.—Marine Biology 137:11–18.

Schweitzer, C. E., & R. M. Feldmann. 2000. New species of calappid crabs from western North America and reconsideration of the Calappidae *sensu lato*.—Journal of Paleontology 74:230–246.

Silberman, J. D., S. K. Sarver, & P. J. Walsh. 1994. Mitochondrial DNA variation and population structure in the spiny lobster *Panulirus argus*.—Marine Biology 120:601–608.

Squires, H. J. 1990. Decapod Crustacea of the Atlantic coast of Canada.—Canadian Bulletin of Fisheries and Aquatic Sciences 221:1–532.

———. 1992. Recognition of *Pandalus eous* Makarov, 1935, as a Pacific species not a variety of the Atlantic *Pandalus borealis* Krøyer, 1838 (Decapoda, Caridea).—Crustaceana 63:257–262.

Stehlik, L. L., C. L. MacKenzie, Jr., & W. W. Morse. 1991. Distribution and abundance of four brachyuran crabs on the northwest Atlantic shelf.—Fishery Bulletin 89:473–492.

Sternberg, R. von, & N. Cumberlidge. 1998. Taxic relationships within the Grapsidae MacLeay, 1838 (Crustacea: Decapoda: Eubrachyura).—Journal of Comparative Biology 3:115–136.

Strasser, K. M., & W. W. Price. 1999. An annotated checklist and key to hermit crabs of Tampa Bay, Florida, and surrounding waters.—Gulf Research Reports 11:35–50.

Strenth, N. E., & F. A. Chace, Jr. 1995. New records of natant decapods (Crustacea: Palaemonidae) from the south Texas coast.—Texas Journal of Science 47:315–318.

Tavares, M. 1991a [1990]. Espèces nouvelles de Cyclodorippoidea Ortmann et remarques sur les genres *Tymolus* Stimpson et *Cyclodorippe* A. Milne Edwards (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, 4e séries, 12, Section A, nos 3–4:623–648.

———. 1991b. Redéfinition des genres *Rochinia* A. Milne Edwards, *Sphenocarcinus* A. Milne Edwards et *Oxypleurodon* Miers, et établissement du genre *Nasutocarcinus* gen. nov. (Crustacea, Brachyura, Majidae).—Bulletin du Muséum National d'Histoire Naturelle, Paris, 4e séries, 13, Section A, nos 1–2:159–179.

———. 1993. Description préliminaire de quatre nouveaux genres et trois nouvelles espèces de Cyclodorippoidea Amèricains (Crustacea, Decapoda, Brachyura).—Vie Milieu 43:137–144.

———. 1996. Révision systématique des Cyclodorippidae américains (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, 4e séries, 18, Section A, nos 1–2:233–295.

Tucker, A. B. 1998. Systematics of the Raninidae (Crustacea: Decapoda: Brachyura), with accounts of three new genera and two new species.—Proceedings of the Biological Society of Washington 111:320–371.

Tudge, C. C., G. C. B. Poore, & R. Lemaitre. 2000. Preliminary phylogenetic analysis of generic relationships within the Callianassidae and Ctenochelidae (Decapoda: Thalassinidea: Callianassoidea).—Journal of Crustacean Biology 20 (Special no. 2):129–149.

Udekem d'Acoz, C. d'. 1997. Redescription of *Hippolyte obliquimanus* Dana, 1852, and comparison with *Hippolyte williamsi* Schmitt, 1924 (Decapoda, Caridea).—Crustaceana 70:469–479.

Vargas, R., & J. Cortés. 1999. Biodiversidad marina de Costa Rica: Crustacea: Decapoda (Penaeoidea, Sergestoidea, Stenopodidea, Caridea, Thalassinidea, Palinura) del Caribe.—Revista de Biología Tropical 47:877–885.

Veloso, V. G. 1998. Malacostraca–Eucarida. Porcellanidae. Pp. 399–405 *in* P. S. Young, ed. Catalogue of Crustacea in Brazil. Museu Nacional, Rio de Janeiro. (Série Livros n. 6).

Wagner, H. P. 1990. The genera *Mithrax* Latreille, 1818 and *Mithraculus* White, 1847 (Crustacea: Brachyura: Majidae) in the western Atlantic Ocean.—Zoologische Verhandelingen (Leiden) 264:1–65.

Wass, M. L. 1963. New species of hermit crabs (Decapoda, Paguridae) from the western Atlantic.—Crustaceana 6:133–157.

Wigley, R. L., R. B. Theroux, & H. E. Murray. 1975. Deep-sea red crab, *Geryon quinquedens,* survey off northeastern United States.—Marine Fisheries Review 37:1–21.

Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas.—Fishery Bulletin 65:1–298.

———. 1983. The mud crab, *Panopeus herbstii,* s.l. partition into six species (Decapoda: Xanthidae).—Fishery Bulletin 81:863–882.

———. 1984. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., 550 pp.

———. 1988. Notes on decapod and euphausiid crustaceans, continental margin, western Atlantic, Georges Bank to western Florida, USA.—Fishery Bulletin 86:67–76.

———. 1993. Mud shrimps, Upogebiidae, from the western Atlantic (Crustacea: Decapoda: Thalassinidea).—Smithsonian Contributions to Zoology 544:1–77.

———, & C. A. Child. 1989. Comparison of some genera and species of box crabs (Brachyura: Calappidae), southwestern North Atlantic, with description of a new genus and species.—Fishery Bulletin 87:105–121.

———, & D. L. Felder. 1986. Analysis of stone crabs: *Menippe mercenaria* (Say), restricted, and a previously unrecognized species described (Decapoda: Xanthidae).—Proceedings of the Biological Society of Washington 99:517–543.

———, & J. J. McDermott. 1990. An eastern United States record for the western Indo-Pacific crab, *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae).—Proceedings of the Biological Society of Washington 103:108–109.

———, & R. Wahle. 1992. Distinguishing juvenile stages of Jonah and Atlantic rock crabs, *Cancer borealis* and *C. irroratus* (Decapoda: Cancridae).—Journal of Crustacean Biology 12:464–466.

———, & R. L. Wigley. 1977. Distribution of decapod Crustacea off northeastern United States based on specimens at the Northeast Fisheries Center, Woods Hole, Massachusetts.—NOAA Technical Report NMFS Circular 407:1–44.

Note Added in Proof

Recent revision of the Albuneidae (Boyko 2002) provided new information for three species included in the present checklist. Western Atlantic specimens identified as *Albunea paretii* Guérin-Méneville, 1853 in Williams (1984) included two species, *A. paretii* and *A. catherinae* Boyko, 2002. Of these, only *A. catherinae* occurs in the region (see account below). *Albunea paretii* ranges from the Florida Keys southward through the Caribbean to Rio Grande do Sul, Brazil, and should be removed from the checklist. According to Boyko (2002), all eastern Atlantic references to *A. paretii* refer to *A. elegans*. Boyko (2002) included additional distributional information for *Lepidopa websteri* that extends this species range to Texas.

Based on new data for *A. paretii* and *A. catherinae,* 52 species are new to the checklist. Thirteen of these have been discovered and described since publication of Williams (1984), and seven species previously recorded from the region are no longer considered part of the regional decapod assemblage.

Family Albuneidae Stimpson, 1858

▶ *Albunea catherinae* Boyko, 2002

Remarks.—Boyko (2002:343) provided a description, diagnosis, illustrations, and size information for this species. *Albunea catherinae* occurs at depths less than 64 m.

Known range.—Western Atlantic: Virginia to Palm Beach County, Florida; Collier County, Florida, through the Gulf of Mexico, to southern Texas; absent from the Florida Keys (Boyko 2002).

Literature Cited

Boyko, C. B. 2002. A worldwide revision of the recent and fossil sand crabs of the Albuneidae Stimpson and Blepharipodidae, new family (Crustacea: Decapoda: Anomura: Hippoidea).—Bulletin of the American Museum of Natural History 272:1–396.

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A new caridean shrimp of the family Alvinocarididae from thermal vents at Menez Gwen on the Mid-Atlantic Ridge

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Abstract.—A new species of alvinocaridid shrimp, *Alvinocaris williamsi,* is described from the Menez Gwen hydrothermal vent field on the Mid-Atlantic Ridge. The new species is most similar to another relatively shallow water alvinocaridid, *A. stactophila* Williams, known only from a cold seep area off the coast of Louisiana, but differs in details of the rostrum and appendages. *Alvinocaris williamsi* is also morphologically similar to two species of the genus recently described from the Mid-Okinawa Trough, Japan. Molecular phylogenetic studies of *A. williamsi,* the eighth described member of the genus, may provide significant insights into the role that deep-sea hydrothermal vents at mid-ocean ridges and hydrocarbon seeps on continental margins have played in the evolution of fauna endemic to these chemosynthetic habitats.

The caridean shrimp family Alvinocarididae was originally proposed by Christoffersen (1986) to accommodate a number of morphologically similar shrimp known from hydrothermal vents and hydrocarbon seeps. The family was further diagnosed by Segonzac et al. (1993) in a footnote, and also by Vereshchaka (1996a, 1996b, 1997) (see Martin & Davis 2001). To date, five genera have been proposed for the family. In the order in which they were proposed, they are: *Alvinocaris* Williams & Chace, 1982; *Rimicaris* Williams & Rona, 1986; *Chorocaris* Martin & Hessler, 1990; *Opaepele* Williams & Dobbs, 1995; and *Iorania* Vereshchaka, 1996b (see Shank et al. 1998 for the synonymy of *Iorania* and *Rimicaris*). A sixth genus of vent shrimp, *Mirocaris* Vereshchaka, 1997, was proposed by Vereshchaka (1997) for *Chorocaris fortunata* Martin & Christiansen (1995) and for a new species (*M. keldyshi* Vereshchaka, 1997); however, this genus was transferred to the newly created family Mirocarididae by Vereshchaka (1997).

The type genus of the Alvinocarididae, *Alvinocaris,* is the most diverse genus of the family and contains five hydrothermal vent-endemic species: *A. brevitelsonis* Kikuchi & Hashimoto, 2000, from the Minami-Ensei Knoll in the Mid-Okinawa Trough off Japan; *A. leurokolos* Kikuchi & Hashimoto, 2000, also from the Minami-Ensei Knoll; *A. longirostris* Kikuchi & Ohta, 1995, from the Iheya Ridge off Japan; *A. lusca* Williams & Chace, 1982, from the Galapagos Rift in the eastern Pacific; and *A. markensis* Williams, 1988, from the Mid-Atlantic Ridge. Another two species of *Alvinocaris* are endemic to chemosynthetic habitats associated with hydrocarbon and brine seeps: *A. muricola* Williams, 1988, from the West Florida Escarpment; and *A. stactophila* Williams, 1988, from the Louisiana Slope in the northern Gulf of Mexico. The study of additional collections, including undescribed hydrothermal-associated shrimp specimens from the Edison Seamount of the Bismark Archipelago in Papua New Guinea (Shank et al. 1999; K. Baba, pers. comm.), from the Logatchev vent field of the Mid-Atlantic Ridge (A. Vereshchaka, pers. comm.), and several recently recovered from active seamounts north of the Bay of Plenty (northern North Island, New Zealand) (Rick Webber and Neil Bruce, pers. comm., http://www.niwa.co.nz/pubs/bu/05/blind) may yield additional new species of *Alvinocaris*. The pan-equatorial biogeographic distribution of the genus is noteworthy. *Alvinocaris* species occur in almost every biogeographic vent province (except the Northeast Pacific vents; Shank et al. 1999). However, recent initial investigations of hydrothermal vents in the Indian Ocean did not reveal the presence of *Alvinocaris* shrimp despite the common appearance of the other dominant Atlantic and Pacific genera *Rimicaris* and *Chorocaris* (Hashimoto et al. 2001, Van Dover et al. 2001). The *Alvinocaris* species described herein occupies the northernmost extent of the generic range, as it inhabits the Menez Gwen vent site, the most shallow vent field (850 m) and the most northern known active deep-sea hydrothermal site along the Mid-Atlantic Ridge (37°50.5′N, 31°31.3′W) (Gebruk et al. 1997, Colaço et al. 1998, Comtet & Desbruyères 1998, Desbruyères et al. 2001). Below, we describe a new species of *Alvinocaris* from the Menez Gwen hydrothermal vent field, and suggest evolutionary relationships with other alvinocarid species.

Materials and Methods

All specimens were collected using the human occupied submersible *DSV Alvin* at the Menez Gwen hydrothermal vent field, northern Atlantic Ocean. Shrimp were collected from a cluster of active individuals among clumps of mussels, *Bathymodiolus azoricus* Von Cosel, Comtet & Krylova, within vent flow with a 30 cm × 30 cm square "black net" (BN) operated using the manipulator arm by the pilots of *DSV Alvin*. A total of 14 specimens were collected (from a single net sample) from areas of most intense diffuse fluid within the central portion of a hydrothermally-active mussel bed community that included a more abundant alvinocaridid species, *Mirocaris keldyshi*, amphipods, *Luckia striki* Bellan-Santini & Thurston, gastropods, e.g., *Lepetodrilus* spp. and *Protolira valvatoides* Waren & Bouchet, polychaetes, e.g., *Branchipolynoe seepensis* Pettibone, and crabs, *Segonzacia mesatlantica* (Williams, 1988) and *Chaceon affinis* (A. Milne-Edwards & Bouvier, 1894). Specimens were brought to the surface in an insulated container and placed in chilled water on-board ship. Whole shrimp were sorted by morphotype and either preserved in 4% buffered formalin in seawater and subsequently transferred to 70% ethanol or frozen at −70°C and subsequently transported on dry ice and stored at −80°C. Carapace length (CL) of each individual was measured in millimeters (mm) from the orbital margin to the posteriomedial margin of the carapace. We recognize that the description of new species within this family from relatively few individuals can be risky (see Shank et al. 1998); however, preliminary results of mitochondrial DNA sequence data (Shank, pers. obs.) complement morphological evidence that distinction of this species from other *Alvinocaris* species is warranted. The holotype and paratypes are deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). The remaining specimens are cryo-preserved at the Woods Hole Oceanographic Institution for ongoing molecular phylogenetic investigations by TMS.

***Alvinocaris williamsi*, new species**

Figs. 1–3

Material examined.—14 females CL: 8.2, 8.2, 8.5, 8.7, 8.9, 8.9, 9.3, 9.5, 9.5, 9.5, 9.6, 9.6, 9.7, 10.1, *DSV Alvin*, Dive 3117, Menez Gwen hydrothermal vent field, North Atlantic Ocean, 37°50.5′N, 31°31.3′W, 850 m, 7 Jul 1997.

Types.—All from *DSV Alvin* Dive 3117.

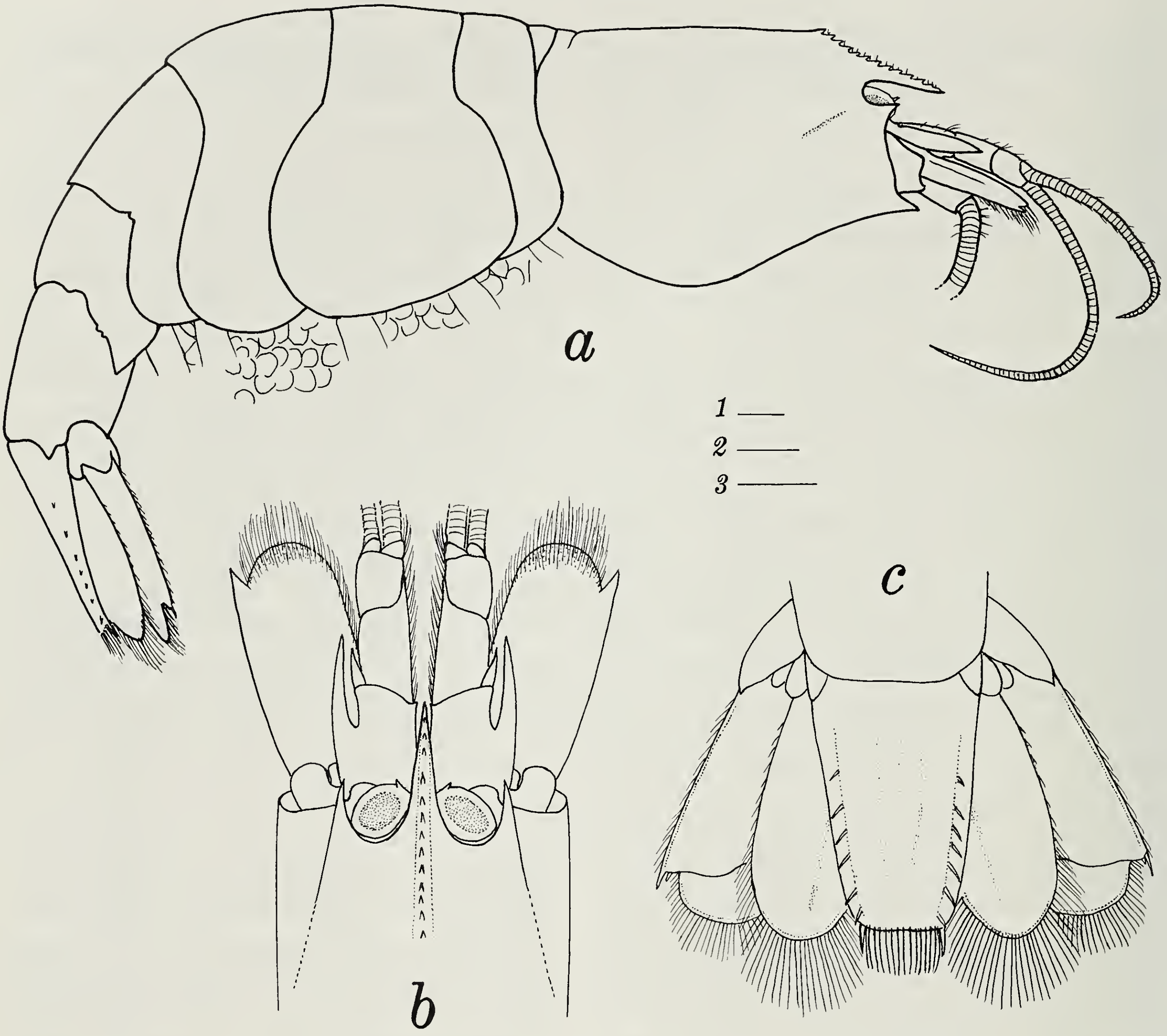

Fig. 1. *Alvinocaris williamsi*, new species, holotype ovigerous female, USNM 1009651. *a*, body, cephalic appendages, and abdomen, lateral view; *b*, anterior region of carapace, including eyes and antennae, dorsal view; *c*, telson and uropods, dorsal view. Scale bars equal 1.0 mm (bar 1 for *a*, bar 2 for *b*, bar 3 for *c*).

Holotype: adult female CL 9.5 mm, ovigerous (specimen ID: BN 70), USNM 1009651. Paratypes: 2 adult females CL 9.3, 9.7 (specimen ID: BN 68 and BN 51, respectively), abdomen torn from body, tail fan missing, USNM 1009652, USNM 1009653.

Description.—Integument thin, shining, minutely punctuate. Rostrum (Fig. 1a, b) almost straight, imperceptibly elevated above horizontal in distal half; sharply pointed tip (broken or slightly blunted in all specimens) reaching at least to level of articulation between first and second peduncular segment of second antenna or sometimes to midlength of second segment; dorsal margin raised into thin serrate crest containing 13 or 14 teeth of nearly equal strength in central sector of row, about 0.5 length of crest continued onto carapace, deflecting from dorsal line of carapace at approximate 45° angle; ventral margin less prominent, straight, and unarmed or with 1 minute subterminal tooth; lateral carina (not visible in Fig. 1a) broadened proximally and confluent with orbital margin. Carapace (Fig. 1a) with buttressed and distinct antennal spine; pterygostomian spine prominent, acuminate. Anterior antennal carina curving posteroventrally from near base of antennal spine to intersect at about midlength of carapace with carina extending posteriorly from pterygostomial spine, its associated groove (not visible in Fig. 1b) continuing indistinctly posteriorly.

Abdomen of female broadly arched dorsally, gradually tapering posteriorly, height of sixth somite about half that of first somite. Pleura of third somite broadly rounded, that of fourth somite irregularly rounded, flanked dorsally by single remote obsolescent spine; fifth pleuron with strong acute triangular posteroventral tooth flanked dorsally by cluster of 2 or 3 remote small spines on margin; sixth somite with middorsal length about 1.4–1.9 that of fifth somite, broad-based posterolateral tooth overlapping base of telson, smaller posterolateral spine acute. Telson (Fig. 1c) elongate, subrectangular, length (not including posterior teeth) about 2.0–2.7 anterior width, 3.2–3.7 posterior width, about 1.3–1.5 length of sixth somite; armed with 5–7 dorsolateral spines of nearly uniform size, occasionally unequal in number on either side; posterior margin slightly convex, armed with 1 spine at each corner and 12 feathered strong setae on posterior margin between them.

Eyes (Fig. 1a, b) with cornea imperfectly developed; unfaceted though diffusely pigmented; ovate in outline though fused to each other mesially beneath rostrum, each with upturned spine on anterodorsal surface.

Antennular peduncle (Fig. 1b) extending slightly short of end of antennal scale; basal segment 2.1 length of second segment and about 2.2–2.5 length of third, all measured on dorsal margin; stylocerite well separated from peduncle, tapering to slender elongate tip variably reaching as far as midlength of second segment; basal segment with distodorsal margin exceeded by rostral tip though extended laterally into strong lateral spine reaching level nearly equal to that of stylocerite and closely appressed to second segment, much smaller distomesial spine slightly divergent; shorter second segment with stronger mesiodistal spine. Antennal scale (scaphocerite) broadly rounded distally, with broad triangular tooth on distolateral border extending to same level as rounded distal border.

Mouthparts (Fig. 2) fairly typical for the genus. Mandible (Fig. 2a, b) with 6 blunt, uneven, terminal teeth plus one slightly sharper dorsal subterminal tooth along cutting border, and with long, blunt, posterior tooth ("molar process" of some authors) separated from cutting edge by a wide gap; mandible deeply excavate on internal (posterior) surface just above this blunt posterior tooth; mandibular palp 2-segmented, distal article bearing numerous plumose setae; basal article with 2 plumose setae on distal border. First maxilla (Fig. 2c) with 2 endites; coxal (distalmost) endite with row of evenly spaced and evenly sized blunt spines (arrow) in addition to dense plumose and simple setae; basial endite (proximal endite) with longer, curved setae but lacking spine row; palp unsegmented, with 2 short and 1 long terminal setae as illustrated. Second maxilla (Fig. 2d) scaphognathite with dorsal lobe broad, distally almost truncate, and lined with evenly spaced plumose setae; posterior lobe of scaphognathite tapering posteriorly, almost triangular, with setae increasing in length posteriorly, each seta angled and minutely serrate (for grooming); coxal lobe simple, blunt, setose; basial endite bilobed, each lobe fringed with plumose setae; palp thin, narrow, strap-like. First maxilliped (Fig. 2e) phyllopodous; coxal endite distally blunt and slightly recurved; basial endite bilobed, with distal lobe approximately twice length of proximal lobe; palp thin, tapering to acute distal tip bearing short setae and visible only in posterior view; exopod broad, expanded and rounded distally, lined on either side with evenly spaced plumose setae; epipod bilobed at base, fused distally, with dorsolateral lobe bearing weak posterior projection. Second maxilliped (Fig. 2f) pediform, 6-segmented; coxa expanded and rounded on medial surface, which bears nu-

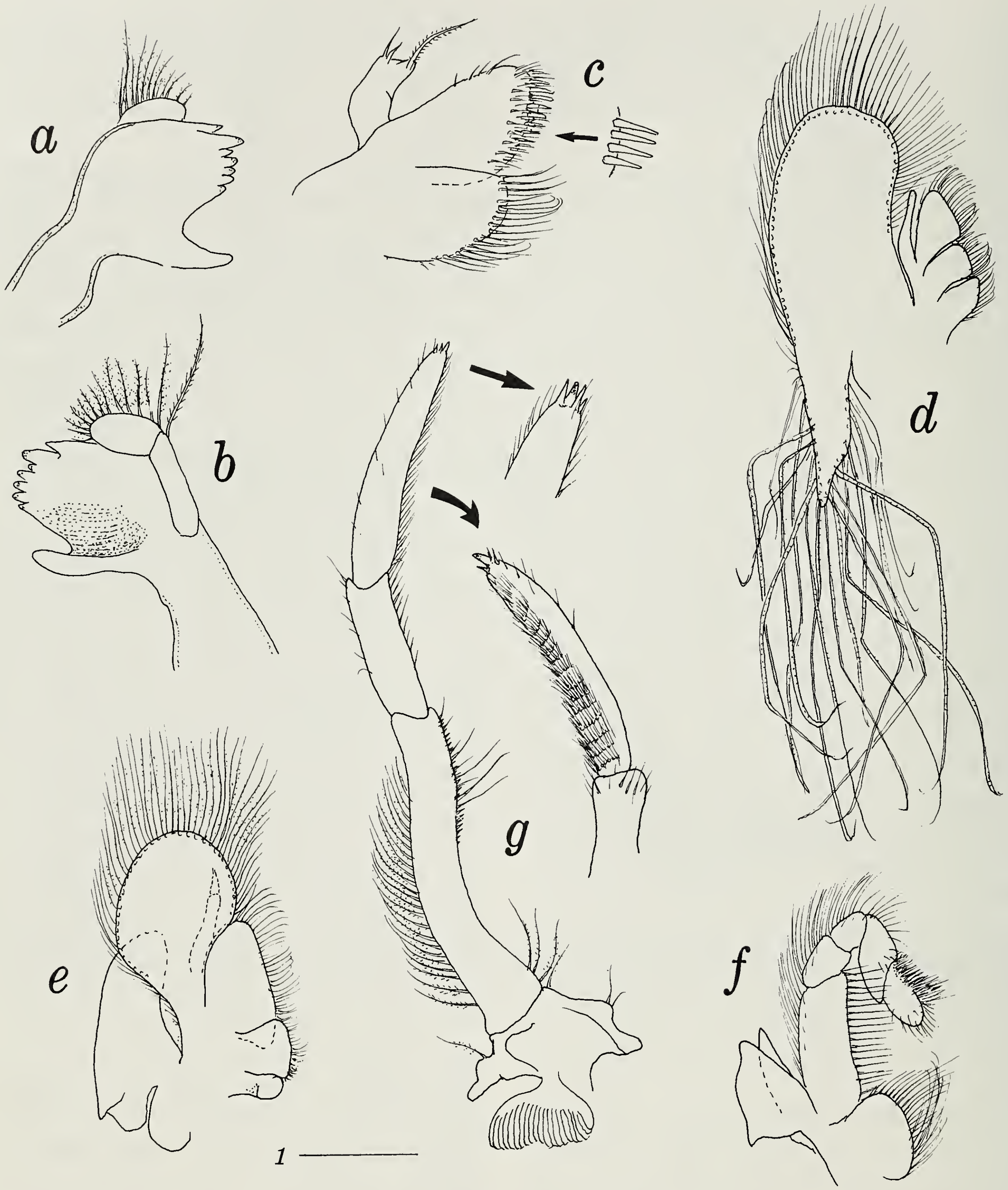

Fig. 2. *Alvinocaris williamsi,* new species, paratype female, USNM 1009653. Mouthparts, right side. *a,* mandible, outer (external) view; *b,* mandible and palp, inner view; *c,* first maxilla, with row of evenly spaced spines magnified and indicated by arrow; *d,* second maxilla; *e,* first maxilliped; *f,* second maxilliped; *g,* third maxilliped, with tip enlarged (upper arrow) and inner surface with rows of setae displayed (lower arrow). Scale bar 1 equals 0.5 mm (*a, b, c*), and 1.0 mm (*d, e, f, g*).

merous plumose setae; fused basi-ischium with evenly spaced plumose setae along medial border; merus and carpus short; propodus trapezoidal; dactylus short, distally rounded, with brush like patch of dense setae on proximal region. Epipod nearly triangular, with weak lobe coming off posterior surface. Third maxilliped (Fig. 2g) pediform, elongate, 4-segmented; coxal segment short, with minute epipod bearing 1 or 2 setae; distal 3 segments elongate and pediform; basal of these with plumose setae on proximal medial border and row of plumose setae along dorsolateral border; dactylus tipped with acute sclerotized spines surrounding central claw-like tip (arrow), and with evenly spaced densely packed rows of stiff, minutely serrulate setae on ventro-medial surface (curved arrow).

First pereopods (Fig. 3a, b) chelate, subequal; fingers curved ventrally and slightly laterally; dactylus more slender than fixed finger, tips varying slightly in relative length, mesial surface of each finger concave; cutting margins uniformly offset, closing without gape, each armed with row of almost uniform teeth so closely set as to be almost contiguous, line of sensory setae

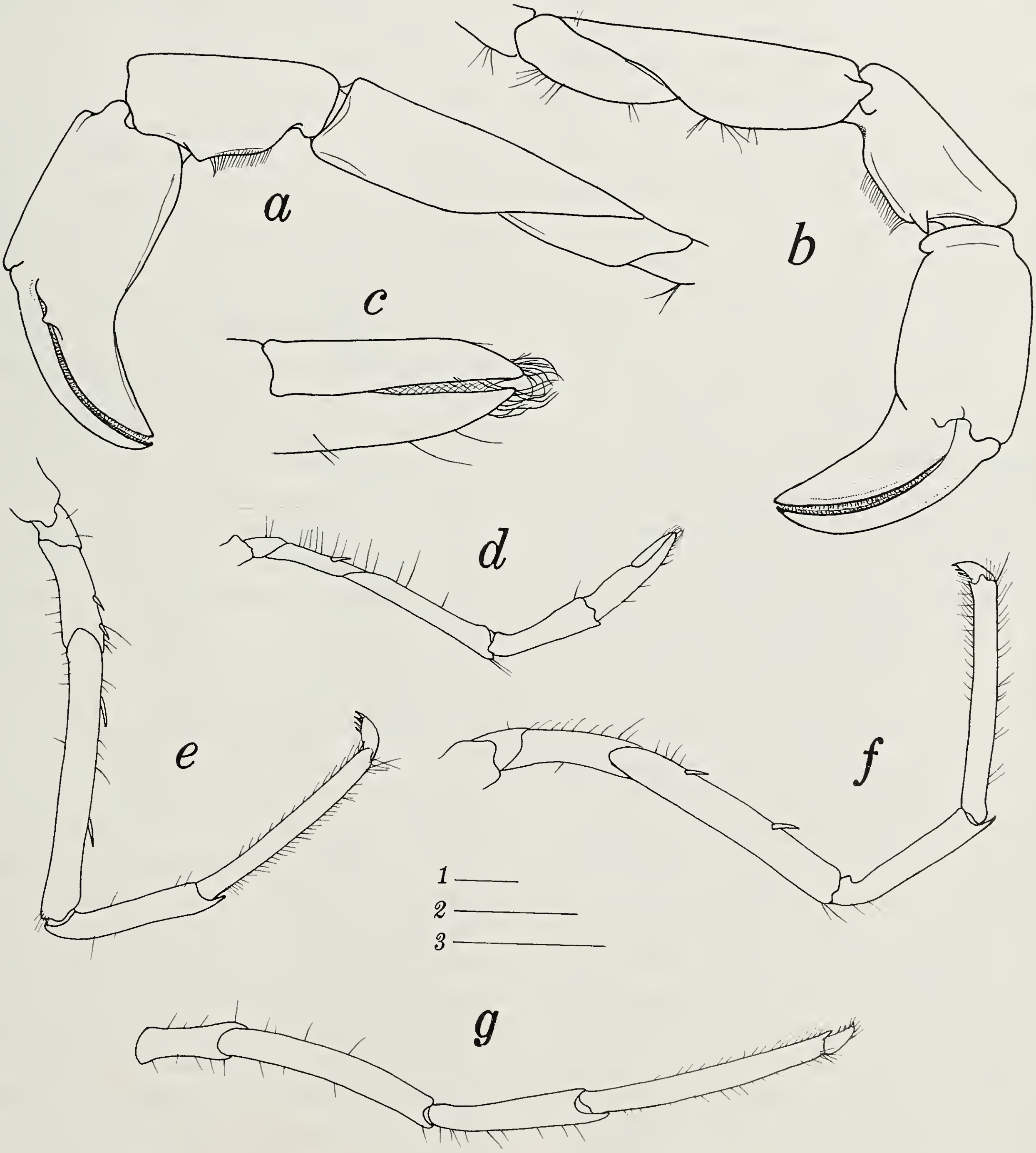

Fig. 3. *Alvinocaris williamsi,* new species, paratype female, USNM 1009652. *a,* right first pereopod (cheliped), inner view; *b,* right first pereopod, outer view; *c,* left second pereopod, tip of chela; *d,* left second pereopod; *e,* left third pereopod; *f,* left fourth pereopod; *g,* left fifth pereopod. Scale bars 1 and 2 equal 1.0 mm; scale bar 3 equals 0.5 mm (bar 1 for *d, e, f, g*; bar 2 for *a, b*; bar 3 for *c*).

mesial to cutting edges, acute tip of dactylus slightly spooned by elongate teeth slanted posteriorly and curving around external edge; entire leg slightly shorter than third maxilliped. Palm inflated but not elongate, approximately equal in length to fingers. Carpus measured along dorsal border slightly longer than palm, bearing oblique ventral crest, ending in strong distolateral spine (Fig. 3b) and flanked mesially by patch of setae on polygonal raised area; notch above spine smoothly concave, opposing low ridge ending in small rounded spine on heel of palm; shallowly concave anteromesial margin of carpus leading dorsally to 2 low rounded lobes. Merus swollen in distal half, distinct from ischium but fused to it, neither armed.

Second pereopod (Fig. 3c, d) shorter and more slender than first, reaching to between midlength and end of antennal peduncle; finger slightly longer than palm, similar in size and shape, opposed margins without gape, each pectinate with single row of teeth in distal half directed obliquely distally and increasing slightly in size to end in noticeably stronger tooth crossing opposite member when closed, but spineless proximally; carpus slender, about 1.2 times longer than chela; merus unarmed, ischium with stout spine at approximately 0.75 length.

Third to fifth pereopods (Fig. 3e, f, g) similar in length and structure, third reaching beyond antennal scale by about 0.3 the length of the propodus. Segments of these pereopods composed of: short dactylus armed with about 6 corneous spines on flexor surface, grading from small proximally to longest and strongest distally; ventral row of spines on propodus leading to base of dactylus; carpus of each leg with distodorsal extension variously projecting as a stop along proximal part of propodal extensor surface; third leg with ischium and merus stronger than on fourth and fifth leg, merus of third with ventral spine at 0.3 and 0.6 length, distal spine tending to be strongest, and ischium with 2 spines in line with those on merus; fourth leg with similar spines on merus but ischium not always bearing spines; fifth leg without spines on merus or ischium but with ventral row of small spines on propodus preceding base of dactylus.

Pleopods (not illustrated) well developed, first pair with endopods about half length of exopods; endopods tapering to acute tip.

Uropods (Fig. 1c) with rami subequal in length, slightly exceeding posterior margin of telson; lateral ramus of exopod with movable spine mesial to larger distolateral tooth, diaeresis sinuous.

Etymology.—The species name commemorates the late Austin B. Williams, Research Scientist of the Systematics Laboratory and National Marine Fisheries Service at the National Museum of Natural History, Smithsonian Institution (see Lemaitre & Collette 2000). We are all beneficiaries of his ceaseless pursuit of excellence in his contribution to the taxonomy, systematics, biogeography, and evolution of various decapod groups, including vent shrimp and crab species.

Remarks.—*Alvinocaris williamsi* appears morphologically most similar to *A. stactophila,* another species from a relatively shallow site (530 m). However, *A. stactophila* is known only from a distant hydrocarbon seep site (as opposed to a hot vent) off the coast of Louisiana, northern Gulf of Mexico. Characters shared by the two species include a rostrum that is unarmed (or occasionally armed with a single tooth) on the ventral margin (a feature also shared with *A. brevitelsonis* and *A. leurokolos* from the western Pacific). The dorsal and ventral margins of the rostrum are heavily toothed in all other described *Alvinocaris* species. Additionally, both *A. williamsi* and *A. stactophila* have a relatively short rostrum that continues posteriorly as a toothed carina that meets the dorsum of the carapace at an angle; this angle is sharper in *A. williamsi* and *A. stactophila* than in any other species except for *A. longirostris,* the distinctive rostrum of which, because of its length and armature, could not be confused with that of either *A. stactophila* or *A. williamsi*. However, *A. williamsi* can be easily separated from *A. stactophila* by the sharper angle of the rostrum and carina where they meet the dorsal line of the carapace (approximately 45° in *A. williamsi* vs. approximately 30° in *A. stactophila*), by the relative length and width of the telson (which is considerably longer and narrower in *A. stactophila*), and by the shorter rostrum relative to the carapace in *A. williamsi.*

Based on the absence of ventral teeth on the rostrum and the angle of the rostral carina and carapace, *A. williamsi* is also markedly similar to two species, *A. brevitelsonis* and *A. leurokolos* Kikuchi & Hashimoto (2000), recently described from the relatively shallow (~700 m) Mid-Okinawa Trough. However, Kikuchi & Hashimoto (2000) point out that there is significant variability in rostral characters, especially in *A. brevitelsonis* where the ventral rostral margin is usually toothed (there are seven spines on the ventral rostral margin of the holotype) but may be unarmed, especially in young individuals. *Alvinocaris leurokolos* lacks teeth on the ventral rostral margin, and is thus more similar to the new species *A. williamsi. Alvinocaris williamsi* is readily distinguishable from both of those species in having a lightly pigmented eye; the eye is unpigmented in both *A. brevitelsonis* and *A. leurokolos.*

The distribution of *Alvinocaris* species within the global biogeographic vent provinces is centered in lower-latitude regions (Shank et al. 1999), and the strong morphological similarities among extant *Alvinocaris* species living in relatively shallow water vent and seep environments (<800 m) in the Atlantic and Gulf of Mexico is striking. Gebruk (1997) and others have hypothesized that vent-endemic shrimp species are derived from shallow-water seep ancestors. A molecular phylogenetic approach to this hypothesis by Shank et al. (1999) suggested that the analyzed vent-endemic *Alvinocaris* (i.e., *A. markensis, A. lusca,* and undescribed Edison Seamount specimens) were derived from the *A. stactophila* (seep) lineage. This suggests that the extant *Alvinocaris* lineages share a common seep ancestor. However, other vent-endemic lineages are basal to *Alvinocaris,* suggesting that vent lineages gave rise to a seep lineage that in turn gave rise to other extant vent lineages. Based on morphology, *A. williamsi* from the relatively shallow Menez Gwen site more closely resembles a seep-endemic species (i.e., *A. stactophila*) than other hot vent species, and therefore molecular genetic comparisons of *A. williamsi* with congeners from deep-sea hydrothermal vents, seamounts, back-arc basins, and hydrocarbon seeps would markedly improve our understanding of the evolution and radiation of these shrimp among diverse chemosynthetic environments throughout the world's oceans.

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We owe an enormous debt of gratitude to Austin B. Williams, whose early work on shrimp from hydrothermal vents established the general framework within which all subsequent work on these shrimp is now viewed, and who unfortunately did not live to see the completion of this species description. Special thanks to Ruth Gibbons for persevering to make sure that several manuscripts, including this one, begun by A. B. Williams before his death were brought to fruition, and to M. Oremland and K. Hiratsuka Moore for providing illustrations. We thank the crews and pilots of the *R/V Atlantis* and the *DSV Alvin* for their skillful collecting efforts, A. Gebruk for shipboard expertise, and the co-chief scientists of the expedition, R. C. Vrijenhoek and R. A. Lutz; some of the shared funding was via the National Science Foundation (OCE-96-33131). Finally, we thank T. Komai and A. L. Vereshchaka, and two anonymous reviewers, for suggestions that greatly improved the manuscript. This is contribution No. 10700 of the Woods Hole

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Literature Cited

Christoffersen, M. L. 1986. Phylogenetic relationships between Oplophoridae, Atyidae, Pasiphaeidae, Alvinocarididae fam. n., Bresiliidae, Psalidopodidae and Disciadidae (Crustacea Caridea Atyoidea).—Bolletim de Zoologia 10:273–281.

Colaço, A., D. Desbruyères, T. Comtet, & A.-M. Alayse. 1998. Ecology of the Menez Gwen hydrothermal vent field (Mid-Atlantic Ridge/ Azores Triple Junction).—Cahiers de Biologie Marine 39:237–240.

Comtet, T., & D. Desbruyères. 1998. Population structure and recruitment in mytilid bivalves from the Lucky Strike and Menez Gwen hydrothermal vent fields (37°17′N and 37°50′N on the Mid-Atlantic Ridge).—Marine Ecology Progress Series 163:165–177.

Desbruyères, D., et al. 2001. Variations in deep-sea hydrothermal vent communities on the Mid-Atlantic Ridge near the Azores plateau.—Deep-Sea Research 48(5):1325–1346.

Gebruk, A. V., S. V. Galkin, A. L. Vereshchaka, L. I. Moskalev, & A. J. Southward. 1997. Ecology and biogeography of the hydrothermal vent fauna of the Mid-Atlantic Ridge.—Advances in Marine Biology 32:93–144.

Hashimoto, J., O Suguru, T. Gamo, H. Chiba, T. Yamaguchi, S. Tsuchida, T. Okudaira, H. Watabe, T. Yamanaka, & M. Kitazawa. 2001. First hydrothermal vent communities from the Indian Ocean discovered.—Zoological Science 18(5): 717–721.

Kikuchi, T., & J. Hashimoto. 2000. Two new caridean shrimps of the family Alvinocarididae (Crustacea, Decapoda) from a hydrothermal field at the Minami-Ensei Knoll in the Mid-Okinawa Trough, Japan.—Species Diversity 5:135–148.

———, & S. Ohta. 1995. Two caridean shrimps of the families Bresiliidae and Hippolytidae from a hydrothermal field on the Iheya Ridge, off the Ryukyu Islands, Japan.—Journal of Crustacean Biology 15(4):771–785.

Lemaitre, R., & B. B. Collette. 2000. Austin Beatty Willliams (17 October 1919–27 October 1999). Biographical summary. Proceedings of the Biological Society of Washington 113:1–12.

Martin, J. W., & J. C. Christiansen. 1995. A new species of the shrimp genus *Chorocaris* Martin & Hessler, 1990 (Crustacea; Decapoda; Bresiliidae) from hydrothermal vent fields along the Mid-Atlantic Ridge.—Proceedings of the Biological Society of Washington 108:220–227.

———, & G. E. Davis. 2001. An updated classification of the Recent Crustacea.—Natural History Museum of Los Angeles County, Science Series No. 39:1–124.

———, & R. R. Hessler. 1990. *Chorocaris vandoverae,* a new genus and species of hydrothermal vent shrimp from the Western Pacific.—Contributions in Science, Natural History Museum of Los Angeles County 417:1–11.

Milne-Edwards, A., & E.-L. Bouvier. 1894. Brachyoures et anomures. Crustacés décapodes provenant des campagnes du yacht l'*Hirondelle* (1886, 1887, 1888). Première partie.—Résultats des campagnes scientifiques accomplies sur son yacht par Albert Ier, Prince Souverain de Monaco 7:1–112.

Segonzac, M., M. de Saint Laurent, & B. Casanova. 1993. L'énigme du comportement trophique des crevettes Alvinocarididae des sites hydrothermaux de la dorsale medio-atlantique.—Cahiers de Biologie Marine 34:535–571.

Shank, T. M., R. A. Lutz, & R. C. Vrijenhoek. 1998. Molecular Systematics of shrimp (Decapoda: Bresiliidae) from Deep-Sea Hydrothermal Vents: enigmatic "Small Orange" Shrimp from the Mid-Atlantic Ridge are juvenile *Rimicaris exoculata.*—Molecular Marine Biology and Biotechnology 7(2):88–96.

———, M. B. Black, K. Halanych, R. A. Lutz, & R. C. Vrijenhoek. 1999. Miocene radiation of deep-sea hydrothermal vent shrimp (Caridea: Bresiliidae): evidence from mitochondrial cytochrome oxidase subunit I.—Molecular Phylogenetics and Evolution 13(2):244–254.

Van Dover, C. L., S. E. Humphris, D. Fornari, C. M. Cavanaugh, R. Collier, S. K. Goffredi, J. Hashimoto, M. D. Lilley, A. L. Reysenbach, T. M. Shank, K. L. Von Damm, A. Banta, R. M. Gallant, D. Gotz, D. Green, J. Hall, T. L. Harmer, L. A. Hurtado, P. Johnson, Z. P. McKiness, C. Meredith, E. Olson, I. L. Pan, M. Turnipseed, Y. Won, C. R. Young, III, & R. C. Vrijenhoek. 2001. Biogeography and ecological setting of Indian Ocean hydrothermal vents.—Science 294:818–823.

Vereshchaka, A. L. 1996a. Comparative analysis of taxonomic composition of shrimps as edificators of hydrothermal communities in the Mid-Atlantic Ridge.—Doklady Biological Sciences 351(1):576–578.

———. 1996b. A new genus and species of caridean shrimp (Crustacea: Decapoda: Alvinocarididae) from North Atlantic hydrothermal vents.—Journal of the Marine Biological Association of the United Kingdom 76(4):951–961.

———. 1997. A new family for a deep-sea caridean shrimp from North Atlantic hydrothermal vents.—Journal of the Marine Biological Association of the United Kingdom 77:425–438.

Williams, A. B. 1988. New marine decapod crustaceans from waters influenced by hydrothermal discharge, brine, and hydrocarbon seepage.—Fishery Bulletin 86:263–287.

———, & F. A. Chace, Jr. 1982. A new caridean shrimp of the family Bresiliidae from thermal vents of the Galápagos Rift.—Journal of Crustacean Biology 2:136–147.

———, & F. C. Dobbs. 1995. A new genus and species of caridean shrimp (Crustacea: Decapoda: Bresiliidae) from hydrothermal vents on Loihi Seamount, Hawaii.—Proceedings of the Biological Society of Washington 108:228–237.

———, & P. A. Rona. 1986. Two new caridean shrimps (Bresiliidae) from a hydrothermal field on the Mid-Atlantic Ridge.—Journal of Crustacean Biology 6:446–462.

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New brachyuran crabs (Crustacea: Decapoda) from the Upper Pliocene Yorktown Formation of southeastern Virginia

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Abstract.—Six new species of crabs, representing three families and one new genus, are described and illustrated from the Upper Pliocene Yorktown Formation of southeastern Virginia. They are remarkable for their state of preservation and represent the first fossil record for three of these living genera in Virginia's rich Neogene marine deposits. The presence of *Stenocionops* along with the common occurrence of *Persephona* in these deposits suggests that warm temperate waters covered southeastern Virginia during the deposition of late Yorktown sediments.

Introduction

In 1935, Mary J. Rathbun published the first comprehensive paper on the fossil crustaceans, principally decapods, of the Atlantic Gulf Coastal Plain of Eastern North America. In this landmark paper she describes or mentions all of the fossil decapod, stomatopod and isopod crustaceans from this region made available to her at that time from a host of sources (Rathbun 1935:1). Of the 25 families, 67 genera, and 167 species covered, and for the most part illustrated, in her paper only eight species representing six genera and six families were listed and treated from Virginia from deposits of Miocene, Pliocene and Pleistocene age. All but one were listed as occurring in deposits of the Yorktown Formation which at that time was regarded as Miocene. However the Neogene stratigraphy of southeastern Virginia has evolved considerably since 1935 (Hazel 1971a, Ward & Blackwelder 1980, Ward & Gilinsky 1993), and consequently only *Cancer borealis* Stimpson, 1859, *Panopeus herbstii* Milne-Edwards, 1834, and *Libinia dubia* Milne-Edwards, 1834, are listed from localities that are now regarded as old as Miocene.

With the exception of *Cancer borealis* Stimpson, 1859, the remaining species—*Callianassa suffolkensis* Rathbun, 1935; *C. atlantica* Rathbun, 1926; *Persephona punctata* (Linné, 1758); *Callinectes sapidus* Rathbun, 1896; *Panopeus herbstii* Milne-Edwards, 1834; and *Libinia dubia* Milne-Edwards, 1834—are all listed from localities now regarded as Upper Pliocene. *Callinectes sapidus* Rathbun, 1896 is the only species listed from the Pleistocene.

In the present paper six additional taxa, *Hepatus bottomsi*, n. sp., *Pterocarcinus baileyi*, n. gen, n. sp., *Persephona niemeyeri,* n. sp., *P. rodesae*, n. sp., *Stenocionops dyeri*, n. sp., and *Euprognatha ricei*, n. sp. are described as new and illustrated from deposits of late Pliocene age in the same general geographic area as that treated by Rathbun 67 years ago. Unlike Rathbun's material, which is very fragmentary, often consisting only of fingers, the taxa presented in this paper are remarkable for their state of preservation and completeness. All are represented by their original exoskeleton, and many even exhibit a uniform color similar to that of their living relatives.

The material studied in this paper was collected from the Moore House Member of the upper part of the Yorktown Formation from three localities in southeastern

Virginia. They are: The Lone Star Lakes, near Chuckatuck, Suffolk; Riddick Pit, borrow pit east side Virginia Routes 10/32, 4.4 km southeast of Benns Church; and Rices Pit, a now flooded borrow pit in Hampton (Ward & Blackwelder 1980). Detailed locality data for the these localities are provided in Appendix 1.

With the exception of one female paratype of *Stenocionops,* the gender of the remaining specimens described in this paper could not be determined.

Stratigraphy & Paleoenvironment

Mansfield (1943) expanded on his earlier biostratigraphic division of the Yorktown Formation into Zones I and II and regarded both units as entirely Miocene. His zonation, though flawed, was very workable in the field for many years. Hazel (1971a) divided the Yorktown into three ostracode zones of which the uppermost or *Puriana mesacostalis* zone, he regarded as Pliocene. Ward & Blackwelder (1980) refined the stratigraphy of the Yorktown Formation by redefining and dividing it into two formations: the Upper Miocene Eastover Formation overlain by the Lower Pliocene Yorktown Formation. The latter was further divided into four members which in ascending order were named: Sunken Meadow, Rushmere, Mogarts Beach, and Moore House. Ward & Blackwelder (1980:44), in defining the uppermost member state, "the Moore House Member, representing the regressive phase of the Yorktown Formation, reflects a renewal of higher current and wave energy conditions. The member consists of sandy shell beds and cross-bedded shell hash and locally is cemented to form a very indurated rock." They further (p. 45, 47) state, "The Moore House Member is found only east of the Surry Scarp," and "The Moore House Member reflects a progressively shallowing, regressive sea. Molluscan assemblages indicate normal salinities, but some of the highest beds in the Williamsburg area contain a few brackish-water mollusks. Locally large offshore bars were the site of rapid, large-scale, cross-bedded sand deposition." All of the specimens studied in this paper and the strata at the localities from which they were derived are now regarded by L. W. Ward as belonging to the Moore House Member and of late Pliocene age (Ward, pers. comm., 26 November 2002). Kier (1972), in a study of the echinoids from two (Chuckatuck and Rices Pit) of the three localities covered in this paper, gives a late Miocene age for his material. This age, though now regarded as incorrect, was based on the ostracode zones of Hazel (1971a) and the work of Gibson (1967). A late Miocene age for strata found at these localities was also the consensus of Neogene molluscan workers at that time. Kier's interpretation of the life habits of the Yorktown echinoids is a valuable resource for understanding the paleoenvironmental conditions that existed during the deposition of the Yorktown at Rices Pit and particularly at the Chuckatuck Bar. (See Johnson & Coch 1969, Johnson 1969 and Campbell 1993 for a detailed description of the structure, extent and mollusks of the Chuckatuck Bar, which includes the deposits at the Riddick Pit).

Kier (1972:3) states, "The Yorktown echinoids, like the ostracodes, indicate a past climate warmer than now" . . . "Although some of these living species range into cooler waters, they all occur in subtropical regions, suggesting that the fossil echinoids they resemble lived in waters warmer than the mild-temperate waters now occurring off the coast of Virginia" Earlier, Hazel (1971b) in a detailed study of the Yorktown ostracodes coupled with his own detailed studies of Western Atlantic Recent ostracodes concluded that the climate of the Yorktown Sea was much warmer than Virginia's coastal waters are today. Kier (1972: 2) in summarizing Hazel (1971b) states, "This equable thermal regime is markedly different from that of any province and concomitant climate zone now extant along the Atlantic coast of the United States. The temperatures varied from about 12°C to 15°C in the winter to about 17.5°C to 20°C and finally to 20°C to 25°C in summer." Ward & Gilinsky (1993:26) state, "The Yorktown Sea supported a large, warm-temperate to subtropical molluscan assemblage." Western Atlantic species of the spider crab *Stenocionops* are not reported north of Cape Hatteras, North Carolina but inhabit warmer waters further south, some to Brazil (see Rathbun 1925; Williams 1965, 1984 for geographic ranges). The purse crab, *Persephona mediterranea* (Herbst, 1794) though reported from as far north as New Jersey and the southern Chesapeake Bay, is not commonly found there but is commonly found in warmer more southern waters from off Cape Hatteras to Brazil. The crabs of the Yorktown Sea, like the mollusks and other invertebrates found at the localities cited here, are representative of similar taxa that would be found today in warm-temperate to subtropical, open marine waters of normal salinity.

Terms and Conventions

The minute mushroom-shaped structures found on the surfaces of numerous brachyurans, and referred to by French authors for more than 100 years as "champignons" (mushrooms) in reference to their "mushroom-like" appearance, are here referred to as bolitimorphs after the Greek bolites (mushroom) in combination with the Greek morphe (form, shape). Bolitimorph as here defined is intended to replace the phrases "mushroom-like structure" or "mushroom-shaped structure". At least one living species, *Merocryptus boletifer* Milne-Edwards & Bouvier, 1894, from the Azores was named for this common feature.

Haj & Feldmann (2002) observed similar structures in members of the family Raninidae and introduced the term "fungiform" for their mushroom shaped structures that form a "pebbled surface" and stated, "This pebbled surface has not been recognized in any other decapod taxon, nor has its structure and function been described previously." These structures have, however been known for some time as noted above, and both their development and function studied in great detail (Serène 1954, Guinot 1979). Given the vast range of shapes suggested by the term Fungi, the term bolitimorph is more specific and is preferred here to denote mushroom-shaped structures.

Repositories.—Primary and secondary types are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, and The Virginia Museum of Natural History, Martinsville, Virginia as indicated.

Abbreviations.—NMNH, National Museum of Natural History, Smithsonian Institution; S.I., Smithsonian Institution; USGS, U.S. Geological Survey (when used with number indicates a locality; see locality register at end of paper); USNM, abbreviation for catalogue numbers of the former U.S. National Museum now the National Museum of Natural History; VMNH, Virginia Museum of Natural History.

Measurements

Measurements are expressed in millimeters. Abbreviations are as follows: cl, carapace length, maximum longitudinal measurement; cw, maximum transverse measurement; prl, propodus length, length of palm or combined length of palm and fixed finger; prh, propodus height; prt, propodus thickness.

Systematic Paleontology

Family Calappidae

Subfamily Matutinae

Genus *Hepatus,* Latreille, 1802

Hepatus bottomsi, new species

Fig. 1

Diagnosis.—Carapace arcuate (shaped like a drawn bow), front prominent, strongly elevated, produced well beyond orbits and anterolateral margin; dorsal surface

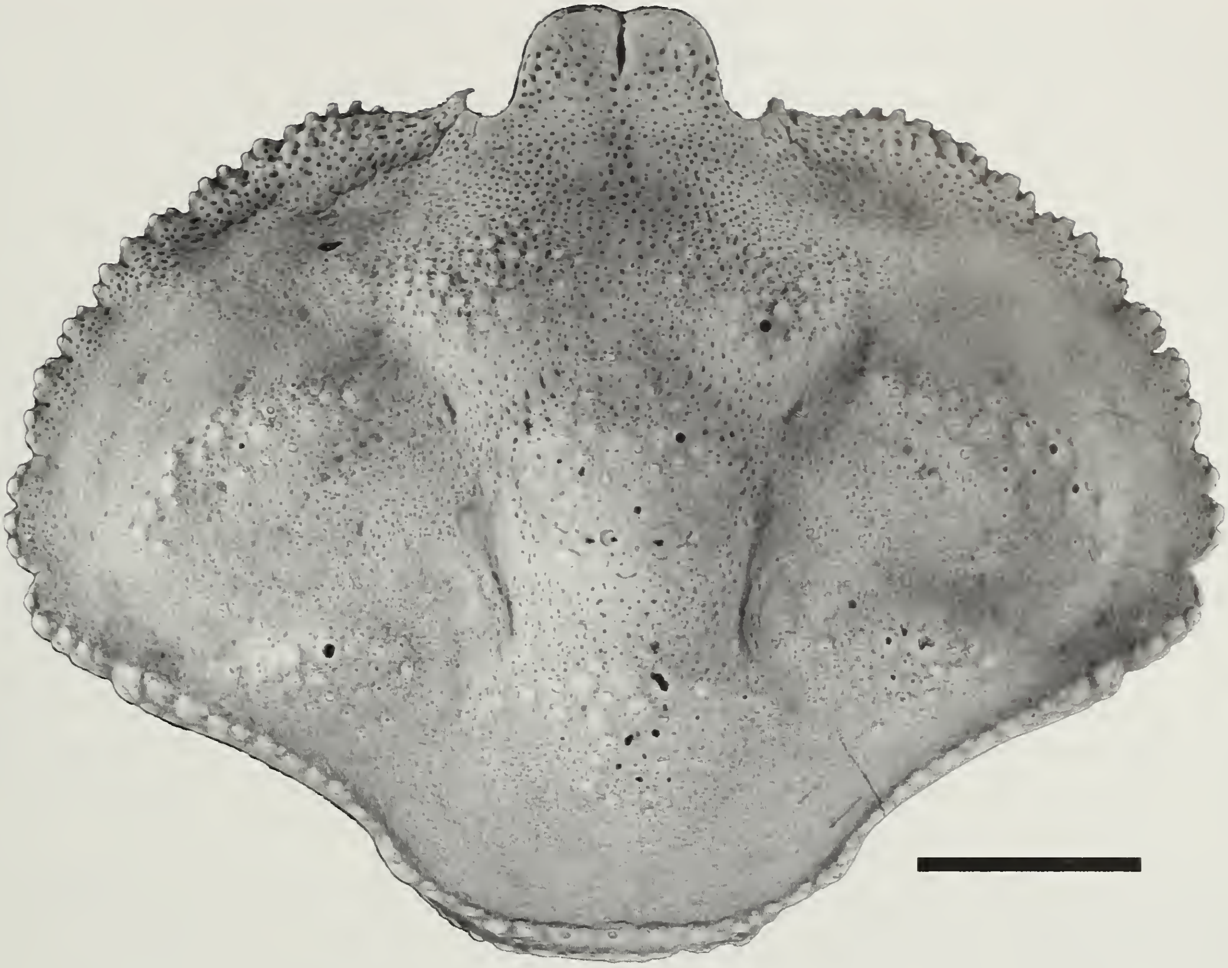


Fig. 1. *Hepatus bottomsi* Holotype (USNM 520705) dorsal view. Scale = 10 mm.

with eight distinct, pustulate protuberances; suborbital flank deeply depressed above descending, weakly sinuous anterolateral margin; surfaces everywhere pitted, particularly anteriorly where appearing eroded.

Description.—Carapace arcuate, strongly narrowing posteriorly, broad, length about three-fourths width, widest just forward of anterior-lateral angle, strongly convex longitudinally and highly arched transversely, appearing tripartite in frontal view, gastric and branchial regions distinctly swollen, regions moderately well defined, greatly elevated in younger individuals; dorsal surface with eight prominent, pustulate protuberances. Surfaces everywhere pitted, giving an eroded appearance; pits most abundant on anterior one-third of carapace particularly on front, eyes, orbits, post orbital and anterolateral margins, and adjacent surfaces. Surfaces somewhat smoother in larger, more mature individuals. Fronto-orbital width between one-fourth and one-third carapace width. Front prominent, thick, bilobate, strongly projecting beyond orbits and anterolateral margin (and placed well above anterolateral continuation of borders of carapace); lobes truncate with lateral margins rounded anteriorly, dorsally divided by deep sulcus, ventrally fused or closed along entire length. Antennules very obliquely set. Orbit small, subcircular, defined by slightly raised wide rim; rim composed of three lobes, base of eye in orbit level with front; orbits directed obliquely downward parallel to slope of thick, rounded dorsal margin above suborbital depression. Anterolateral margin comprised of about 40 blunt denticles situated on from 12 to 13 or more teeth; teeth separated by closed incisions, most of which begin with a deep pit; teeth bidentate anteriorly otherwise most often tridentate with median denticle strongest. Margin, where descending anteriorly to buccal cavity, weakly sinuous, comprised of single row of denticles of subequal strength. Posterolateral margin straight, strongly convergent posteriorly; anterior portion of margin, just posterior to strong tooth defining anterolateral angle, with a long low-angle tooth directed obliquely forward, tooth with double or triple close set rows of low tubercles; tubercles continue as a single or double row to distinct, though small, subacute tooth defining posterolateral angle; single row of tubercles continue transversely across posterior margin of carapace where it eventually continues along the opposing lateral margins until returning to the opposite side of the buccal cavity from which it began. Posterior margin high, narrow, width about one-seventh to one-fifth carapace width; margin defined above by slightly convex row of tubercles continuous with row of posterolateral margin, and submarginal row of tubercles below. Postfrontal surface with medial, broad, very shallow sulcus leading to base of frontal lobes. Epigastric region defined by minute pustules on either side of base of postfrontal sulcus. Hepatic region depressed, bordered anteriorly by thick, rounded carapace margin leading to orbit. Remaining dorsal regions defined by eight prominent, pustulate protuberances distributed as follows: paired protogastric, one mesogastric, one cardiac, paired epibranchial, and paired mesobranchial. Protogastric and mesogastric regions large, of subequal size, subcircular. Epibranchial regions developed into oblique ridges directed toward marginal tooth of anterolateral angle. Mesobranchial regions developed into ridges aligned roughly with anterior ridge of cardiac region to form a transverse line of protuberances aligned with first posterolateral tooth. Anterior face of ridges, smooth, steep. Intestinal region weakly inflated, indistinct. Posterior gastric pits minute, closely spaced.

Color.—Rust or yellowish brown to brownish gray when dry, gray or dark gray when wet. Recent species in alcohol are usually gray.

Etymology.—This species is named for E. Edward Bottoms, paleoanthropologist of Portsmouth, Virginia, in recognition of his numerous writings on Paleo Indians of the Eastern United States, for his years of teaching regional history on all student levels in the Tidewater Area, and for stimulating the author's early interest and development in paleontology.

Holotype.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia. USGS 26891; (USNM 520705) cl 42.88 mm, cw 54.92 mm. *Paratypes*: (USNM 520706), cl 49.97 mm, cw 66.18 mm. USGS 26891 as above; (USNM 520707), cl 33.63 mm, cw 42.77 mm. USGS 26891 as above. (VMNH I3546), cl 47.24 mm, cw 64.19 mm. Same geographic locality as USGS 26891 as above.

Occurrence.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia.

Remarks.—Recent comparisons: The greatly produced front of *H. bottomsi* immediately separates it from all living species of *Hepatus* but may confuse it with species of the genus *Hepatella,* Smith, in Verrill, 1869, type species *H. amica,* from which it differs as follows. Adult specimens of *Hepatus bottomsi* have eight low dorsal protuberances compared to the six greatly elevated dorsal protuberances found in adults of *Hepatella,* and as Rathbun, 1937 notes, *Hepatella* lacks the suborbital depression found in members of the genus *Hepatus.* This feature is distinct in *H. bottomsi.*

Fossil comparisons: *Hepatus bottomsi* differs from the middle Miocene *H. nodosus* Collins & Morris, 1976, of Trinidad, the only fossil species with which it might be confused, in having a greatly produced front and obliquely directed epibranchial ridges. In *H. nodosus* the front is marginal and the epibranchial ridges are transverse.

Individuals of *H. bottomsi* become smoother and their dorsal protuberances lower and much less pronounced as they grow larger and older.

Leucosiidae
Subfamily Ebaliinae
Pterocarcinus, new genus

Diagnosis.—Carapace suboctagonal, wing like; "wing" or branchial region extending laterally well beyond basis of legs; margins very thin, carinate; front narrow with two very weak rostral "horns"; cardiac region most prominent, a raised, subcircular platform or "mesa" surrounded by a deep, wide sulcus; posterior margin broad, bilobate.

Type species.—*Pterocarcinus baileyi,* n. sp. by present designation and monotypy.

Related species.—?*Ebalia rotundata* (A. Milne-Edwards, 1880); See A. Milne-Edwards & E. L. Bouvier, 1902 for figures. Generic status uncertain.

Etymology.—*Ptero* from the Greek, pteron, wing, in combination with the generic name *Carcinus* derived from the Greek, karkinos, or crab. Gender masculine.

Remarks.—In outline *Pterocarcinus* resembles a number of species currently placed in *Ebalia* Leach, 1817; *Lithadia* Bell, 1855 and *Speloeophorus* A. Milne-Edwards, 1865, but it differs dramatically in overall shape and form from the type species of all of these genera. It does not possess the subhemispherical form of the type species of *Ebalia, E. tuberosa* (Pennant, 1777). Nor does it exhibit the outline, "thick" wings, and caverns of the type species of *Speloeophorus, S. nodosus* (Bell, 1855), and it does not exhibit the highly elevated and excavated form represented by the type of *Lithadia, L. cumingii* Bell, 1855. (See Rathbun 1937, for figures of North and South American species placed in these genera). In overall form and outline *P. baileyi* most closely resembles *Ebalia rotundata* (A. Milne-Edwards, 1880), a species clearly not in the genus *Ebalia,* but one which might be its closest living relative. *Ebalia rotundata,* though very similar to this new species, differs in having very thick or rotund branchial "wings" unlike the thin carinate wings of *Pterocarcinus* and in having the cardiac and urogastric regions joined and not completely separated by a deep sulcus as in *Pterocarcinus* (Fig. 2A). In the absence of the first right pleopod of a male and other features present in living material, the true relationship of this new fossil genus to other leucosiids may never be fully understood, but its form is quite different from all known genera. Fragments of this new genus are fairly common in strata of Pliocene age along the Atlantic Coastal Plain. Given this situation it seems best to give this unusual leucosiid a distinct generic name.

Pterocarcinus baileyi, new species
Figs. 2–4

Diagnosis.—As for genus.

Description.—Carapace suboctagonal, wing-like, length about eight-tenths width, broadest at anterolateral angle; regions moderately well defined; dorsal ridge from front along midline to and including intersecting diagonal branchial ridges; hepatic and cardiac regions and posterior lobes distinct to prominent, ridges greatly elevated; irregular inner margin of elevated hepatic region deeply excavated. Cardiac region most prominent (Figs. 2A, 3B, F), a raised, subcircular or oval free-standing "mesa-like" platform completely surrounded by a deep, wide sulcus filled with scattered, tall bolitimorphs (Fig. 3B, D); "mesa" slightly elevated above ridge of branchial region and strongly produced posteriorly. Most surfaces of carapace covered with pavement of low, closely spaced or abutting bolitimorphs (Fig. 2A); bolitimorphs separate or free standing in depressions adjacent to ridge leading to front, along and anterior to diagonal ridge of branchial region, and in sulcus completely surrounding cardiac "mesa-like" region as well as ventral surfaces of pterygostomian and branchial regions where they are highest and most dis-

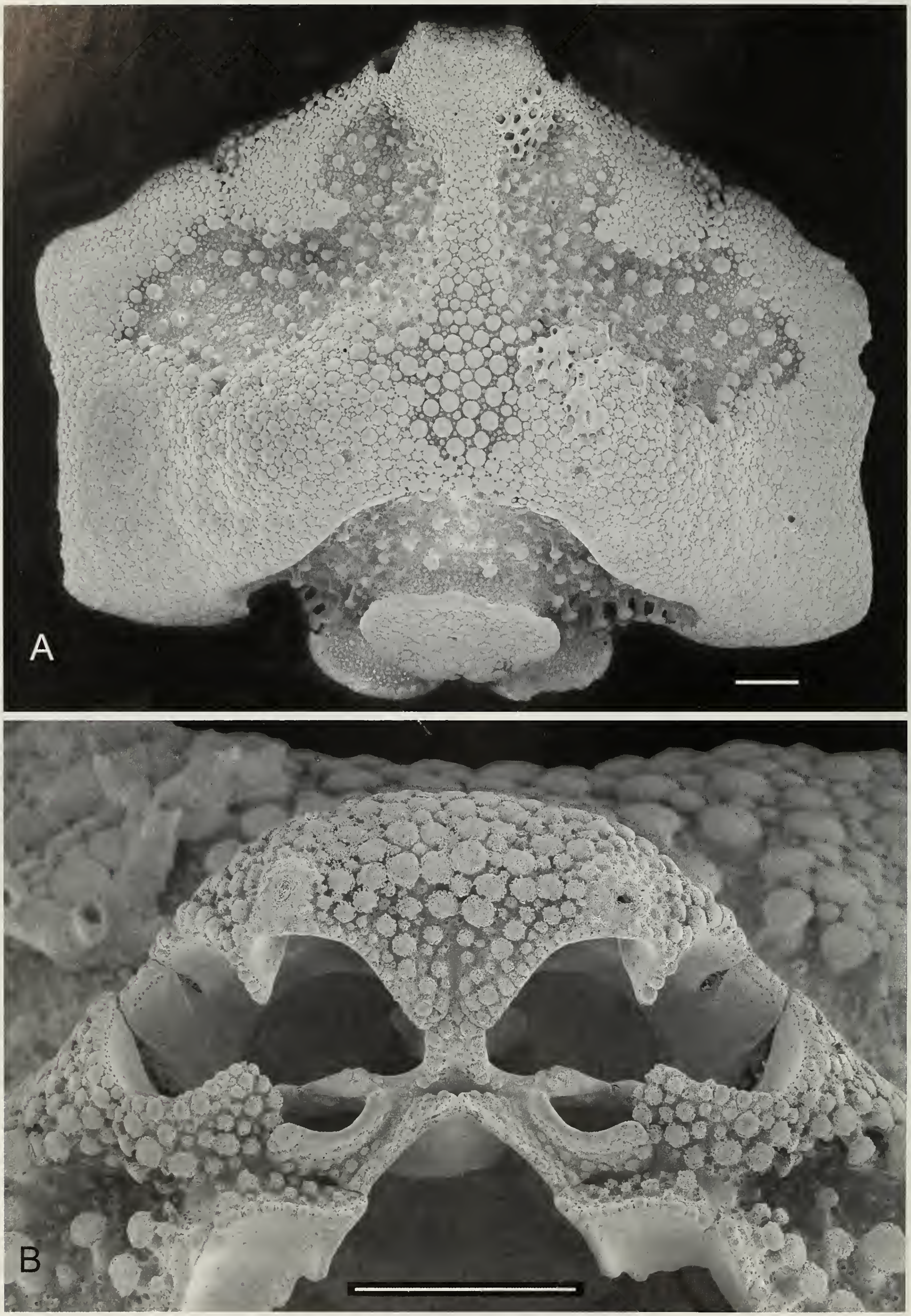


Fig. 2. *Pterocarcinus baileyi* Holotype (VMNH I3547) A. dorsal view; B. frontal view, close up. Scale = 1 mm.

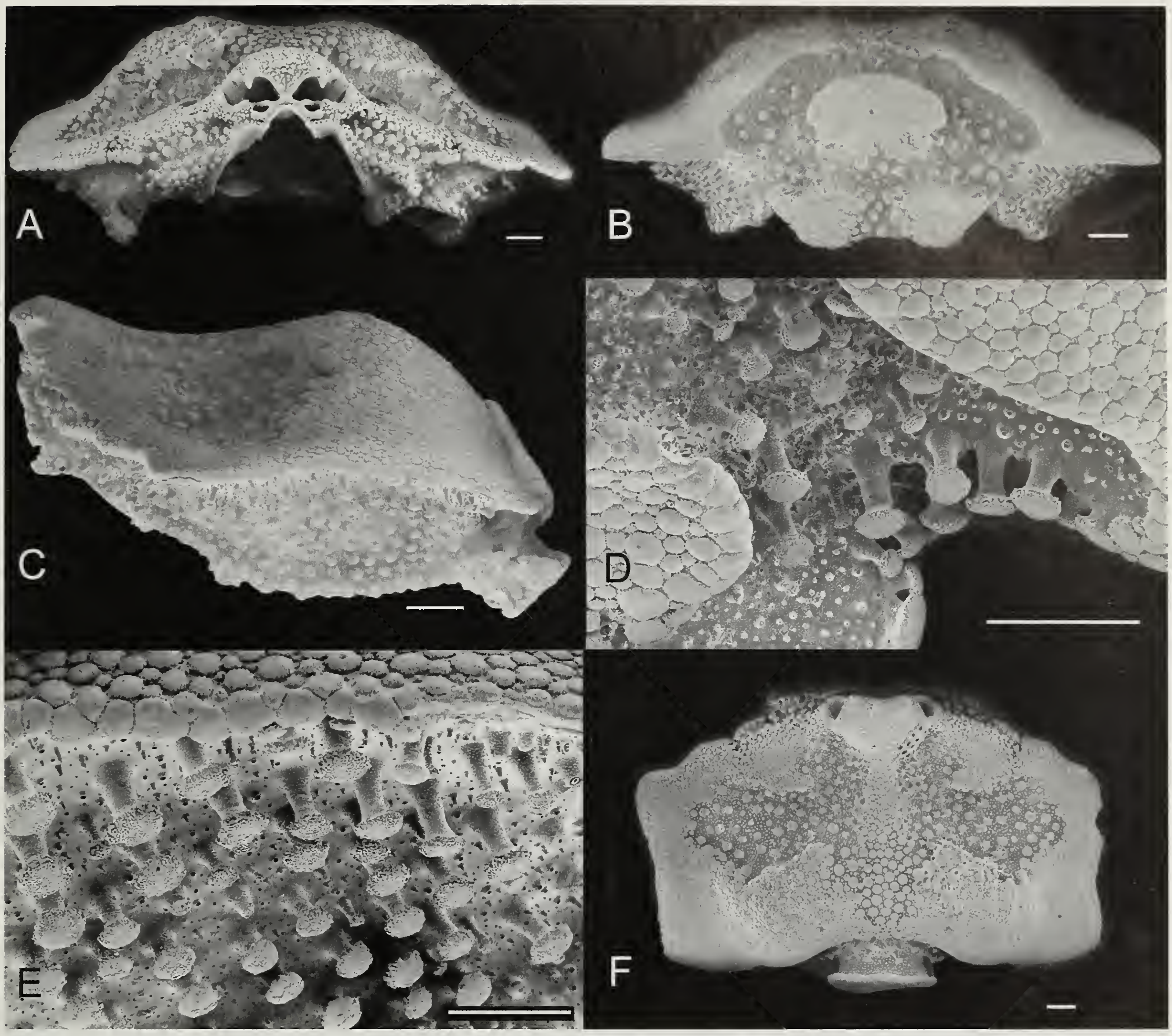


Fig. 3. *Pterocarcinus baileyi* Holotype (VMNH I3547) A. anterior view; B. posterior view; C. left lateral view; D. oblique posterior view. Scale = 1 mm. E. left lateral view of ventral surface beneath branchial "wing". Scale = 0.5 mm. F. oblique frontal view to show height of cardiac "mesa". Scale = 1 mm.

tinct. Front truncate, elevated, narrow, width slightly less than one-sixth width of carapace, lateral margins defined by very short, rounded, blade-like "horns" (Fig. 2A, B); front weakly projecting. Horns appearing more distinct in younger individuals. Fronto-orbital width about one-fourth carapace width. Orbit sub-circular, marginal, with three sutures, slightly produced at ex-orbital margin. Orbit and antennule fossae openly connected; basal antennal segment not present (not preserved); antennule fossae oblique. Bolitimorphs on fronto-orbital surfaces closely spaced forming pavement (Fig. 2B).

Pterygostomian region developed into long ridge subparallel to anterolateral margin (Fig. 3A); ridge composed of free standing rows of bolitimorphs of median length that cluster to form a downward, obliquely directed tooth before terminating posteriorly. Buccal cavity triangular, anterior margins of afferent channels with minute pustules, margin curving downward laterally to a narrow notch or sulcus. Branchial "wings" extending laterally well beyond basis of ambulatory legs and chela (Fig. 3A–C); legs probably not visible in dorsal view. "Wings" ventrally covered with distinctly separated tall bolitimorphs

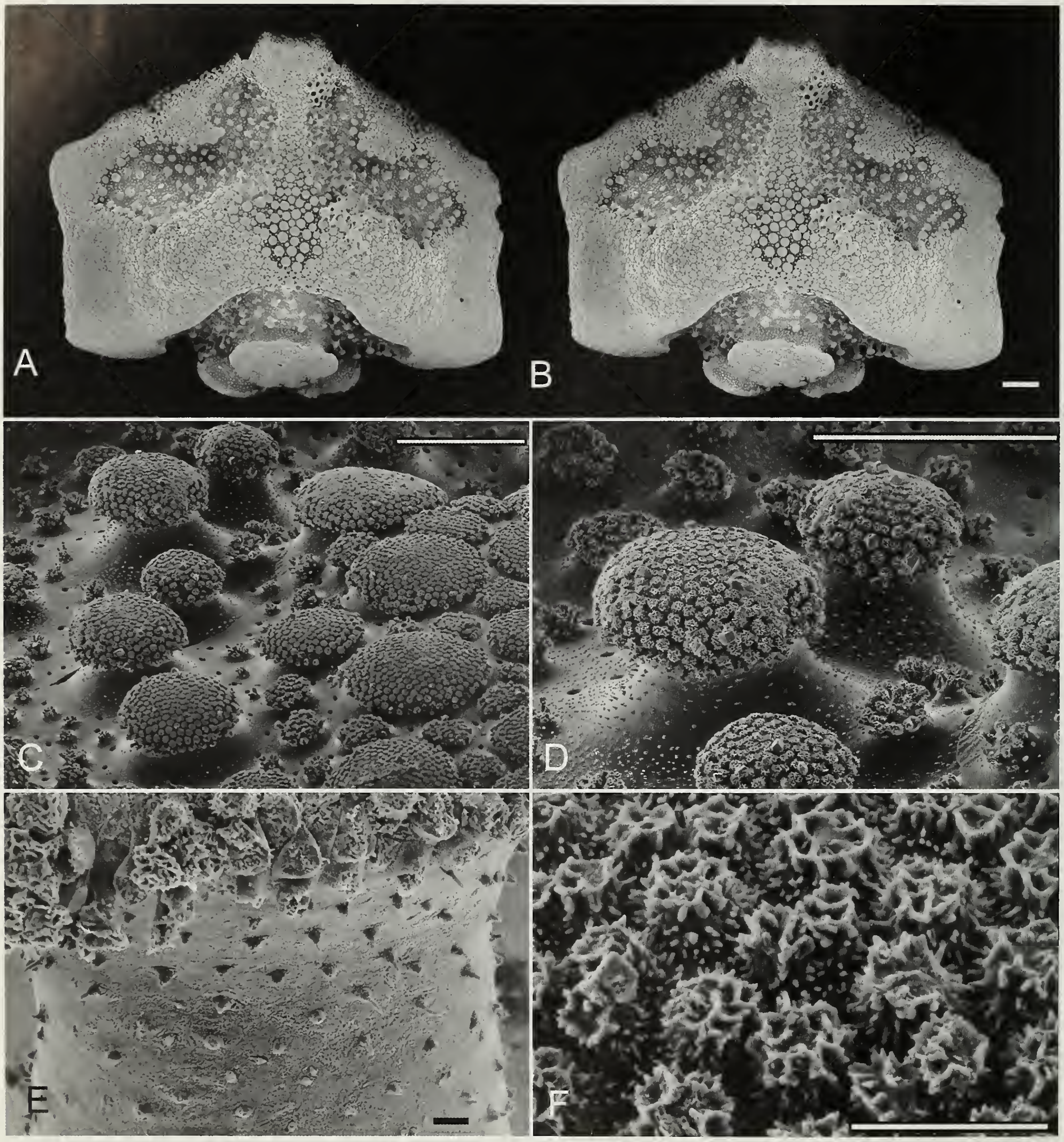


Fig. 4. *Pterocarcinus baileyi* Holotype (VMNH I3547) A., B. stereo pair in dorsal view. Scale = 1 mm. *Pterocarcinus baileyi* Paratype (USNM 520708) C., D. close-up of bolitimorphs in post-hepatic depression. Scale = 200 μm. *Pterocarcinus baileyi* Holotype (VMNH I3547) E. close-up of stalk of bolitimorph to show dagger-like structures that might function to hold sediment in place. Scale = 10 μm. *Pterocarcinus baileyi* Paratype (USNM 520708) F. high magnification to show unique structure of crown of bolitimorph seen in figures C. and D. above. Scale = 20 μm.

(Fig. 3E); bolitimorphs much shorter and abutting around margins at insertion of ambulatory legs and chela. Anterolateral, lateral, and posterolateral margins very thin, carinate (Fig. 3A–C); leading edge of each curving downward like an airfoil; edge appearing beaded below where bordered by a single row of minute bolitimorphs. Anterolateral margin longest, convergent anteriorly, set at 40 degrees to longitudinal axis; margin interrupted medially by a very distinct fissure between hepatic and branchial regions; margin anterior to fissure thickened and posterior to fissure sinuous; anterolateral angle rounded to subacute. Lateral margin about two-thirds length of anterolateral margin, distinctly concave in dorsal view and raised medially in lateral view; anterior half weakly divergent anteriorly; posterior half subparallel to longitudinal axis and terminating in a subacute angle. Posterolateral margin perpendicular to longitudinal axis, length less than one-half length of anterolateral margin; margin separated from posterior lobes by deep sulcus. Posterior distinctly bilobate, width slightly less than one-half width of carapace; lobes thick, separated by a deep fissure; dorsal surface of each, smooth; lobes moderately produced posteriorly, margin of each terminating in a thin, raised, beaded rim.

Apparent posterior gastric pits distinct, very widely spaced, set on branchial ridges just anterior to gastro-cardiac sulcus (Fig. 2A).

Color.—Brown, buff, or sometimes weathered bluish grey.

Etymology.—This species is named for Richard H. Bailey, geologist and paleontologist, Professor, Northeastern University, Boston, Massachusetts, for his research contributions to Atlantic Coastal Plain geology and paleontology, for his many years of superb teaching, and especially for his years of encouragement and field assistance to the author.

Holotype.—Riddick Pit, about 4.4 km southeast of Benns Church, Isle of Wright County, Virginia. Same geographic locality as USGS 26892 (VMNH I3547), cl 10.04 mm, cw 12.75 mm. *Paratypes*: (VMNH I3548), cl 10.77 mm, cw 13.36 mm estimate, incomplete. Same geographic locality as USGS 26892 above. (USNM 520708), cl 9.16 mm, cw 10.22 mm, USGS 26891, The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia; (USNM 520709), cl 8.79 mm, cw 10.95 mm, USGS 26891 as above.

Occurrence.—Riddick Pit, about 4.4 km southeast of Benns Church, Isle of Wright Co., Virginia, and The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia.

Remarks.—The function of the boletimorphs found on *Pterocarcinus baileyi* and other crabs probably differs with each of the taxa on which they occur. Given the difficulty of cleaning specimens covered with these boletimorphs, it is obvious to this author that their primary function is most probably one of concealment, in that they very effectively trap sand particles and hold them in the grooves and excavations of the carapace, thus obscuring the crab's outline and allowing it to blend into the substrate. Such concealment would allow it to hide from predators and ambush prey as well. These sometime very ornate, even flower-like, surface structures might also aid in anchoring the crab in the substrate. They also undoubtedly have a structural advantage in their reinforcement of the carapace. Serène (1954) elaborates on their development and Guinot (1979) discusses their development and presents the hypothesis that they serve to channel water to the bases of the legs and that they aid in concealment as well. My own observations have indicated that their individual form can be species specific and therefore of particular use to paleontologists in the identification of crab fragments.

Subfamily Iliinae

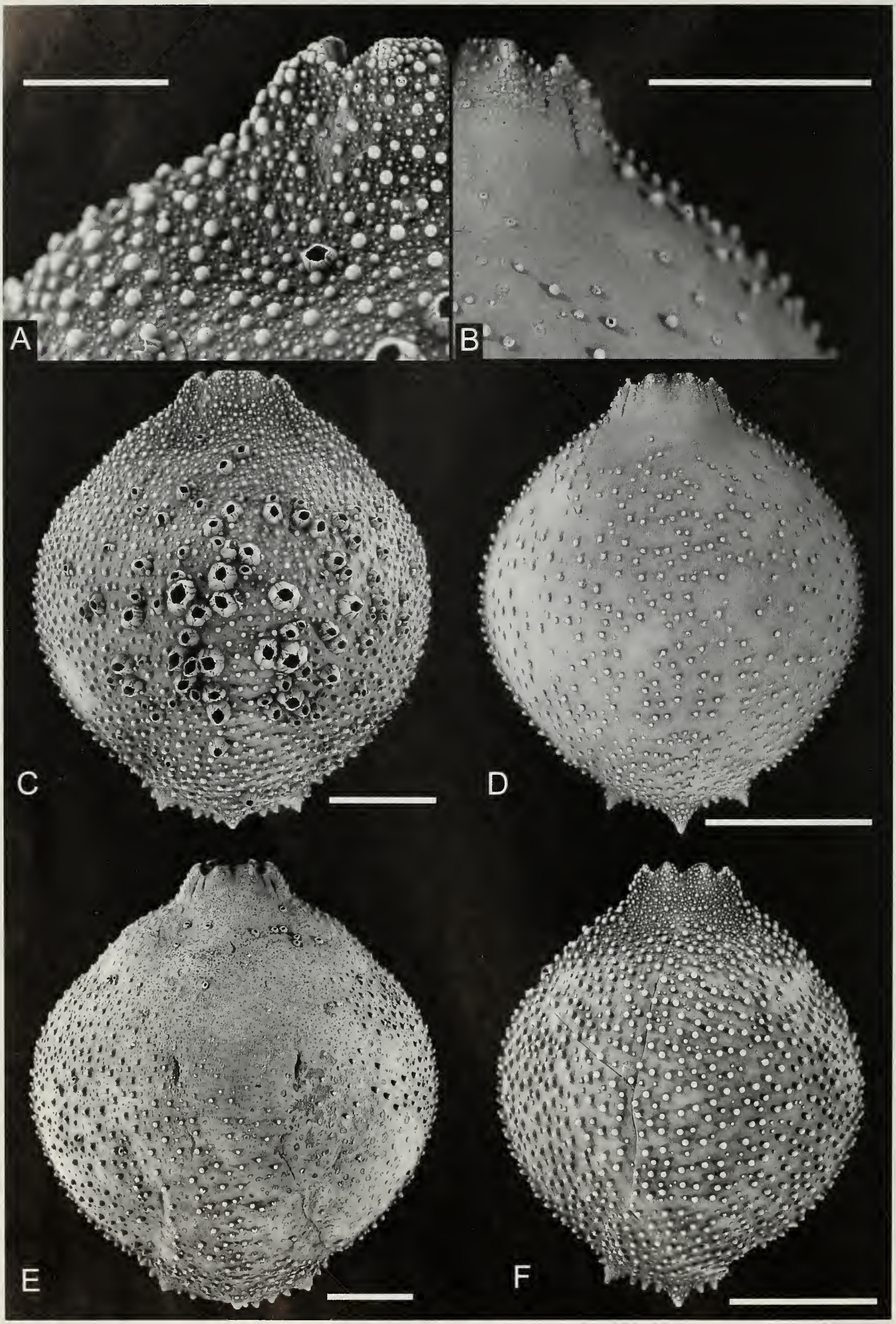
Genus *Persephona* Leach, 1817

Persephona niemeyeri, new species

Figs. 5A, C, E, F

Diagnosis.—Carapace hemispherical with three posterior spines; front bilobate, elevated, produced with orbits well beyond anterolateral margin; post frontal, hepatic and all other dorsal surfaces thickly covered with relatively high, subacute tubercles of various sizes; tubercles strongest along lateral and posterior margins, and highly concentrated on front, orbits and adjacent areas where developed into bolitimorphs.

Description.—Carapace hemispherical, width about nine-tenths of length, regions


A
B
C
D
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F

very weakly defined, front and orbits advanced well beyond anterolateral margins; posterior with three equally spaced recurved spines, two marginal, and one median above margin. Dorsal surfaces thickly covered with relatively high, subacute tubercles of various sizes; tubercles strongest along lateral and posterior margins, most concentrated below plural suture, where very low and closely spaced, and highly concentrated on front, orbits and adjacent areas where developed into bolitimorphs. Front very narrow, width about 0.09 width of carapace, bilobate, lobes separated by distinct v shaped sulcus, laterally defined by raised clusters of tubercles; anterior margins of lobes blunt, denticulate. Orbit very small, divided by three deep, narrow, open sutures creating four lobes. Minute, elongate tubercles span sutures from both sides, creating a pectinate appearance. Supraorbital eave and median lobe meet at a steep angle to form a broad v as seen from above. Large distinct bolitimorphs concentrated on outer lobe. Suborbital lobe with afferent channel below; channel deeply notched at anterolateral angle, inner angle rounded distally, margin pustulose and channel produced beyond front and orbits as seen in dorsal view. Hepatic region slightly swollen, weakly defined, thickly covered with tubercles. Superior margin of subhepatic region with low ridge of concentrated tubercles; ridge not joining but rather descending just below tubercles of anterolateral margin. Anterior and posterior lateral margins of carapace continuous, defined by a row of larger tubercles beginning at orbit and continuing along upper edge of plural suture to a point just above tooth of posterolateral angle; row poorly separated from dorsal tubercles, sometimes indistinct or appearing as double row where intermixed with dorsal tubercles; area below plural suture covered with closely spaced low tubercles, surface appearing very rough, bordered below by distinct row of strong tubercles just above bases of ambulatory legs. Posterior margin slightly more than one-third carapace width, produced posteriorly, laterally defined by a broad, stout, triangular, acute recurved spine at each corner; margin between spines comprised of from seven to 10 large recurved tubercles; intestinal margin above with a single medially placed, stout, recurved spine. Spines coarsely granulate. Posterior gastric pits not evident.

Color.—Reddish orange to yellow when dry.

Etymology.—This species is named for Antonio B. Niemeyer, Jr., science teacher, retired, of Chesapeake, Virginia, in recognition of his contribution to science through his many years of teaching science in the public schools of tidewater Virginia and for the fundamentals of general science that he instilled in this author so many years ago.

Holotype.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia. USGS 26891, (USNM 520710) cl 52.30 mm, cw 48.13 mm; *Paratypes*: (USNM 520711) cl 43.69 mm, cw 38.85 mm, USGS 26891 as above; (USNM 520712) cl 30.06 mm, cw 25.91 mm, USGS 26891 as above; (USNM 520713) cl 23.02 mm, cw 18.07 mm. Fragment of anterior portion of carapace only. USGS 26891 as above; (VMNH I3549) cl 36.83 mm, cw 33.27 mm. Same geographic locality as USGS 26891 above.

Occurrence.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia.

Remarks.—Recent comparisons: *Perse-*

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Fig. 5. *Persephona niemeyeri* Paratype (USNM 520711) A. closeup of left anterior surface in dorsal view. Scale = 4 mm. *Persephona rodesae* Holotype (USNM 520714) B. closeup of right anterior surface in dorsal view. Scale = 5 mm. *Persephona niemeyeri* Paratype (USNM 520711) C. dorsal view. Scale = 10 mm. *Persephona rodesae* Holotype (USNM 520714) D. dorsal view. Scale = 10 mm. *Persephona niemeyeri* Holotype (USNM 520710) E. dorsal view of geronic specimen, bare areas are a result of wear and abrasion. Scale = 10 mm. *Persephona niemeyeri* Paratype (USNM 520712) F. dorsal view. Scale = 10 mm.

phona niemeyeri is most similar to the Recent western Atlantic purse crab, *P. mediterranea* (Herbst, 1794) (see: Williams 1984 for synonymy) from which it can be immediately separated on the basis of its dense tuberculate covering alone.

Fossil comparisons: *Persephona niemeyeri* most closely resembles *P. rodesae* described below from which it can be separated as follows: 1.) *Persephona niemeyeri* has far more dorsal tubercles than *P. rodesae,* especially anteriorly on the postfrontal, frontal, and orbital surfaces; 2.) these tubercles are much higher and more acute than those of *P. rodesae*; 3.) the densely tuberculate hepatic region of *P. niemeyeri* differs considerably from that of *P. rodesae* which possesses only a few tubercles; and 4.) the lateral row of tubercles just above the plural suture of *P. niemeyeri* is poorly separated from the dorsal tubercles with which it inner grades, where as this row in *P. rodesae* is well separated from the dorsal tubercles.

Specimens of isolated "arms" referred to *P. punctata* (Linné, 1758) by Rathbun (1935:106), from her Virginia localities will probably, in time, be shown to represent *P. niemeyeri* and/or *P. rodesae.* The right posterior spine of paratype (USNM 520712) was broken off prior to photography but has since been restored. The barren surfaces seen on the figure of the holotype (USNM 520710) of *P. niemeyeri* are the apparent result of abrasion on this gerontic specimen. Remnants of the dense covering of these tubercles and bolitimorphs can be seen on the actual specimen.

Persephona rodesae, new species
Fig. 5B, D

Diagnosis.—Carapace hemispherical with three posterior spines; front bilobate, elevated, produced with orbits well beyond anterolateral margin; post frontal surface barren of tubercles, hepatic region and all other dorsal surfaces sparsely covered with relatively low, small, obtuse to subacute tubercles of subequal size; tubercles strongest along lateral and posterior margins, and very small to minute where highly concentrated on distal surface of front, and around orbits.

Description.—Carapace hemispherical, width about nine-tenths of length, regions very weakly defined, front elevated, produced with orbits well beyond anterolateral margin; posterior with three equally spaced recurved spines, two marginal, and one median above margin. Dorsal surfaces sparsely covered with relatively low, blunt to subacute tubercles of subequal size; tubercles strongest along lateral and posterior margins, most concentrated below plural suture, where very low, rounded and closely spaced; very small to minute tubercles highly concentrated on front and orbits where some are developed into small bolitimorphs; post frontal surfaces and adjacent areas behind orbits nearly barren, void of tubercles. Front very narrow, width about 0.11 width of carapace, bilobate, lobes separated by distinct v-shaped sulcus, laterally defined by low ridge formed by raised clusters of tubercles; anterior margins of lobes blunt, denticulate. Orbit very small, divided by three deep, narrow, open sutures creating four lobes. Minute, elongate tubercles span sutures from both sides, creating a pectinate appearance. Supraorbital eave and median lobe meet at a steep angle to form a broad v as seen from above. A few very small bolitimorphs are present along margin of outer lobe and just posterior to orbit along anterolateral margin. Hepatic region slightly swollen, weakly defined, surface with only a few tubercles. Subhepatic region not preserved in type series. Anterior and posterior lateral margins of carapace continuous, defined by a distinct row of larger tubercles beginning at orbit and continuing along upper edge of plural suture to a point just above tooth of posterolateral angle; row of tubercles usually well ordered and well separated from dorsal tubercles, particularly anteriorly; posteriorly row may inner grade with some dorsal tubercles and appear as a double row; area below plural suture covered with pavement of closely spaced low tubercles, surface appearing very rough. Posterior margin slightly more than one-third carapace width, produced posteriorly, laterally defined by a broad, stout, triangular, acute recurved spine at each corner; margin between spines comprised of from seven to 11 large recurved tubercles; intestinal margin above with a single medially placed, stout, recurved spine. Spines coarsely granulate. Posterior gastric pits not evident.

Color.—Pale yellow when dry.

Etymology.—This species is named for Mary Betty Rodes, science teacher, deceased, formerly of Portsmouth, Virginia, in recognition of her contribution to science through her many years of teaching science in the public schools of tidewater Virginia. In addition Miss Rodes provided the author with his first formal introduction to paleontology.

Holotype.—Rices Pit, Hampton, Virginia. USGS 26893, (USNM 520714) cl 27.05 mm, cw 23.86 mm. *Paratypes*: (USNM 520715) cl 32.05 mm, cw 28.39 mm, USGS 26893 as above; (USNM 520716) cl 32.60 mm, carapace incomplete, cw 35.50 mm, USGS 26893 as above; (USNM 520717) cl 15.47 mm, cw 16.41 mm, fragment of anterior portion of carapace only, USGS 26893 as above; (VMNH I3550) cl 27.88 mm, cw 24.95 mm, same geographic locality as USGS 26893 above.

Occurrence.—Rices Pit, Hampton, Virginia.

Remarks.—Recent comparisons: *Persephona rodesae* appears most similar to the Recent Western Atlantic purse crab, *P. mediterranea* (Herbst, 1794) (see: Williams 1984 for synonymy) from which it differs in having: 1.) relatively high, obtuse to subacute tubercles, compared to the very low rounded tubercles of *P. mediterranea*; 2.) small to minute tubercles concentrated on its front and orbits unlike *P. mediterranea* where these areas are all but barren; 3.) fewer, though stronger tubercles on its hepatic region; 4.) fewer, though stronger tubercles along its lateral margins; 5.) a much rougher surface below its lateral margins; and 6.) far fewer and much stronger tubercles along its posterior border.

Fossil comparisons: *Persephona rodesae* most closely resembles *P. niemeyeri* described above. See remarks for *P. niemeyeri* for comparison.

Persephona rodesae and *P. niemeyeri* have not been found at the same locality or in similar sediments. *Persephona rodesae* has been found in the shelly sands of Rices Pit, a much calmer, much less violent environment during its deposition than that seen at the Chuckatuck Bar where *P. niemeyeri* is found. The morphological differences between these two species therefore appear directly related to these environmental differences.

Family Majidae

Subfamily Inachinae

Genus *Euprognatha* Stimpson, 1871

Euprognatha ricei, new species

Fig. 6

Diagnosis.—Carapace pyriform in outline, surface with five unusually long narrow blunt spines, mesogastric and cardiac spines longest, surface between base of mesogastric spine and protogastric regions exhibiting a distinct, pentagonal array of granulations mimicking the shape of a royal crown; intestinal spine present, well developed; interantennular spine absent.

Description.—Carapace pyriform in outline; fronto-orbital region strongly projecting, narrow, occupying less than one-fourth width of carapace; regions well defined, moderately swollen. Front bidentate, projecting; projections represent superior surface of "shoe-shaped" antennual fossae below; projections broadly triangular or obtuse distally, divided by a shallow sulcus extending posteriorly where terminating at an inverted v-shaped row of eight granules. Orbit circular, margins vertical, subparallel; supraorbital eave covered with triangular

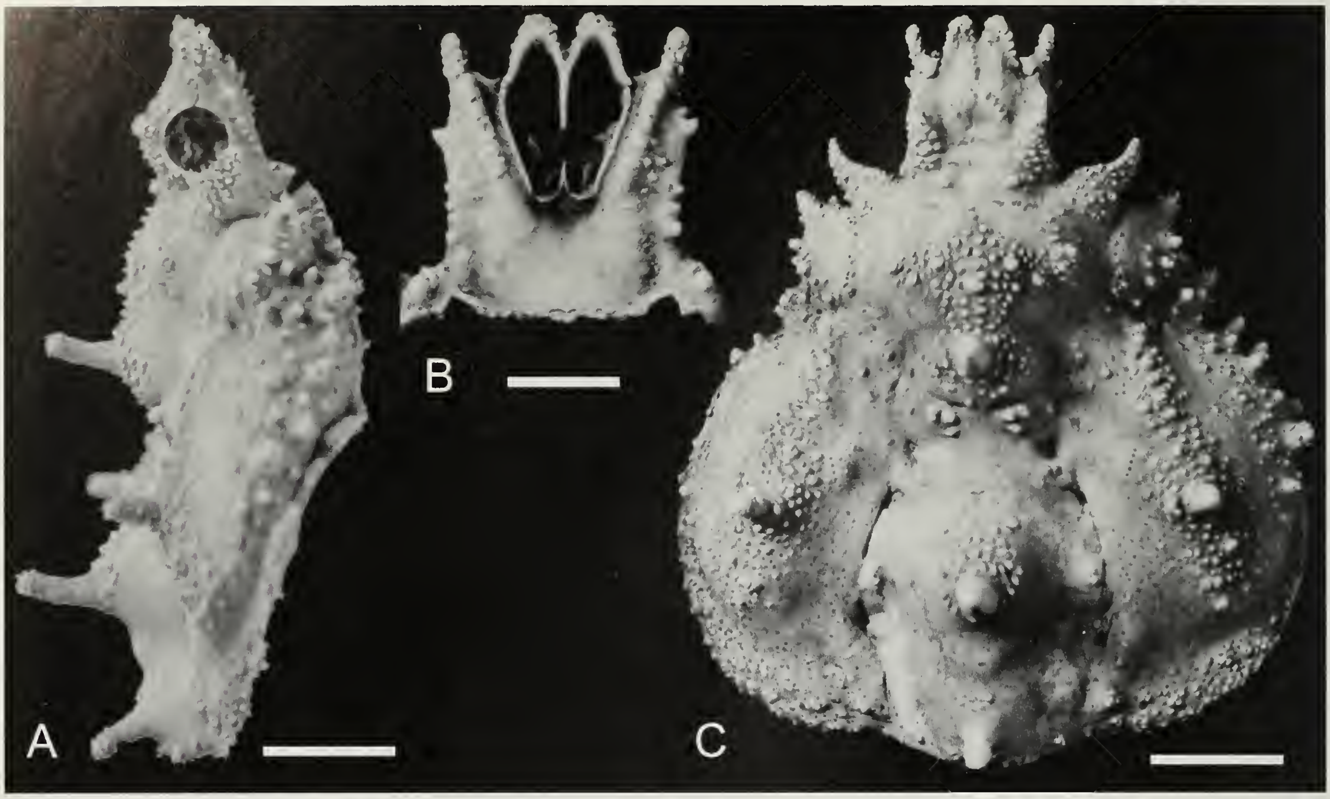

Fig. 6. *Euprognatha ricei* Holotype (USNM 520718) A. right lateral view. Scale = 2 mm. B. ventral closeup of antennule fossae, and long basal segment of antenna. Scale = 1 mm. C. dorsal view. Scale = 2 mm.

field of granules posteriorly; point of field distal where defined by a strong tubercle on orbital margin. Eyes apparently on long stalks, resting within depression of postorbital spine. Postorbital spine very strong; broad basally, tapering to a point distally, obliquely directed forward. Basal antennal article with inner and outer rows of granules of which several are developed into short, obtuse spines (tubercles); article directed only slightly obliquely forward, terminating in a granulated spine subequal in advancement to the front. Antennal sternum weak, not produced; interantennular spine absent. Outer margin of pterygostomian region with rows of coarse granules; superior row with large blunt tooth posteriorly. Buccal cavity broadest anteriorly, lateral margins divergent, width about one-third width of carapace. Hepatic region conical, sparsely covered with rounded granules or small tubercles, terminating obliquely in a strong blunt spine; spine produced laterally to a distance subequal to advancement of post orbital spine. Mesogastric, cardiac, intestinal, and branchial regions each surmounted with a single prominent cylindrical blunt spine; mesogastric spine longest, vertically directed; cardiac spine subequal to mesogastric spine, slightly directed posteriorly; intestinal and branchial spines much shorter and of subequal length; the former obliquely directed posteriorly; latter obliquely directed laterally. Spines smooth laterally with their distal ends granulated. Surface of carapace noticeably punctate, otherwise relatively smooth except for concentrations of low tubercles or rounded granules along frontal margins, supraorbital eaves, postorbital spines, hepatic regions, lateral margins, and bases of prominent spines. Irregular concentrations of tubercles and granules appearing as a distinct anteriorly directed row on each branchial region; row beginning just posterior to prominent spine of branchial region and converging anteriorly where tapering to a point at branchial-hepatic junction. Surface between base of mesogastric spine and protogastric regions defined by a very distinct pentagonal array of granulations arranged in the shape of a royal crown. Tubercles strongest on or near hepatic and anterolateral margins. Posterior gastric pits distinct, close set at base of mesogastric region, each bounded posteriorly by cluster of three granules. Distinct broad, smooth, groove separating cardiac and intestinal regions from branchial region.

Branchial region posterolaterally produced into a relatively wide, flattened, granulated margin. Posterior margin moderately produced posteriorly, width about one-third carapace width.

Color.—Ash white when dry, or gray when wet.

Etymology.—This species is named in honor and appreciation of Mr. William M. Rice, deceased, of Hampton, Virginia, who allowed the author unrestricted access to his borrow pit and who, with his wife, Madeline, and family built a museum on his property for the purpose of educating students in the Hampton Roads area. This small museum, known as The Kenneth E. Rice Memorial Museum (after his youngest son), the borrow pit behind it, and the tutorage of Mr. Rice served more than five thousand students of all ages each year. His positive impact on the paleontology of the area is unsurpassed.

Holotype.—Rices Pit, Hampton, Virginia. USGS 26893, (USNM 520718) cl 10.31 mm, cw 9.01 mm. *Paratypes*: (USNM 520719) cl 4.41 mm, cw 3.46 mm, USGS 22209 same geographic locality as USGS 26893 above; (VMNH I3551) cl 7.75 mm, cw 6.83 mm, USGS 26893 as above.

Occurrence.—Rices Pit, Hampton, Virginia.

Remarks.—Recent comparisons: Of the known living species of *Euprognatha, E. ricei* appears most similar in overall form, number and placement of prominent dorsal spines and distribution of tubercles and granules to *E. gracilipes* A. Milne-Edwards, 1878b (Florida Keys to Barbados, Rathbun 1925). *Euprognatha ricei* can however be easily separated from *E. gracilipes* as follows: 1.) the prominent spines of *E. ricei* are much longer than those of *E. gracilipes* and *E. ricei* unlike *E. gracilipes* possesses an intestinal spine; and 2.) the dorsal surface of *E. ricei* is much less granulate than the evenly, coarsely granulated surface of *E. gracilipes.* The presence of long mesogastric, branchial, and cardiac spines, and in particular a long intestional spine in combination with its sparsely granulated surface, the absence of an interantennular spine and the presence of a pentagonal array of granules in the shape of a royal crown on its mesogastric region easily separate *E. ricei* from all other living species of *Euprognatha.*

Fossil comparisons: Rathbun (1935) identified two left dactyls from the Miocene of Liberty County, Florida as *Euprognatha* sp., p. 112, pl. 24, figs. 16–19. Lacking associated chela, the type specimens of *E. ricei* cannot be compared with Rathbun's material.

The distal end of the left basal antennal article was broken and lost by the author in handling the specimen after the photograph was completed.

Subfamily Mithracinae
Genus *Stenocionops* Desmarest, 1823
Stenocionops dyeri, new species
Fig. 7

Diagnosis.—Carapace oblong-ovate, strongly arched anteriorly; superior lateral marginal spines three; frontal depression laterally bordered by 10 to 18 small spines; cardiac region greatly elevated, armed with an irregular pentagonal array of five short spines.

Description.—Carapace oblong-ovate, strongly arched anteriorly, surface uneven, regions well defined. Length from rostral notch along middorsal line from 1.33 to 1.41 times greatest width, broadest across middle of branchial regions; greatest height approximately one-half that of width. Rostral horns basally divergent, laterally subparallel, short, flattened, slightly upturned distally. Frontal depression deep, ovate, lat-

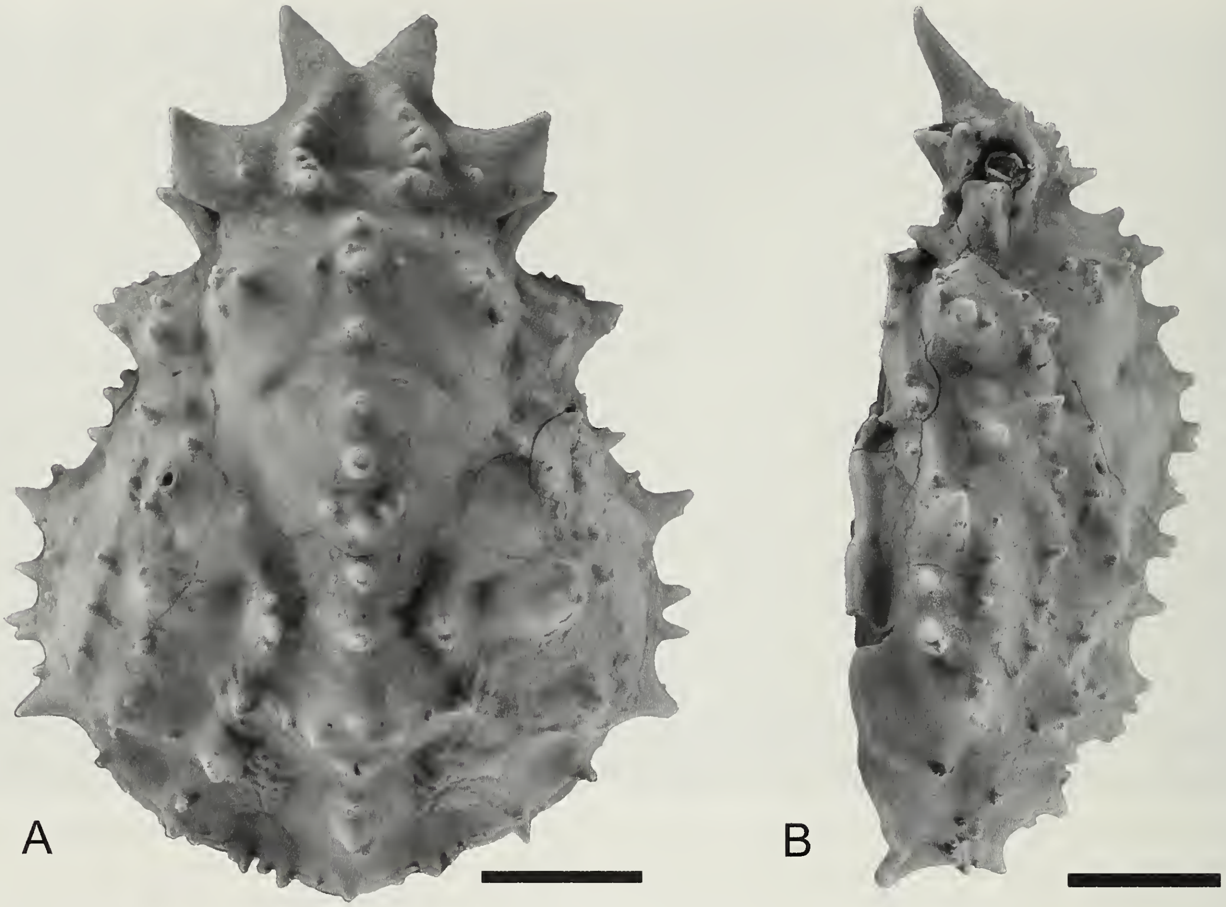

Fig. 7. *Stenocionops dyeri* Holotype (USNM 520720) A. dorsal view and B. left lateral view. Scale = 10 mm.

erally bordered by 10 to 18 small spines decreasing in height anteriorly. Fronto-orbital region broad, more than one-half times that of width; orbits strongly projecting. Eyes small, retractable within deep tubular orbits; preocular spine superior, a small distinct spine or tubercle medial to its base; postocular spine smaller, acute. Orbit completed below by a blade-like lateral expansion of basal antennal article. Basal antennal article broader than long, armed with 3 spines, one anterior-external, short, acute, barely visible dorsally; another, posterior-external, usually very weak; and last, anterior-internal, strong, acute, extending forward and obliquely downward from basal insertion of second antennal article. Second antennal article not extending forward to or beyond rostral notch. Opening of green gland oval, noticeably raised, a prominent, obliquely downward-directed, acute spine near its external-lateral border. Pterygostomian region triangular, armed with two small outer marginal spines; anterior longest. Inner margins raised, rim like, anteriorly terminated by an anvil-like process. Buccal frame broader than long, widest anteriorly; width about one-third width of carapace width. Superior lateral marginal spines three; one hepatic and two branchial. Secondary lateral marginal spines common, may exceed ten, their number apparently increasing with age. Hepatic region swollen, very distinct, reaching beyond fronto-orbital width, armed laterally with a cluster of five or more spines; superior inner margin with two spines, posteriormost longest and strongest. Mid-dorsal line slightly raised, ridge-like. Gastric region greatly arched anteriorly; armed with from eight to 10 short spines, of which four are usually mesogastric, two metagastric, and three urogastric. Posterior gastric pits faint, bordered by curved row of spines just distal to cervical groove.

Cardiac region greatly elevated, usually armed with a characteristic irregular pentagonal array of five small spines, posteriormost two, often close set. Cardio-intestinal and metabranchial regions separated by deep furrows. Intestinal region armed with two distinct spines along midline, posteriormost largest; spines aligned perpendicular to a lower horizontal row of from two to five smaller spines and/or tubercles, their number apparently decreasing with age; row of spines bordered below by wide, shallow sulcus. Posterior margin rounded, narrow, slightly projecting, width less than one-half fronto-orbital width. Branchial regions uneven, moderately spinous. A distinct, armed, broadly conical prominence on each epibranchial, mesobranchial and metabranchial region, which when roughly aligned with rostral notch, forms an inverted V of approximately 30°. Epibranchial prominence usually with two secondary spines or tubercles. A prominent ridge armed with three low spines, posterior longest, occupying inter-lateral margin of metabranchial region.

Lower margin of entire carapace terminating in a rounded rim. Entire surface of body (chelipeds—excepting distal half of fingers) closely covered with minute, circular pores.

Coxa, basis, and ischium of chelipeds and ambulatory legs, unarmed. Merus of cheliped quadrangular in section, armed with four distinct lateral rows of spines, the dorsal row being most prominent with four superior spines and as many as five smaller spines or tubercles. Carpus smooth. Hand elliptical in section, highest proximally, smooth to finely granulate. Fingers less than one-half length of palm, not gaping. Ambulatory legs circular in section; merus of first and second pair moderately tuberculate above; third and fourth pairs smooth. Legs decreasing in length posteriorly.

Color.—Ash white with faint patches of pink when dry, gray when wet. Some living species of *Stenocionops* are dark red, such as *Stenocionops furcata coelata* (A. Milne-Edwards, 1878a). See Williams (1984:339).

Etymology.—This species is named for Brian J. Dyer, microbiologist, Old Dominion University, Norfolk, Virginia for his contribution to science through his years of research and teaching and especially for his years of encouragement and field assistance to the author.

Holotype.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia. USGS 26891, (USNM 520720) cl including rostrum 58.38 mm, excluding rostrum 54.47 mm, cw including spines 44.65 mm, excluding spines 40.03 mm. *Paratypes*: (USNM 520721) Female: cl including rostrum 53.91 mm, excluding rostrum 49.96 mm, cw including spines 41.70 mm, excluding spines 37.72 mm, right propodus: prl 21.63 mm, prh 6.09 mm, prl 3.15 mm, left propodus, prl 20.96 mm, prh 5.13 mm, prt 3.22 mm, USGS 26891 as above; (VMNH I3552) cl including rostrum 42.95 mm, excluding rostrum 39.21 mm, cw including spines 32.22 mm, excluding spines 27.75 mm, same geographic locality as USGS 26891 above.

Occurrence.—The Lone Star Lakes, near Chuckatuck, Suffolk, Virginia.

Remarks.—Recent comparisons: *Stenocionops dyeri* appears most similar in shape and overall character to *S. spinosissima* (Saussure, 1857) from which it can be easily separated as follows: 1.) *Stenocionops dyeri* has three strong lateral spines compared to the five found in *S. spinosissima*; 2.) *S. dyeri* has short, flattened rostral horns compared to the much longer, more acute horns of *S. spinosissima*; and 3.) *S. dyeri* has between 13 to 15 short median spines, of which those on the cardiac region are arranged in an irregular pentagonal array in contrast to *S. spinosissima* which exhibits 10 median spines of which only two are found on the cardiac region. *Stenocionops dyeri* also superficially resembles a much smaller species of *Stenocionops, S. triangulata* (Rathbun, 1892) which also possesses three lateral spines. These spines in *S. dyeri,* however, are shorter and much less acute. *Stenocionops dyeri* also differs from this species in having: 1.) much flatter, shorter and less divergent rostral horns; 2.) 13 to 15 median spines compared to about nine on *S. triangulata*; and 3.) an irregular pentagonal array of five spines on its cardiac region compared to only one or two on this region in *S. triangulata.* In reference to *S. triangulata,* Rathbun (1925:461) states: "Known only from small and immature specimens". The pentagonal array of spines on the cardiac region of *S. dyeri* alone sets it apart from all other known species of *Stenocionops.*

Fossil comparisons: Rathbun (1935) described *Stenocionops primus* from the Upper Cretaceous Brownstown Formation, of Howard County, Arkansas and *Stenocionops suwanneeana* from the Eocene Ocala Limestone of Suwannee County, Florida. The chela of these two species may indeed resemble those of adult males of *Stenocionops* or other mature majid chela but in size and coarse granulation they are very different from the nearly smooth diminutive female chela of *S. dyeri.* The chela in both adult male and female species of some living representatives of *Stenocionops* are relatively small, like those of *S. dyeri,* but in reaching maturity the chela in gerontic males can become quite large. The geologic time difference between *S. dyeri* and these geologically much older taxa is such that it would be very unlikely that they represent the same species.

The barnacle, *Balanus* sp., is often found completely covering the dorsal surface of the carapace of *S. dyeri* where it apparently lived as a symbiont during the life of the crab. This barnacle has not yet been found covering the orbital openings of this crab, thus revealing that the crab was indeed alive and able to keep its orbits clear during this relationship. The massive numbers of this barnacle found on some specimens of *S. dyeri* greatly increased the crab's surface area and undoubtedly contributed to its being washed about and buried in the Chuckatuck Bar deposits by strong currents during storms. These same barnacles also strengthened the dorsal aspect of the carapace allowing it to be preserved in this high energy environment of deposition.

Acknowledgments

Mr. H. B. Roberts, deceased, formerly of the Department of Invertebrate Zoology, NMNH, SI, correctly identified *Hepatus bottomsi, Persephona rodesae, Euprognatha ricei* and *Stenocionops dyeri* as new in a letter to the present author, dated 13 October 1964. Given the incomplete and often fragmentary nature of the material presented to him at that time, his identifications are remarkable for their accuracy, a testament to his knowledge and ability. Due to his declining health, Mr. Roberts was unable to pursue descriptions of these and other new taxa (see: Manning & Blow 1980, Blow & Bailey 1992) and passed that task on to this author before his retirement in June 1973. He died 14 March 1979.

I thank E. E. Bottoms for introducing me to a number of fossil decapod localities in the Hampton Roads area in the fall of 1962, and for years of cooperative fieldwork and mutual assistance. I particularly thank my parents, R. V. and C. D. Blow, for years of logistical support, field assistance, and for their own collecting efforts which have benefitted and continue to benefit my research these past 40 years. Mr. W. A. Staylor, Mr. H. F. Saunders and the other men and women of the Lone Star Cement Co. kindly allowed the author unrestricted access to their diggings. R. H. Bailey, B. A. Bedette, B. J. Dyer, L. W. Ward, and the late D. Wilson helped the author in the field on a number of occasions, adding their expertise and collections to the research and writing of the present paper. L. D. Campbell and Svein Nielsen kindly made their collections available to the author for study.

I thank S. Whittaker, of the SEM lab, Smithsonian Institution, for providing the photomicrographs of *P. baileyi,* M. G. Harasewych for providing the digital images of the remaining taxa except for the dorsal and lateral views of *E. ricei,* which were taken by Mr. T. F. Phelan. My sincere thanks to J. A. Sanner for enhancing the images in Adobe Photoshop and constructing the finished digital plates. In addition B. A. Bedette read the manuscript and offered numerous suggestions and corrections. T. R. Waller provided space in his laboratory, and scientific and editorial advice throughout the preparation of this manuscript.

Literature Cited

Bell, T. 1855. A Monograph of the Leucosiadæ, with observations on the relations, structure, habits, and distribution of the family; a revision of the generic characters; and descriptions of new genera and species, Horæ Carcinologicæ, or Notices of Crustacea, I.—Transactions of the Linnean Society 21:277–314 + pls. 30–34.

Blow, W. C., & R. H. Bailey. 1992. *Chasmocarcinus robertsi,* a new crab species from the Miocene of Virginia, with notes on the genus *Falconoplax* (Crustacea, Decapoda, Goneplacidae).—Tulane Studies in Geology and Paleontology 25(4):175–185.

Campbell, L. D. 1993. Pliocene molluscs from the Yorktown and Chowan River Formations in Virginia.—Virginia Division of Mineral Resources Publication 127:1–259.

Collins, J. S. H., & S. F. Morris. 1976. Tertiary and Pleistocene crabs from Barbados and Trinidad.—Palaeontology 19(1):107–131.

Desmarest, A. G. 1823. Malacostracés. Pp. 158–425 *in* Dictionnaire des Sciences Naturelles, vol. 28. Strasbourg.

Gibson, T. G. 1967. Stratigraphy and paleoenvironment of the phosphatic Miocene strata of North Carolina.—Geological Society of America Bulletin 78(5):631–650, pls. 1, 2.

Guinot, D. 1979. Morphologie et phyogenèse des Brachyoures.—Mémoires du Muséum national d'Histoire naturelle (Paris), new series A (zoology) 112:1–354.

Haj, A. E., & R. M. Feldmann. 2002. Functional morphology and taxonomic significance of a novel cuticular structure in Cretaceous raninid crabs (Decapoda: Brachyura: Raninidae).—Journal of Paleontology 76(3):472–485.

Hazel, J. E. 1971a. Ostracode biostratigraphy of the Yorktown Formation (upper Miocene and lower Pliocene) of Virginia and North Carolina.—Geological Survey Professional Paper 704:1–13.

———. 1971b. Paleoclimatology of the Yorktown Formation (upper Miocene and lower Pliocene) of Virginia and North Carolina: Pp. 361–375 *in* H. J. Oertli, ed., Paléoécologie Ostracodes, Pau, 1970.—Bulletin Centre Recherche Pau-SNPA, 953 pp., 3 tab.

Herbst, J. F. W. 1794. Versuch einer Naturgeschichte der Krabben und Krebse, nebst einer systematischen Beschreibung ihrer verschiedenen Arten 2(5):147–162 + pls. 37–40.

Johnson, G. H. 1969. Guidebook to the geology of the York-James Peninsula and south bank of the James River.—College of William and Mary Department of Geology Guidebook No. 1. Atlantic Coastal Plain Geological Association, Tenth Annual Field Conference and First Annual Geological Field Conference: 1–33.

———, & N. K. Coch. 1969. A Coquina facies in the Yorktown Formation near Chuckatuck, Virginia and its geological implications.—(Abs.) Geological Society America Special Paper 121: 448.

Kier, P. M. 1972. Upper Miocene echinoids from the Yorktown Formation of Virginia and their environmental significance.—Smithsonian Contributions to Paleobiology 13:1–41. Smithsonian Institution Press, Washington.

Latreille, P. A. 1802. Histoire naturelle générale et particulière des Crustacés et des Insects 3:13–467. Paris.

Leach, W. E. 1817. Malacostraca Podophthalma Britanniæ; or descriptions of the British species of crabs, lobsters, prawns, and of other Malacostraca with pedunculated eyes. James Sowerby, London, XIV, 5 p., unpaged + pls 16, 25 and 44.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentii, synonymis, locis, 10th edition. Laurentius Salvius, Stockholm 1:1–824.

Manning, R. B., & W. C. Blow. 1980. Henry B. Roberts 1 September 1910–14 March 1979.—Crustaceana 39(1):104–107, pl. 1.

Mansfield, W. C. 1943 [1944]. Stratigraphy of the Miocene of Virginia and the Miocene and Pliocene of North Carolina. Pp. 1–19 *in* J. Gardner, ed., Mollusca from the Miocene and Lower Pliocene of Virginia and North Carolina: Pt 1, Pelecypoda.—U.S. Geological Survey Professional Paper 199-A:1–178.

Milne-Edwards, A. 1865. Description de quelques Crustacés nouveaux on peu connus de la famille des Leucosiens.—Annales Société Entomologique de France 4(5):148–159, pl. 6.

———. 1878a. Note sur quelques Crustacés nouveaux appartenant au groupe des Oxyrhynques.—Bulletin de la Société Philomathique de Paris 7(2): 222–225.

———. 1878b. Études sur les Xiphosures et les Crustacés de la Région Mexicaine.—In Mission Scientifique au Mexique et dans l'Amerique centrale part 5(4):121–184, pls. 21–27, 29–30.

———. 1880. Études préliminaires sur les Crustacés, l ere partie. In reports on the results of dredging under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, '78, '79 by the U.S. Coast Survey Steamer "Blake," Lieut. Commander C. D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., Commanding.—Bulletin of the Museum of Comparative Zoölogy at Harvard College 8(1): 1–68, pls. 1, 2.

———, & E. L. Bouvier. 1894. Brachyures et Anomoures. *In* Crustacés décapodes provenant des campagnes du yacht l'Hirondelle (1886, 1887, 1888), Première Partie. Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert 1 er, Prince Souverain de Monaco 7:1–112, pls. 1–11.

———, & E. L. Bouvier. 1902. Les Dromiacés et Oxystomes. *In* reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1978–79), and along the Atlantic Coast of the United States (1880), by the U. S. Coast Survey Steamer "Blake", Lieut. Com. C. D. Sigsbee, U. S. N., and Commander J. R. Bartlett, U. S. N., Commanding, XXXIX.—Memoirs of the Museum of Comparative Zoölogy at Harvard College 27(1):1–127, pls. 1–25.

Milne-Edwards, H. 1834. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux 1:1–468. Paris.

Pennant, T. 1777. Crustacea, Mollusca, Testacea. British Zoology, edition 4, 4:London, 1–154, pls. 1–93.

Rathbun, M. J. 1892. Catalogue of the crabs of the family Periceridae in the U.S. National Museum.—Proceedings of the United States National Museum 15(901):231–277, pls. 28–40.

———. 1896. The genus *Callinectes*.—Proceedings of the United States National Museum 18(1070): 349–375, pls. 12–28.

———. 1925. The spider crabs of America.—United States National Museum Bulletin 129:1–613, pls. 1–283.

———. 1926. The fossil stalk-eyed Crustacea of the Pacific slope of North America.—United States National Museum Bulletin 138:1–155, pls. 1–39.

———. 1935. Fossil Crustacea of the Atlantic and Gulf Coastal Plain.—Geological Society of America, Special Papers 2:1–160, pls. 1–26.

———. 1937. The Oxystomatous and allied crabs of America.—United States National Museum Bulletin 166:1–278, pls. 1–86.

Saussure, H. de. 1857. Diagnoses de quelques Crustacés nouveaux de l'Amérique tropicale.—Revue et Magzin de Zoologie Pure et Appliquée, 2(9):501–505.

Serene, R. 1954. Sur quelques especes rares de Brachyures (Leucosidae) de l'Indo-Pacifique.—Treubia 22(3):453–499, pls. 7–10.

Stimpson, W. 1859. Notes on North American Crustacea, No. 1.—Annals of the Lyceum of Natural History of New York 7(1862)(2):49–93, 1 plate.

———. 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L. F. de Pourtales, Assistant United States Coast Survey. Part 1. Brachyura.—Bulletin of the Museum of Comparative Zoology at Harvard College 2(2):109–160.

Verrill, A. E. 1869. On the parasitic habits of Crustacea.—American Naturalist 3:239–250. [*Hepatella amica* Smith described as footnote p. 250]

Ward, L. W., & B. W. Blackwelder. 1980. Stratigraphic revision of Upper Miocene and Lower Pliocene beds of the Chesapeake Group, Middle Atlantic Coastal Plain.—Contributions to Stratigraphy, Geological Survey Bulletin 1482-D:1–61, pls. 1–5.

———, & N. L. Gilinsky. 1993. Molluscan assemblages of the Chowan River Formation, Part A, Biostratigraphic analysis of the Chowan River Formation (Upper Pliocene) and adjoining units, The Moore House Member of the Yorktown Formation (Upper Pliocene) and the James City Formation (Lower Pleistocene).—Virginia Museum of Natural History Memoir 3, Part A: 1–32, plate 1. Tables 1, 2, & 4–6 & fig. 6 not paginated (in pocket).

Williams, A. B. 1965. Marine decapod crustaceans of the Carolinas.—Fishery Bulletin 65(1):1–298.

———. 1984. Shrimps, lobsters, and crabs of the Atlantic Coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., 550 pp.

Appendix 1

Locality register

USGS 26891 The Lone Star Lakes, formerly Lone Star Cement Company open-pit mine, about 1 km north of Chuckatuck, Suffolk, Virginia. USGS Chuckatuck, 7½-minute quadrangle map, 1965 photorevised 1979.

USGS 26892 Open-pit mine, locally known as Riddick Pit, about 4.4 km southeast of Benns Church, on east side of Va. route 10/32, Isle of Wright County, Virginia. USGS Benns Church 7½-minute quadrangle map, 1965 photorevised 1986.

USGS 26893 Rices Pit belonging to Mr. William M. Rice, about 0.4 km north of intersection of Fox Hill Road (Rte. 167) and Harris Creek Road, Hampton, Virginia. USGS Hampton, 7½-minute quadrangle map, 1965 photorevised 1986.

USGS 22209 Same geographic locality as 26893 above but collected by a large group of Smithsonian scientists lead by G. A. Cooper in 1966.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Columbasellus acheron, a new genus and species of subterranean isopod from Washington (Crustacea: Isopoda: Asellidae)

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Abstract.—*Columbasellus acheron*, new genus, new species, is described from a male specimen discovered during the cleaning of the municipal water well of Kalama, Washington. The genus *Columbasellus* is geographically closest to the genera *Caecidotea, Calasellus* and *Salmasellus,* but is morphologically more similar to the Eurasian *Asellus aquaticus/hilgendorfii* complex of species, with which it shares a male pleopod 2 that possesses a relatively large labial spur and basal spur, and fully formed, ovate exopods in pleopods 4 and 5. *Columbasellus acheron* inhabits the hyporheic zone of the Kalama River. Evidence is presented that indicates widespread use of stream gravel interstices by subterranean isopods in the Pacific Northwest, including the first record of *Salmasellus howarthi* from Oregon.

In the eastern United States there are about 65 described species of subterranean asellid isopods, mostly known from caves (Henry et al. 1986, Lewis & Bowman 1995), although a significant number have now been described that apparently live in soil or gravel interstices (Lewis 1982, 2000; Lewis & Bowman 1981; Lewis & Holsinger 1985). The situation is different west of the Rocky Mountains, where caves and karst are much less commonplace and only five subterranean asellids have been described: *Caecidotea sequoiae* Bowman, 1975, *Calasellus californicus* (Miller, 1933), *C. longus* Bowman, 1981, *Salmasellus steganothrix* Bowman, 1975 and *S. howarthi* Lewis, 2001.

It is becoming increasingly apparent that subterranean isopods are more widespread in western North America than the number of described species might indicate. We add to the growing body of evidence (Lewis 2001) that subterranean isopods are common in the hyporheic zone of western streams with the description of *Columbasellus acheron,* the first record of *Salmasellus howarthi* from Oregon, and several other records of undetermined eyeless, unpigmented isopods.

It is with some chagrin that we make this addition by describing a new genus and species of subterranean isopod that was discovered during the process of trying to eradicate it. The city of Kalama, Washington, currently obtains groundwater from sands and gravels below the Kalama River, which is located approximately 3.2 km east of the confluence of the Kalama and Columbia rivers near the Modrow Bridge (Fig. 1). The water withdrawal is accomplished via a Ranney well collection system that consists of three horizontal pipes extending below the Kalama River at a depth of five meters. The isopods were flushed from the municipal well during the process of cleaning it with superchlorination, scouring and vacuuming. Of dozens of isopods emerging from the well, only one was collected. This single specimen is recognized here as a unique subterranean isopod flushed from its hyporheic habitat.

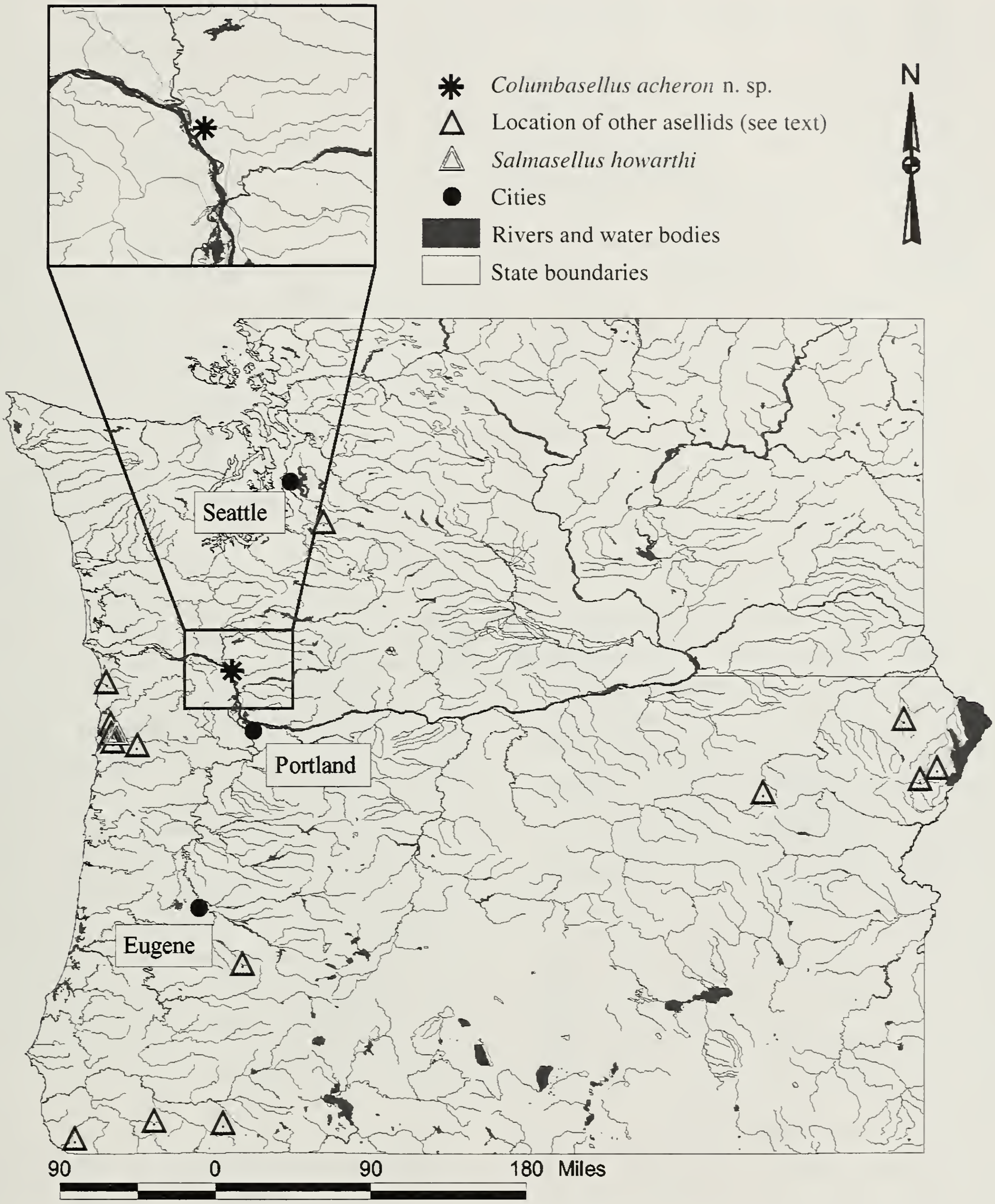

Fig. 1. Map of the Pacific northwest showing collection localities of subterranean asellid isopods.

Family Asellidae G. O. Sars, 1897

***Columbasellus,* new genus**

Diagnosis.—Eyeless, unpigmented. Head without rostrum or lateral incisions. Mandible with 3-segmented palp, 4-cuspate incisors and lacinia mobilis. Maxilla 1 inner lobe with 5 apical setae. Pereopods, coxae visible in dorsal view; male pereopod 1 propodus slender, palm without processes; dactyls 1–7 with accessory unguis. Male pleopod 1 with retinacula present. Male pleopod 2 endopod with digitiform basal spur, endopodial groove originating from within basal part of endopod, labial spur present, cannula tapering to a subtriangular stylet; exopod with catch lobe. Pleopod 3 exopod with transverse suture. Pleopods 4 and 5 with well formed ovate exopods and endopods.

Morphology and setation pattern of the mandible, maxilla 2, pereopods, uropods, essentially identical to other previously described asellids (e.g., see figures by Williams 1970, Bowman 1981).

Type-species.—*Columbasellus acheron.*

Etymology.—"Columb" from Columbia River + "*Asellus*".

Relationships.—*Columbasellus* is geographically closest to *Caecidotea* from U.S. Pacific coastal states (Williams 1970; Bowman 1974, 1975), *Calasellus* two species from California (Bowman 1981), and *Salmasellus* two species in Washington and Alberta (Bowman 1975, Lewis 2001). However, *Columbasellus* is morphologically more similar to the Eurasian *Asellus aquaticus/hilgendorfii* assemblage discussed by Henry and Magniez (1995). These authors analyzed the Pacific Rim asellids and found anatomical similarities that suggested a common ancestor for the following genera: *Asellus, Calasellus, Mesoasellus, Nipponasellus, Phreatoasellus, Sibirasellus,* and *Uenasellus.* These genera have the following characteristic states, which may be synapomorphic for the group: a first maxilla with 4 or 5 setae on the inner lobe; no processes on the palmar margin of the pereopod 1 propodite; a male second pleopod possessing an exopodite catch lobe, endopodite basal and labial spurs. *Mesoasellus, Phreatoasellus, Uenasellus, Calasellus* comprise a clade characterized by the following shared states: first maxilla with 5 setae on the inner lobe; mandibular palp of three articles. We add *Columbasellus* to this clade. Within the clade, *Columbasellus* is distinguished by the following autapomorphies: labial spur arising from within endopodial groove not from the rim of the endopodial groove as in *Calasellus* and *Sibirasellus*; cannula short and tapering, not elongate and seta-like as in *Calasellus.*

Columbasellus is separated from *Caecidotea* and *Salmasellus* by the absence of basal and labial spurs in the male second pleopod of the latter genera. Basal and labial spurs are present in *Columbasellus* and *Calasellus,* but the structure of the labial spurs are quite dissimilar. *Columbasellus* has a labial spur (see Henry & Magniez 1995) arising from within the endopodial groove, whereas the labial spur of *Calasellus* consists of a tiny cylindrical structure on the rim of the endopodial groove similar to that of *Sibirasellus.* The cannula in *Columbasellus* is a relatively short, tapering subtriangular stylet, while in *Calasellus* it is a seta-like filament that traverses most of the length of the endopod.

Bowman (1981) believed that *Calasellus* was related to *Asellus* (*Phreatoasellus*) Matsumoto, 1962 (five species in Japan, now elevated to generic status), which agrees with the later synthesis of Henry and Magniez (1995). *Columbasellus* and *Calasellus* are separated from *Phreatoasellus* by the dissimilar male pleopod 2 and by the absence of an accessory unguis on the pereopod dactyls. The pleopod 4 exopod of *Phreatoasellus* is ovate in *P. higoensis* and *P. kawamurai,* while pyriform in *P. uenoi, P. iriei* and *P. minatoi* (Matsumoto 1960, 1962, 1978). The pleopod 5 exopod is well developed in all *Phreatoasellus. Columbasellus* is further separated from *Calasellus* by the oval pleopod 4 exopod (pyriform in *Calasellus*) and by the presence of a well formed pleopod 5 exopod (rudimentary or absent in *Calasellus*).

Columbasellus acheron, new species

Figs. 2–4

Material examined.—Washington, Cowlitz Co., Kalama, Ranney Well (approximately 46.00N, 122.82W), about 5 m below Kalama River, collected May 2000, Carl McCrary, 1 male. This 14.5 mm male is the holotype and has been deposited in the collection of the Natural History Museum of Los Angeles County (LACM CR 2000-013.1).

Etymology.—Refers to the River Acher-

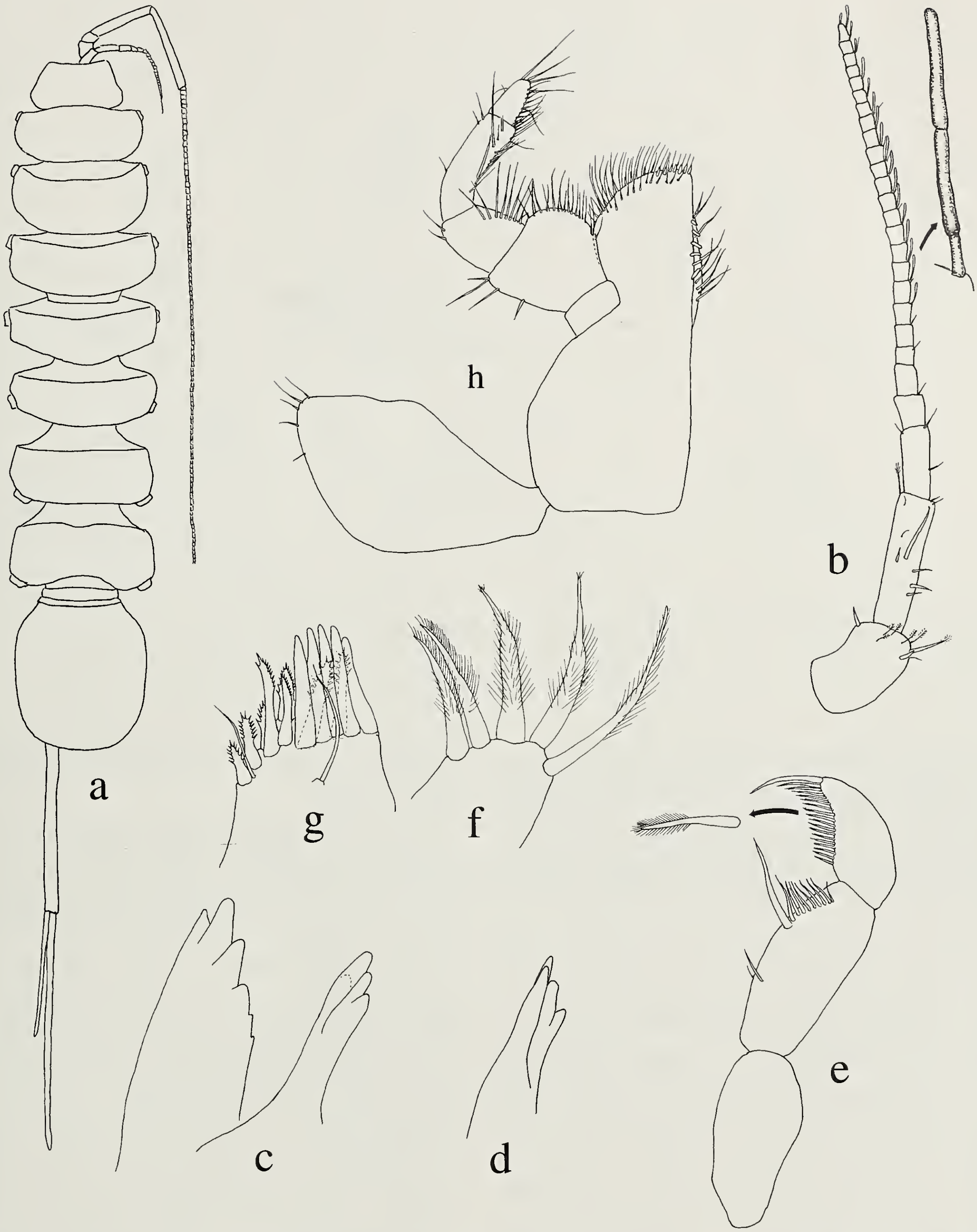

Fig. 2. *Columbasellus acheron*, holotype male. a, habitus; b, antenna 1; c, left mandible, incisor and lacinia mobilis; d, right mandibular incisor; e, mandibular palp; f, maxilla 1, inner lobe; g, same, outer lobe; h, maxilliped.

on of Greek mythology, one of the rivers flowing through the underworld.

Description.—Body linear, about 4.8× as long as wide. Head trapezoidal, about 2× as wide as long, anterior margin slightly concave, postmandibular lobes weakly developed. Pleotelson ovate, about 1.3× as long as wide, false sutures faintly visible on anterior dorsal surface, caudomedial lobe not produced.

Antenna 1 reaching to mid-length of last article of antenna 2 peduncle, flagellum of

Fig. 3. *Columbasellus acheron*, holotype male. a, pereopod 1; b, pereopod 2; c, pereopod 7.

23 articles, esthete formula equivocal due to damage, apparently 3-0-1-0-12. Antenna 2 about 0.8× body length, basal segments slender, linear, cylindrical, specialized modifications absent, flagellum of about 67 articles.

Left mandible with incisor 4-cuspate and 2 minute denticles, lacinia mobilis 4-cuspate, 16 spine-like setae in adjacent row; right incisor 4-cuspate, 17 spine-like setae in row; molars present, unremarkable; palp with rows of plumose setae on articles 2 and 3. Maxilla 1, outer lobe with 13 robust apical spine-like setae and 1 seta, 1 subterminal plumose seta and 1 plumose seta along distal shaft, lateral margins with setules and minute comb spines; inner lobe with 5 stout plumose setae. Maxilla 2 with rows of setae on apical margins, unremarkable. Maxilliped with rows of stout plumose setae and 6 retinacula.

Pereopod 1, propodus about 2.8× as long as wide, palmar margin straight, with 8 spine-like setae, dactyl flexor margin with accessory unguis and 9 spine-like setae. Some pereopods missing or detached from holotype, but dactyls apparently all with accessory unguis.

Pleopod 1 longer than pleopod 2; protopod with 3 retinacula surrounded by minute comb spines; endopod subrectangular, about 2× length of protopod, setae of decreasing length along concave lateral margin, with 8 plumose setae along distolateral margin. Pleopod 2 protopod slightly longer than wide, mesial surface with numerous rows of minute comb spines; exopod proximal segment with 3 lateral plumose setae, distal segment with 20 plumose setae along margins, catch lobe present; endopod, digitiform basal spur present, mostly obscured in dorsal view; endopod produced into a tapering cylindrical process, curving distolaterally; endopodial groove prominent, traversing over half of endopod; labial spur originating from endopodial groove, extending along axis of groove; cannula extending into a robust, tapering stylet. Pleopod 3 exopod with 8 small, non-plumose setae along distal margin. Pleopod 4 exopod with 1 proximolateral seta and brush border

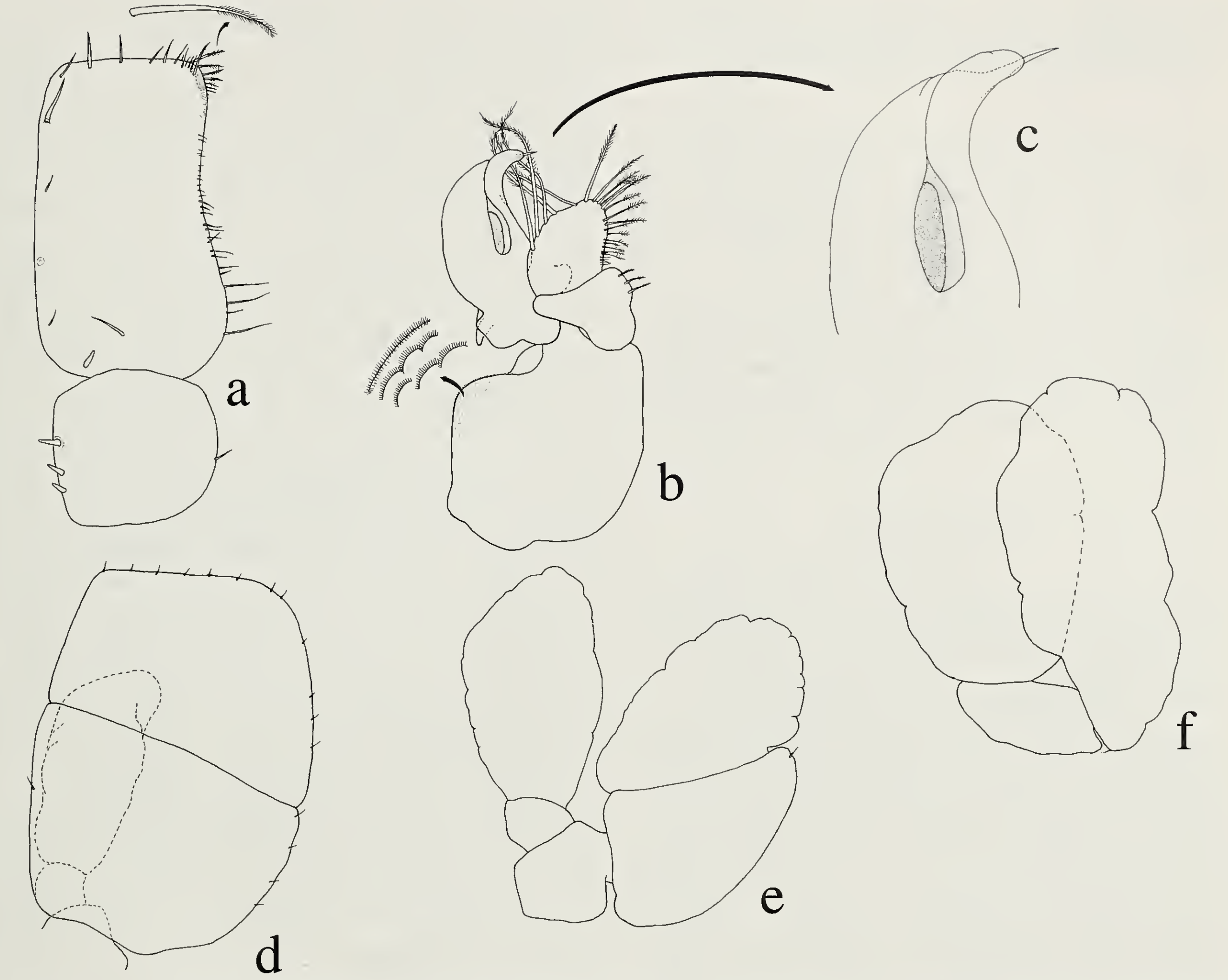

Fig. 4. *Columbasellus acheron,* holotype male. a, pleopod 1; b, pleopod 2; c, same, endopod tip; d, pleopod 3; e, pleopod 4; f, pleopod 5.

of setules, transverse suture present. Pleopod 5 endopod and exopod subequal.

Uropods cylindrical, linear, about 0.6× body length, 2.3× length of pleotelson; protopod about 0.7× length of endopod, endopod 1.9× length of exopod.

Vernacular name.—Columbia groundwater isopod.

Range.—This species is known only from the Kalama River at Kalama, in southwestern Washington, just above its confluence with the Columbia River, approximately 55 km NNW of Portland, Oregon (Fig. 1).

Notes on ecology.—The well from which *Columbasellus acheron* emerged consists of a large diameter concrete caisson that extends approximately 8 meters below grade, with three perforated lateral pipes that extend horizontally approximately 5 meters below the bottom of the Kalama River. The isopods surfaced following superchlorination and high pressure scouring of the lateral pipes. Most of the isopods settled to the bottom of the caisson and were later removed during vacuuming of the well by the contractor hired to conduct the cleaning. Although no additional isopods have been noted, the well is likely a window into the hyporheic habitat. Techniques that penetrate this environment (Pospisil 1992), e.g., Karaman-Chappuis for shallow stream gravel interstices or Bou-Rouch sampling of deeper gravels with pump wells, should allow access to the isopods. It is likely that other subterranean invertebrates (amphipods, bathynellids, etc.) occur with *Columbasellus acheron* and await discovery.

Salmasellus howarthi Lewis, 2001

Material examined.—Oregon: Tillamook Co., Kilchis River drainage, Tilden Creek, 27 Sep 1998, 1 juvenile male.

This species was previously known only from two lava tube cave streams in southwestern Washington. This record extends the range approximately 100 km to the west.

Asellid species

Material examined.—Oregon: Clatsop Co., Sheewash Creek, 24 Aug 1994; Curry Co., Quail Prairie Creek near mouth, Oct 1992; Josephine Co., Howard Creek at mouth, 12 Oct 1997; Jackson Co., Crooked Creek, 13 Oct 1997; Lane Co., Cedar Creek, 25 Sep 1999; Tillamook Co., Clear Creek at mouth, 29 Sep 1998; East Foley Creek at river mile 2.5, 31 Aug 1994; Fall Creek, 29 Aug 1996; tributary to North Fork Kilchis River, 28 Sep 1997; Tilden Creek, 27 Sep 1998; Union Co., Limber Jim Creek at USFS Road 100, 20 Sep 1994; Wallowa Co., Chesnimnus Creek, 28 Aug 1991; Grouse Creek, 25 Aug 1992; Lick Creek, Aug 1992.—Washington: King Co., Lower Rock Creek, 15 Aug 1997; same locality, 1 Oct 1998.

This material consists of unidentifiable juveniles and females of subterranean species collected from stream gravels and presumably represents populations of *Calasellus, Salmasellus* or *Columbasellus*. The collection data are mapped to further illustrate the occurrence of subterranean asellids in the streams of Oregon and Washington (Fig. 1).

Acknowledgments

We sincerely thank Mr. Carl McCrary, Kalama Public Works Director, for collecting this unique isopod, who later gave it to Dr. John T. Longino, Evergreen State College, Olympia, Washington. Dr. Longino recognized the unusual nature of the specimen and transferred it to us for identification. We also thank Jude Van Buren (State of Washington Department of Health) and Richard Hoey (Regional Engineer, Southwest Drinking Water Operations) for information on the collection of the isopod. The new records of other asellids from Oregon and Washington are courtesy of Dr. Robert Wisseman, President, Aquatic Biology Associates, Corvallis, Oregon. We thank David L. White (University of South Carolina) for his help in preparing the map. We would also like to thank Dr. John R. Holsinger and Dr. Brian Kensley for reading the manuscript and making suggestions for its improvement. We also thank Dr. Guy Magniez, who not only read the manuscript, but worked with us on understanding the homologies of the Pacific Rim asellids.

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Literature Cited

Bowman, T. E. 1974. The California freshwater isopod, *Asellus tomalensis*, rediscovered and compared with *Asellus occidentalis*.—Hydrobiologica 44:431–441.

———. 1975. Three new troglobitic asellids from western North America (Crustacea: Isopoda: Asellidae).—International Journal of Speleology 7:339–356.

———. 1981. *Calasellus longus*, a new genus and species of troglobitic asellid from Shaver Lake, California (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 94:866–872.

Henry, J.-P., & G. Magniez. 1995. Novelles donnees sur les Asellidae epiges d'Extreme-Orient (Crustacea, Isopoda, Asellota).—Contributions to Zoology 65:101–122.

Henry, J-P., J. J. Lewis, & G. Magniez. 1986. Isopoda: Asellota: Aselloidea, Gnathostenetroidoidea, Stenetriodea. Pp. 434–464 *in* L. Botosaneanu, ed., Stygofauna Mundi. A faunistic, distributional, and ecological synthesis of the world fauna inhabiting subterranean waters (including the marine interstitial). E. J. Brill, Leiden, 740 pp.

Lewis, J. J. 1982. A diagnosis of the *Hobbsi* group, with descriptions of *Caecidotea teresae*, new species, and *C. macropropoda* Chase and Blair (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 95: 338–346.

———. 2000. *Caecidotea cumberlandensis*, a new species of troglobitic isopod from Virginia, with new records of other subterranean *Caecidotea* (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 113: 458–464.

———. 2001. Three new species of subterranean asellids from western North America, with a synopsis of the species of the region (Crustacea: Isopoda: Asellidae).—Texas Memorial Museum, Speleological Monograph 5:1–15.

———, & T. E. Bowman. 1981. The subterranean asellids (*Caecidotea*) of Illinois.—Smithsonian Contributions to Zoology 335:1–66.

———, & ———. 1995. The subterranean asellids of Texas (Crustacea: Isopoda: Asellidae).—Proceedings of the Biological Society of Washington 109:482–500.

———, & J. R. Holsinger. 1985. *Caecidotea phreatica*, a new phreatobitic crustacean (Asellidae) from southeastern Virginia.—Proceedings of the Biological Society of Washington 98:1004–1011.

Matsumoto, K. 1960. Subterranean isopods of the Kyushu District, with the descriptions of three new species.—Bulletin of the Biogeographical Society of Japan 22:26–44.

———. 1962. Two new genera and a new subgenus of the Family Asellidae of Japan.—Annotationes Zoologicae Japonenses 35:162–169.

———. 1978. Three new species of subterranean asellids from southern Kyushu and the Kii Peninsula, Japan.—Journal of the Speleological Society of Japan 3:20–34.

Miller, M. A. 1933. A new blind isopod *Asellus californicus*, and a revision of the subterranean asellids.—University of California Publications in Zoology 39:94–109.

Pospisil, P. 1992. Sampling methods for groundwater animals of unconsolidated sediments. Pp. 107–134 *in* A. I. Camacho, ed., The natural history of biospeleology. Monografias Museo Nacional de Ciencias Naturales, Madrid, 680 pp.

Williams, W. D. 1970. A revision of the North American epigean species of *Asellus* (Crustacean: Isopoda).—Smithsonian Contributions to Zoology 49:1–80.

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Bahadzia patilarga, a new species of subterranean amphipod crustacean (Hadziidae) from Cuba

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Abstract.—A new species of *Bahadzia* is described from an anchialine cave on the southern coast of Cuba. *Bahadzia patilarga* is the second species of the genus to be described from Cuba. Both Cuban species have eye spots and are found with remipeds and thermosbaenaceans at or near the halocline.

Since the initial description of the genus *Bahadzia* by Holsinger (in Holsinger & Yager 1985) on the basis of two stygobitic species from anchialine caves in the Bahamas and Turks and Caicos, seven more species have been described. These species are found in the Bahamas, Turks and Caicos, Cuba, Hispaniola and on the Yucatan Peninsula. To date, the only species of *Bahadzia* described from Cuba is *B. yagerae* (Ortiz & Pérez 1995). The present paper describes a second species of *Bahadzia* from the southern coast of Cuba. Although both this new species and *B. yagerae* exist in caves approximately 17 km apart, and both have eye spots, they are otherwise morphologically distinct. The following description raises the number of species in the genus to ten.

Systematics

Family Hadziidae Karaman, 1943
Genus *Bahadzia* Holsinger, 1985 (in Holsinger & Yager, 1985)
Bahadzia patilarga, n. sp.
(Figs. 1–4)

Material examined.—CUBA. Metanzas Province: Cueva de los Carboneros, Playa Girón, holotype ♀ (4 mm), A. Pérez, 11 June 1998; 2 paratypes (♀ and juvenile), J. Yager, 14 September, 1992, and 2 paratypes (♂ and ♀), J. Bozanic, 15 September 1992.

The holotype is deposited in the crustacean collection of the Center of Marine Research, University of Havana, Cuba (No. 178). The paratypes are in the collection of John R. Holsinger (H-3242, H-3249).

Diagnosis.—Small to medium sized stygobitic species easily distinguished from other members of the genus except *Bahadzia yagerae* Ortiz and Pérez 1995 by having a tiny, round, pigmentless eye, but differing from *B. yagerae* by having proportionately longer pereopods 6 and 7. Further distinguished from all other species within the genus by possessing a much shorter row of setae on the extreme inner margin of the inner plate of maxilla 2 and fewer setae on anterior margin of the propod of gnathopod 2 of the female. Largest male 6.0 mm; largest female 6.5 mm.

Female.—Head with tiny round, pigmentless eye or eye spot. Antenna 1 approximately 40% longer than body and 2.25 times longer than antenna 2; primary flagellum with up to 39 segments, accessory flagellum 3-segmented, subequal in length

Fig. 1. *Bahadzia patilarga*, n. sp., paratypes from Cueva de los Carboneros. Playa Giron, Cuba. Juvenile (2.5 mm): A, head region with eyespot. Female (6.5 mm): B, left mandible; C, incisor and lacinia mobilis of right mandible F, maxilla 2; G, maxilliped. Male (6.0 mm): D, maxilla 1; E, palp of other maxilla; H, telson; I, lower lip.

to the first 3 primary flagellar segments; peduncular segments becoming progressively shorter distally. Antenna 2: flagellum with up to 14 segments; peduncular segment 4 approximately 15% longer than segment 5. Mandible: molar well developed; spine row with 2 modified tooth-like spines distally and about 10 weakly serrate spines; lacinia mobilis of left mandible 4 dentate, that of right 3 dentate and smaller; incisor of left mandible 5 dentate, that of right 4 dentate and narrower; palp segment 3 as long as combined lengths of 1 and 2, bearing 1 long A seta, long row of approximately 13 D setae and 3–4 apical E setae. Lower lip: inner lobes distinct; lateral processes short, rounded apically. Maxilla 1: inner plate with 15 short, lightly plumose setae; outer plate bearing 9 pectinate spines; left and right palps similar, expanded and rounded distally, broad apex with 11 bladespines and single short, naked setae. Maxilla 2: inner plate narrowing distally, with row of approximately 45 naked submarginal facial setae and row of approximately 5 thicker setae located distally on extreme inner margin. Maxilliped: apex of inner plate even, armed on inner half with 4–5 short spines and a few short setae, inner margin with row of 10 weakly plumose setae; outer plate broader than inner with row of naked setae on inner margin and distally; palp segment 3 pubescent distally, distral inner margin of segment 3 slightly lobate; palp segment 4 almost as long as segment 3, nail small and spine-like.

Gnathopod 1: propod subrectangular about twice as long as broad, posterior margin heavily setose distally, palm short, transverse but lobate at defining angle and bearing 3 spines on lobe; carpus approximately 2 times as long as propod, bearing several clusters of long setae toward distal end; merus weakly lobiform and pubescent; basis with 7 long setae on posterior margin; coxa long and deep with about 9 short setae and 3 short spines. Gnathopod 2: propod subrectangular, palm short, oblique bearing short setae and 3 long setae at defining angle, posterior margin with 4 sets of long setae, anterior margin with a few setae, not in clusters; carpus approximately 28% longer than propod, posterior margin with 9 clusters of long setae; basis with 5 long setae; coxa deeper than broad, margin with about 6 setae and 4 short spines. Pereopod 3: coxa relatively small, deeper than broad, margin with 3 short setae. Pereopod 4: coxa broadly expanded distally and excavate posteriorly, margin with 13 short setae. Pereopod 6 approximately 5% longer than body, approximately 7% longer than pereopod 7 and 90% longer than pereopod 5. Pereopods 5–7: basis relatively narrow, with rather large, bluntly rounded distoposterior lobes. Dactyl of pereopod 5 approximately 50% length of corresponding propod; dactyls of pereopods 6 and 7 respectively, approximately 30% and 13% of corresponding propods. Coxal gills on 2–6 subovate, with short peduncle, very large on pereopods 2–4. Brood plates sublinear, small relative to gills.

Pleonal plates: posterior margins with 1 setule each, posterior corners small but distinct; ventral margin of plate 1 without spines, plates 2 and 3 with 1 spine. Pleopods normal, coupling spines rather long. Uropod 1: inner ramus shorter than peduncle, longer than outer ramus, bearing about 5 spines; peduncle with 12 spines, 1 of which is basofacial in position. Uropod 2: inner ramus approximately 15% longer than peduncle, longer and broader than outer ramus, armed with 13 spines; outer ramus with about 6 spines; peduncle with 9 spines 4 of which form a comb row on dorsodistal end. Uropod 3 approximately 23% length of body; inner ramus slightly longer and broader than outer ramus, margins with short spines and plumose setae; outer ramus with short terminal segment, inner margin with plumose setae and a few spines, outer margin with spines only; peduncle without spines. Telson rather long and narrow, in two separate lobes; lateral margins with about 5 spines each, none in sets of two; medial margins with 3–4 small spines each;

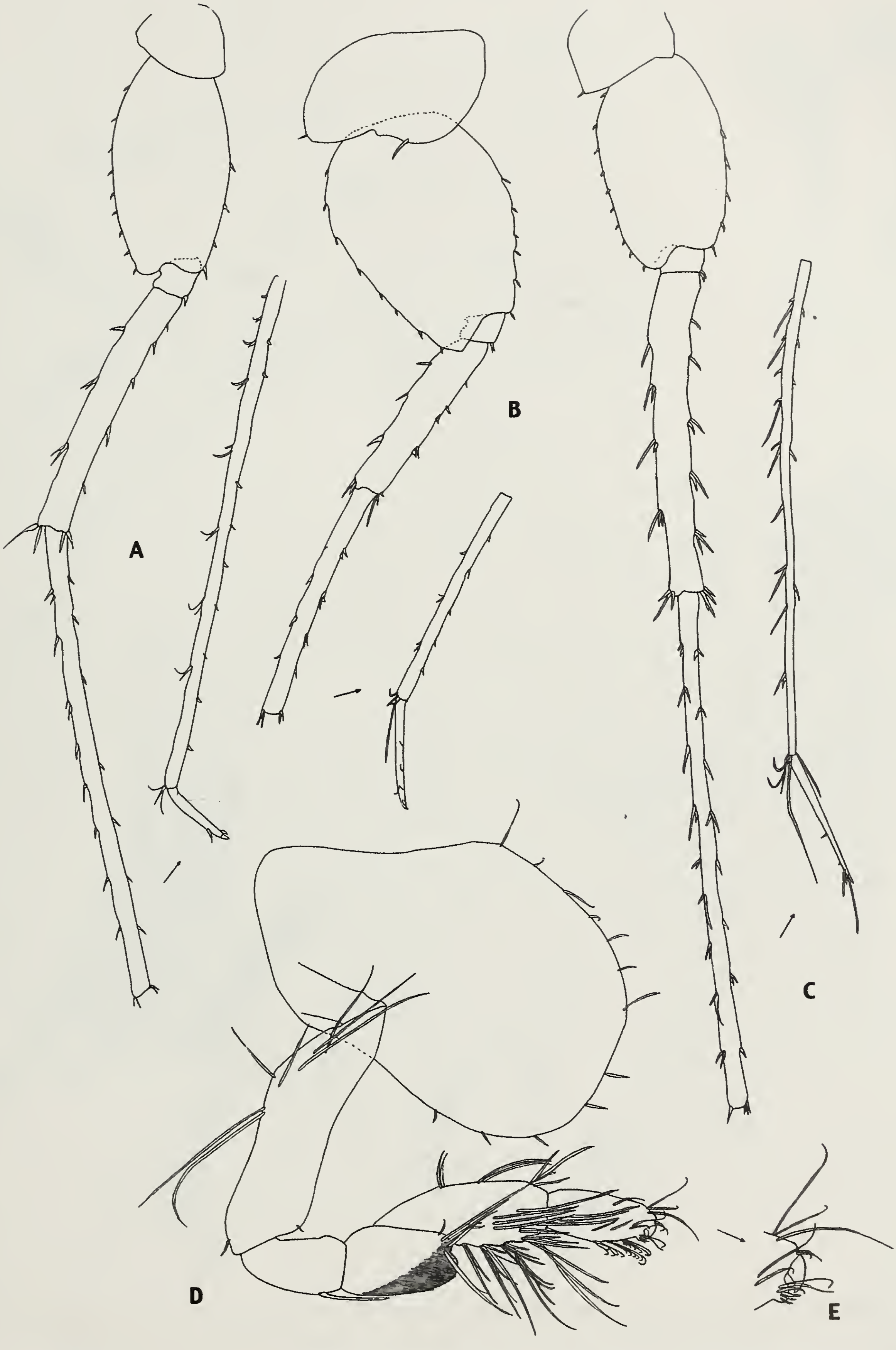

Fig. 2. *Bahadzia patilarga,* n. sp., paratypes from Cueva de los Carboneros, Playa Giron, Cuba. Male (6.0 mm): A, B, C, pereopods 7, 5, 6. Female (6.5 mm): D, gnathopod 1; E, enlarged distal end of propod and dactyl of gnathopod 1.

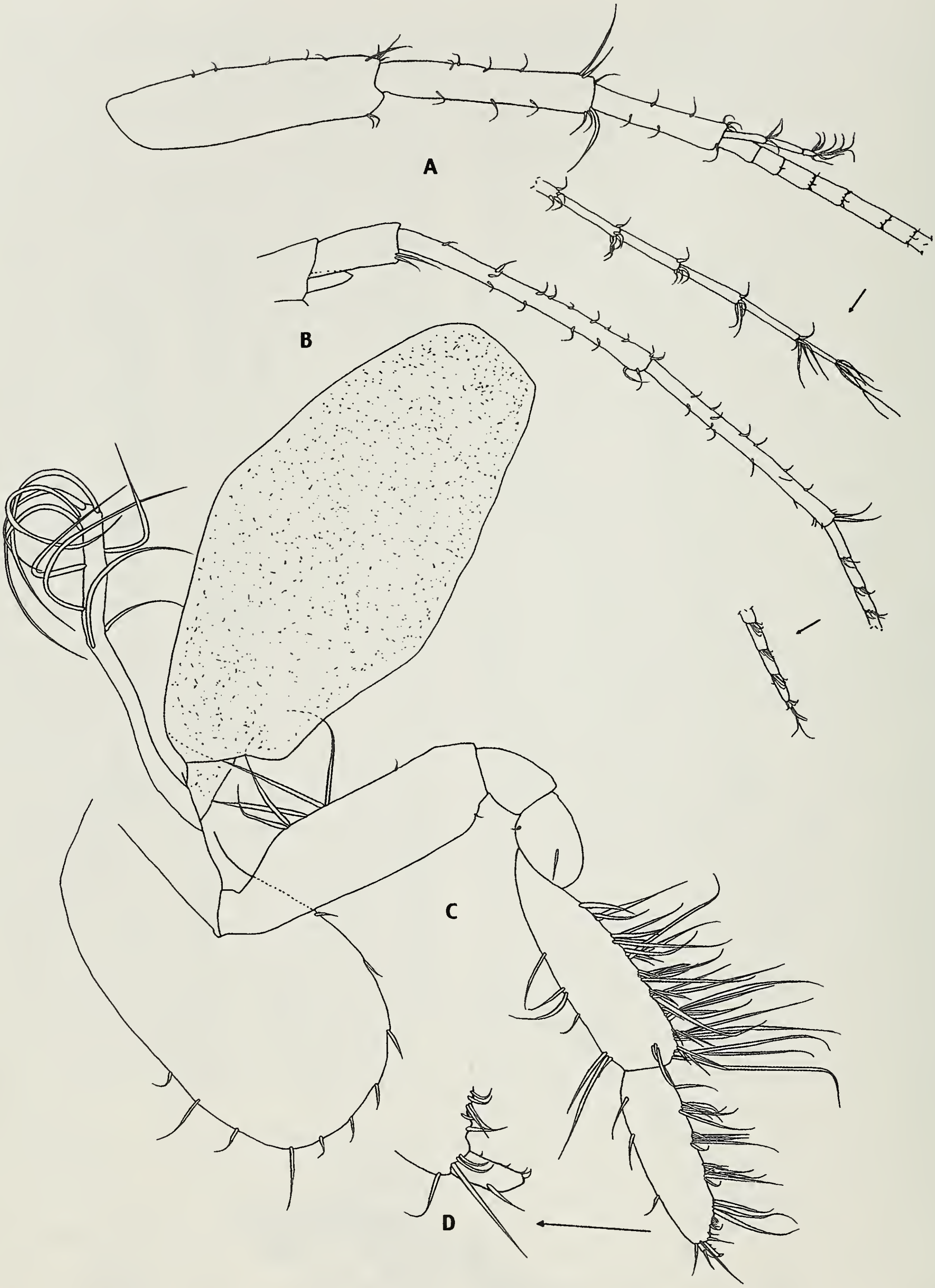

Fig. 3. *Bahadzia patilarga,* n. sp., paratype from Cueva de los Carboneros, Playa Giron, Cuba. Female (6.5 mm): A, B antennae 1,2; C gnathopod 2; D, enlarged distal end of propod and dactyl of gnathopod 2.

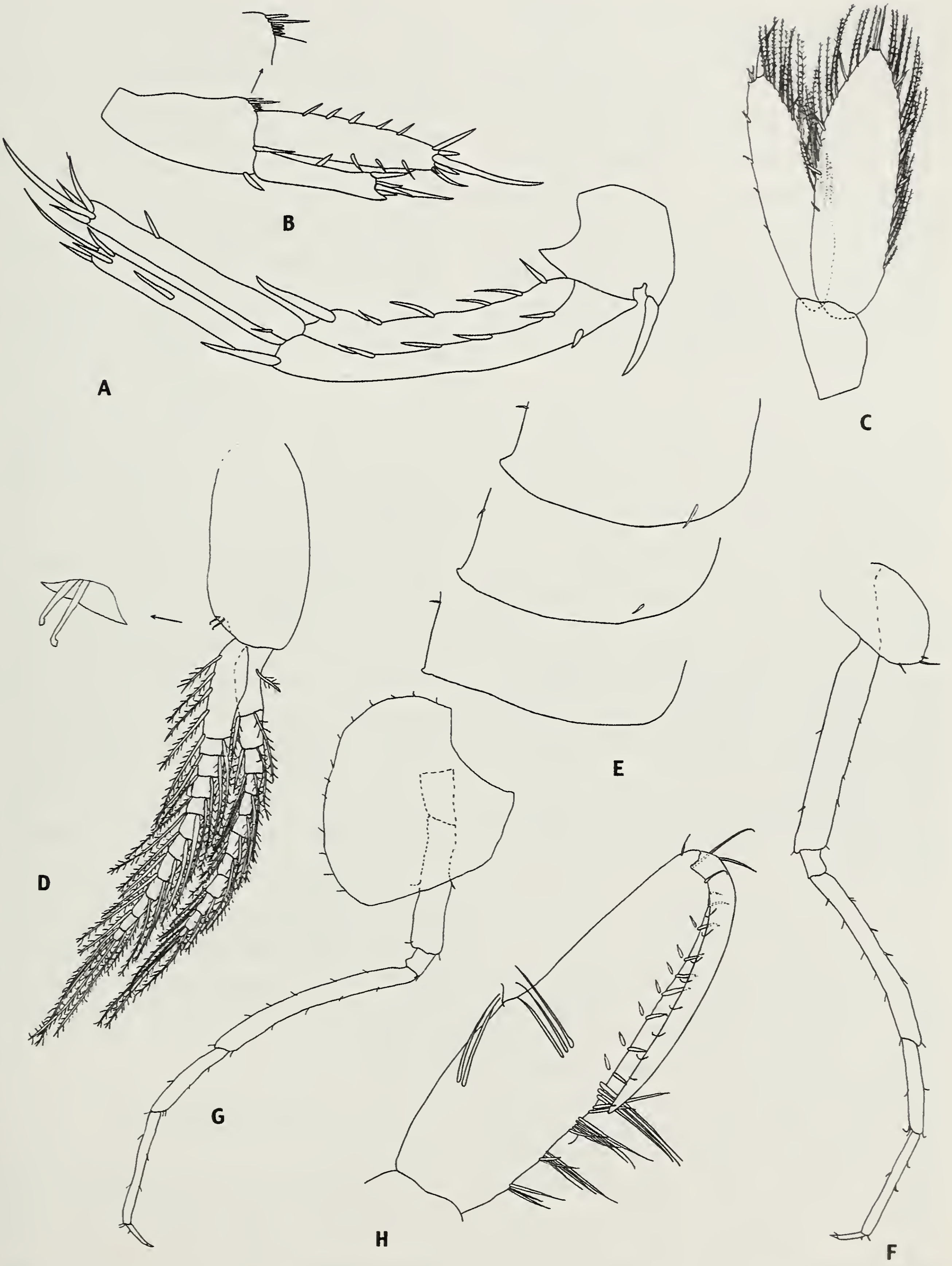

Fig. 4. *Bahadzia patilarga,* n. sp., paratypes from Cueva de los Carboneros, Playa Giron, Cuba. Female (6.5 mm): A, uropod 1; B, uropod 2 (distomedial spine row enlarged); C, uropod 3; D, pleopod 1 (coupling spines enlarged); E, pleonal plates. Male (6.0 mm): F, G, pereopods 3, 4; H, propod and dactyl of gnathopod 2.

apices with 1–2 short spines and 3 long, distally plumose setae.

Male.—Differing from female as follows: maxilla 1 inner plate with 7 short, weakly plumose setae; palp of maxilla 1 with 12 bladespines and without short naked setae. Gnathopod 2: dactyl and propod proportionately longer; propod palm long, oblique with double row of about 9 blunt tipped spines; defining angle with 3 long setae; posterior margin longer than palm, with 4 sets of setae. Distal margin of peduncle of uropod 3 with 2 spines.

Etymology.—The word "patilarga" is Spanish vernacular commonly used in Latin American countries to describe legs that are larger than normal. It is used here as a noun in apposition alluding to the extremely long pereopods 6 and 7 of the species.

Remarks.—*Bahadzia patilarga* was informally referred to as "cubensis" in an article written for a general SCUBA diving magazine and was not intended to be a formal taxonomic publication. Therefore the name "cubensis" is unavailable and invalid and should not be considered a synonym or *nomen nudum.*

Type-locality.—This species is known only from the type-locality, Cueva de los Carboneros.

Discussion

Bahadzia patilarga is recorded to date from a single anchialine cave, Cueva de los Carboneros, which is located in Playa Giron on the southern coast of Cuba in Matanzas Province. Playa Giron is commonly known in America as the Bay of Pigs. Collection of *B. patilarga* was made at or near the halocline, where it occurs sympatrically with remiped and thermosbaenacean crustaceans. This association with remipeds and thermosbaenaceans and its specific microhabitat defined as being near or within the halocline of anchialine caves is very common, although not ubiquitous, for this genus. Based on research in caves of the Yucatan Peninsula, Pohlman et al. (1997) noted that these crustacean taxa might be utilizing a chemoautotrophic energy source existing near the halocline. They suggested that a similar phenomenon may occur in anchialine caves throughout the Caribbean and southern Atlantic, where organisms such as *Bahadzia* exist. Pohlman et al. (1997) noted a dramatic drop in oxygen concentration precisely at the halocline, where they surmised that chemoautotrophism was occurring. Although no field data are available for the oxygen concentration at the halocline in the type locality for *B. patilarga,* it is interesting to note that, as with many (but not all) species of *Bahadzia, B. patilarga* has extremely large gills. Enlarged gills may be an adaptation for living in low oxygen environments.

Based on a track synthesis, Holsinger (1989, 1992) predicted the occurrence of *Bahadzia* in Cuba. The description of *Bahadzia patilarga* above brings the number of species so far discovered on the island to two. Both species exist in single caves a mere 17 km apart. Recent explorations by one of us (TRS) resulted in the discovery of a remiped crustacean in a cave on the northern coast of Cuba, also in Matanzas Province. Based on this discovery and the fact that remipeds and *Bahadzia* are often found living sympatrically, it is predicted that additional populations of *Bahadzia,* quite possibly representing new species, will be found in caves on the northern coast of Cuba.

Acknowledgments

We are grateful to Jeff Bozanic, Jill Yager and the Biokarst Association of Cuba for assistance with collecting specimens, and we thank Tamara Connolly for assistance with preparation of the figures. This study was supported in part by a PEET (Partnerships for Enhancing Expertise in Taxonomy) grant from the National Science Foundation to JRH (DEB-9521752).

Literature Cited

Holsinger, J. R. 1989. Preliminary zoogeographic analysis of five groups of crustaceans from anchialine caves in the West Indian region. Proceedings of 10th International Congress of Speleology, 1:25–26.

Holsinger, J. R. 1992. Two new species of the subterranean amphipod genus *Bahadzia* (Hadziidae) from the Yucatan Peninsula region of southern Mexico, with an analysis of phylogeny and biogeography of the genus.—Stygologia 7:85–105.

Holsinger, J. R., & J. Yager. 1985. A new genus and two new species of subterranean amphipod crustaceans (Hadziidae) from the Bahamas and Turks and Caicos Islands.—Bijdragen tot de Dierkunde 55:283–294.

Karaman, S. 1943. Die unterirdischen Amphipoden Sudserbiens. Srpska Kral'evska Akademiia Posebna Izdan'a, CXXXV Prirodn'achki i Matematichki Spici, 34 (4) Okhridski Zbornik: 163–312.

Ortiz, M. & A. Pérez. 1995. Una Nueva Especie de Anfipodo Cavernícola Hadzioideo (Amphipoda, Gammaridea) de Cuba.—Graellsia 51:165–168.

Pohlman, J. W., T. M. Iliffe, & L. A. Cifuentes. 1997. A stable isotope study of organic cycling and the ecology of an anchialine cave ecosystem.—Marine Ecology Progress Series 155:17–27.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(1):206–214. 2003.

A new species of *Cymbasoma* (Crustacea: Copepoda: Monstrilloida) from the Pacific coast of Costa Rica, Central America

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Abstract.—A new species of monstrilloid copepod belonging to the genus *Cymbasoma* Thompson is described from a female specimen collected in Bahía Culebra, an embayment on the Pacific coast of northwestern Costa Rica, in Central America. The new taxon, *C. concepcionae*, n.sp., is part of a group of species of *Cymbasoma* with a fifth leg represented by a single lobe armed with three setae. An overall comparison of this morphological group is presented. The new species is distinguished mainly by a combination of characters including a short inner seta on the fifth leg, a slightly globous genital double somite, and transverse cuticular striations nearly encircling the cephalic area. Moreover, the species can be easily recognized by a distinctive cluster of rounded cuticular processes on the middle ventral margin of the fifth pedigerous somite and on the anterior half of the genital double somite. The intercoxal sclerite of the first swimming leg shows a peculiar ornamentation not previously described within the group. This is the first record of a monstrilloid copepod species from marine waters of Costa Rica and of Central America, and the fourth species of *Cymbasoma* recorded from the Eastern Tropical Pacific.

Monstrilloid copepods are parasitic crustaceans known mainly by their planktonic, non-feeding adult stage. These usually rare copepods are collected mainly in zooplankton surveys of coastal-neritic systems at all latitudes. The order is represented currently by over 100 nominal species contained in three valid genera: *Monstrilla* Dana, *Monstrillopsis* Sars, and *Cymbasoma* Thompson (Huys & Boxshall 1991, Grygier 1994).

Cymbasoma is a diverse genus with more than 40 nominal species; its species are distributed world-wide. Most of these species have been reported from either the Eastern Atlantic or the Far East (Razouls 1996). To date three species, *C. californiense* Suárez-Morales, 1999, *C. rigidum* Thompson, 1888, and *C. tumorifrons* Isaac, 1974, are known to occur in tropical waters of the Eastern Pacific (Suárez-Morales & Alvarez-Silva 2001). Suárez-Morales & Alvarez-Silva (2001) predicted that the regional list of Monstrilloida recorded for the Eastern Tropical Pacific would increase, most likely from the coastal, near-shore environments where monstrilloid copepods are more frequently collected.

As part of a survey of the coastal areas along the northern Pacific coastline of Costa Rica, in Central America, zooplankton samples were collected in Bahía Culebra, a deep embayment that is part of the Gulf of Papagayo. A taxonomic analysis of the zooplankton samples revealed the presence of an undescribed species of monstrilloid copepod belonging to the genus *Cymbasoma,* which is described and illustrated here, following the current description standards set by Grygier & Ohtsuka (1995) for monstrilloid copepods.

Systematics

Order Monstrilloida Sars, 1903
Family Monstrillidae Giesbrecht, 1892
Genus *Cymbasoma* Thompson, 1888
Cymbasoma concepcionae, new species
(Figs. 1–3)

Material examined.—Holotype: adult female from Bahía Culebra, Costa Rica, undissected, ethanol-preserved. Date of collection: 6 November 1999. Vial deposited in the Collection of Zooplankton at El Colegio de la Frontera Sur (ECOSUR), in Chetumal, Mexico (ECOCH-Z-01211).

Etymology.—The new species honors Mrs. Concepción Morales, mother of the first author (ES-M).

Type locality.—Bahía Culebra (10°36′17.0″N, 85°39′36.6″W), northern part of the Pacific coast of Costa Rica; depth of collection: near surface.

Habitat.—Bahía Culebra is located within the Gulf of Papagayo, in the northwestern part of the Pacific coast of Costa Rica. It is a deep (35 m average depth), relatively small (20 km^2), semi-enclosed embayment. Bahía Culebra is influenced by seasonal variations of the coastal current flowing northward off Costa Rica. Because of wind influence, relatively intense coastal upwelling has been reported in the area (Glynn et al. 1983). The bay has a sandy bottom and scattered patches of coral reef (Jiménez 1998). The mean sea surface temperature in the area is 27.5°C.

Description.—Female: Total body length of holotype: 1.5 mm measured from anterior end of cephalothorax to posterior end of anal somite. Cephalothorax measuring 0.95 mm, representing almost 61% of total body length (Fig. 1A, B). Oral papilla protuberant (Fig. 1E), located ventrally a quarter the length of cephalothorax (Fig. 1B). Pair of ocelli present, pigment cups joined medially, well developed, weakly pigmented in central portion, round in dorsal view (Fig. 1A, F). Cephalothorax with irregularly arranged cuticular protuberances on "forehead" (Fig. 1A, D); sensilla not observed in this area. Longitudinal and oblique cuticular ridges overlying part of region of ocelli on dorsal surface; ridges stretch dorsally and end in a transverse pattern (Fig. 1F). Two pairs of nipple-like processes on anterior ventral surface; anterior pair larger, eccentrically conical in shape, small pair regularly concentric (Fig. 1C, D). Other ventral cuticular ornamentation including pair of mammiform processes on anterior surface between bases of antennules (Fig. 1D) and wide zone of transverse ridges covering most of the surface between the oral papilla and small nipples (Fig. 1A, B, D, E); dorsal and ventral transverse ridge zones at same level, but discontinuous on lateral surfaces.

Antennule length 0.25 mm, relatively short, less than 14% of total body length, and 22% as long as cephalothorax. Antennules four-segmented, armed with 0-I; 1-V; 2-I; 8-VIII setae (Arabic numerals) and spines (Roman numerals) (Fig. 2D, E). In terms of pattern described by Grygier and Ohtsuka (1995) for female monstrilloid antennular armature, setae (Roman numerals) and spines (Arabic numerals), element 1 present on first segment; elements on second segment: $2d_1$, $2d_2$, $2v_1$, $2v_2$, $2v_3$, and IId. Third segment with elements 3, IIId, and IIIv. Segment four bearing element $4v_1$, particularly well developed, asymmetrical, longer on left antennule (Fig. 2D, E); elements $4d_{1,2}$ and $4v_{1-3}$ present, poorly developed, setae IVd, IVv, Vd, Vv, and Vm present. Element 5 absent. Subterminal elements b_{1-6} and 6aes, 6_1, and 6_2 present; 6aes larger on left antennule. Aesthetasc 4aes well developed, on ventral surface (Fig. 2D, E).

First pedigerous somite, fused to cephalothorax, and succeeding three free pedigerous somites each bearing a pair of biramous swimming legs. Pedigerous somites 2–4, together accounting for 21% of total length in dorsal view. Swimming legs 1–4

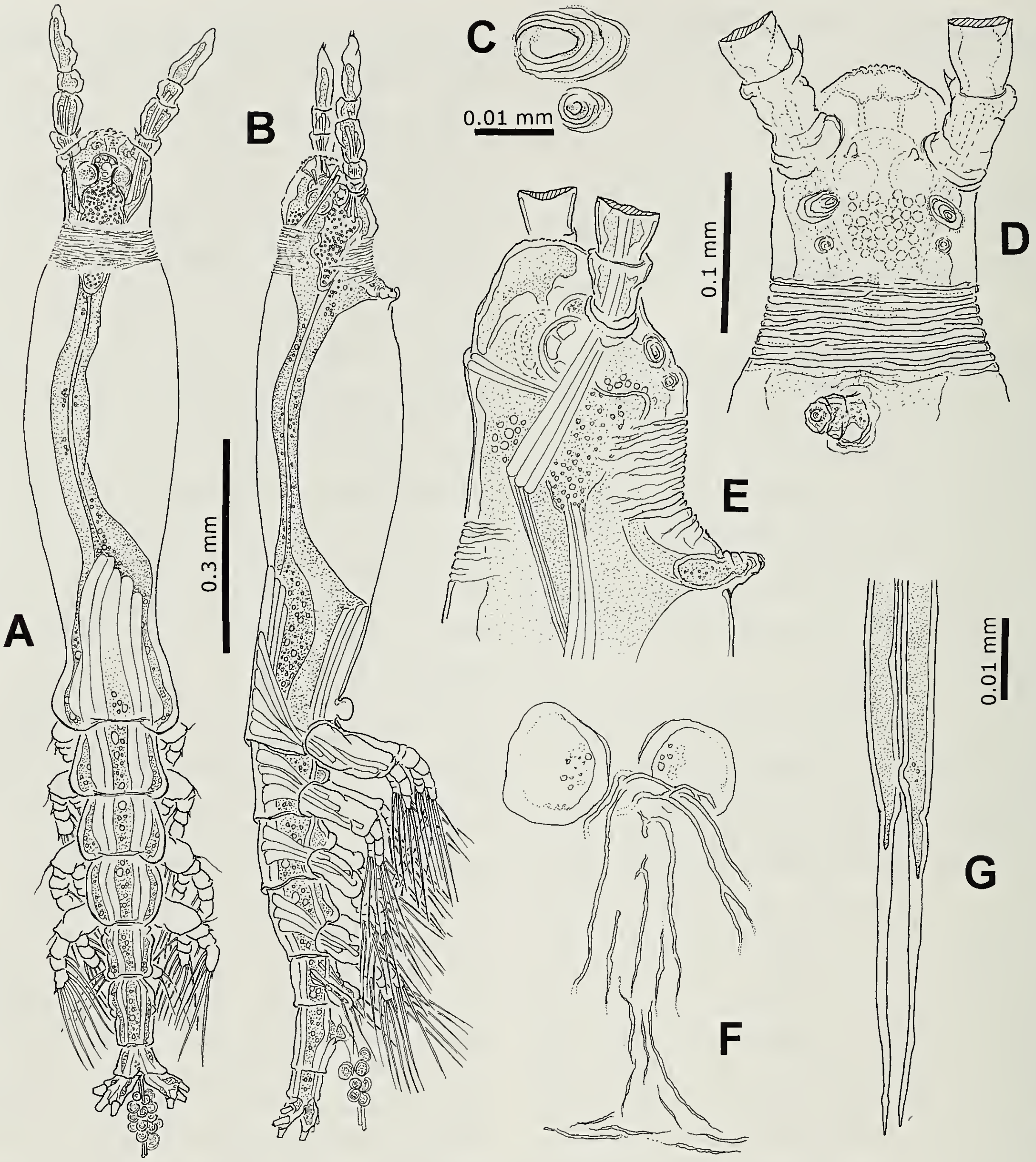

Fig. 1. *Cymbasoma concepcionae,* new species. adult female, holotype from Bahía Culebra, Costa Rica. A. habitus, dorsal; B. habitus, lateral; C. detail of ventral nipple-like processes; D. cephalic area showing ventral cuticular processes; E. cephalic area, lateral view; F. cuticular ridges on dorsal surface posterior to ocelli; G. distal ends of ovigerous spines, ventral.

Table 1.—Armature formula of swimming legs 1–4 of *Cymbasoma concepcionae,* new species. Symbols to left of dash are lateral elements, symbols to right of dash are medial elements; semicolons represent arthrodial membranes of rami; commas separate lateral, terminal, and medial elements on the distal segment of a ramus; Roman numerals are thicker, rigid elements; Arabic numerals are thinner, flexible elements.

	Coxa	Basis	Endopodite	Exopodite
leg 1	0–0	1–0	0–1; 0–1; 1, 2, 2	I–1; 0–1; I, I+1, 2
leg 2	0–0	1–0	0–1; 0–1; 1, 2, 2	I–1; 0–1; I, I+1, 3
leg 3	0–0	1–0	0–1; 0–1; 1, 2, 2	I–1; 0–1; I, I+1, 3
leg 4	0–0	1–0	0–1; 0–1; 1, 2, 2	I–1; 0–1; I, I+1, 3

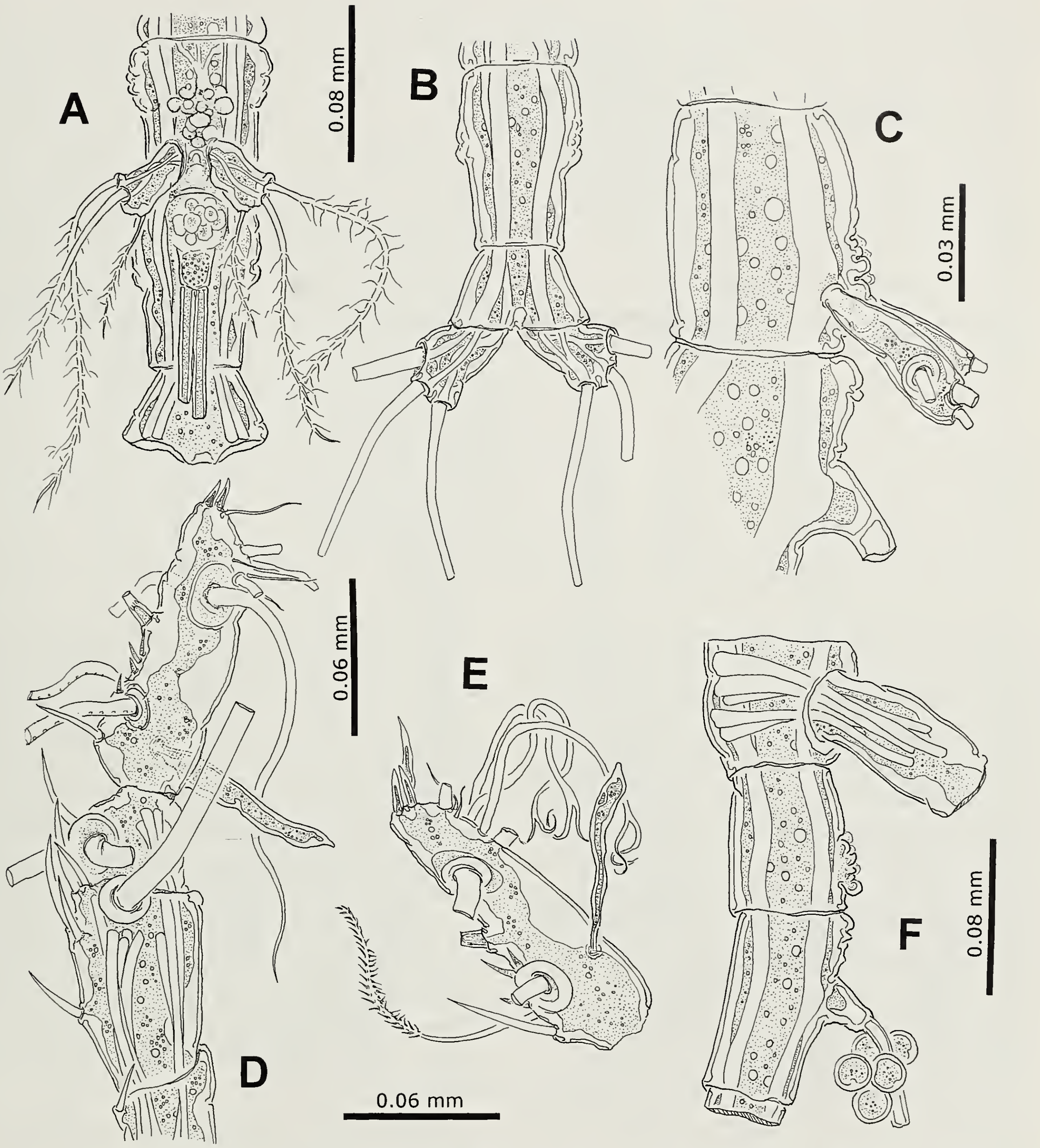

Fig. 2. *Cymbasoma concepcionae,* new species, adult female, holotype from Bahía Culebra, Costa Rica. A. urosome and fifth legs, ventral view; B. genital double somite and anal somite plus caudal rami, dorsal; C. fifth pediger and anterior part of genital double somite, lateral; D. right antennule, dorsal; E. distal segment of left antennule, ventral; F. third free pediger and urosome, lateral view, protoendopod of fourth legs shown, fifth legs omitted to show ventral cuticular processes, caudal rami cut short.

slightly increasing in size posteriorly (Fig. 3A–D), but their intercoxal sclerites decrease in size posteriorly. Intercoxal sclerite of leg 1 with pair of longitudinal semi-cylindrical processes covered with short setae and flanking hairy medial depression. Posterior margin of this intercoxal sclerite flat at middle, with rounded processes on each side (see Fig. 3E). Intercoxal sclerites of legs 2–4 rectangular, without ornamentation on surface or on posterior margin (Fig. 3F). Basis of legs articulating with large, rectangular coxa along diagonal arthrodial membrane. Basis with hair-like lateral seta

Table 2.—Comparison of selected taxonomic features in species of *Cymbasoma* with uriramous fifth leg armed with three setae. GDS = anterior half genital of double somite globose; IS = inner seta of 5th leg smallest; IS <50% = inner seta <50% as long as others; L = longest seta on leg 5; OP on CT = position of oral papilla on cephalothorax; A1/CT = relative length (as a percent) of antennule to cephalothorax; = relative length (as a percent) of position of oral papilla anteriorly on cephalothorax; T = transverse striations on "neck" area. Key to species: (A) *C. concepcionae,* new species; (B) *C. reticulatum* Giesbrecht, 1892; (C) *C. bowmani* Suárez-Morales, 1998; (D) *C. quintanarooense* (Suárez-Morales, 1994) (Suárez-Morales & Escamilla 2001); (E) *C. boxshalli* (Suárez-Morales, 1993) (Suárez-Morales 20001a); (F) *C. bali* Desai & Krishnaswamy, 1962; (G) *C. frondipes* Isaac, 1975; (H) *C. striatum* (Isaac, 1974) (Suárez-Morales 2000); (I) *C. claparedi* Giesbrecht, 1892; (J) *C. tumorifrons* Isaac, 1975.

	A	B	C	D	E	F	G	H	I	J
GDS	yes	no	no	yes	yes	no	no	yes	no	yes
IS	yes	no	yes	no	yes	no	yes	yes	no	yes
IS <50%	no	no	no	no	yes	no	no	yes	no	no
L	outer	none	none	none	outer	middle	none	none	none	outer
OP on CT	23	20–25	15	28	18–20	17	?	18	14	25
A1/CT	22	27–30	23	32	22	27	21	33	29	31
OP/TL	43	89	42	47	42	41	?	34	49	36
T	yes	no	no	no	no	?	?	yes	no	yes

on legs 1–4 (Fig. 3A–D); on leg 3, this seta about 4.5 times longer, lightly setulated from distal half, and slightly thicker than those on the other legs (see Fig. 3C). Endopodites and exopodites of swimming legs 1–4 triarticulated. Ramal setae biserially plumose except spiniform outer seta on exopod 1 and 3, and inner seta of first exopodal segment, these latter being short and sparsely setulated (Fig. 3A–D). Also, outermost apical exopodal setae of swimming legs 1–4 with inner margin naked, outer margin lightly spinulose to tip (Fig. 3A–D). Armature of swimming legs in Table 2.

Fifth legs separated at base, unsegmented, each consisting of relatively large, lobe-like expod (Fig. 2A); 3 setae present, outer 25% longer than terminal; inner seta narrower and shorter, about 50% as long as outer seta. All 3 setae with sparse, biserial setules (Fig. 2A).

Urosome of 3 segments: fifth pedigerous somite, genital double somite and free anal somite. Fifth pedigerous somite with a group of rounded protuberances along middle ventral margin between fifth legs lobes (Fig. 2C, F). Genital double somite relatively large, ratio of its length and anal somite: 69.5:30.5 = 100; anterior half expanded laterally, expansion visible in both ventral (Fig. 2A) and dorsal (Fig. 2B) views, with rounded protuberances along lateral margins of expanded anterior half. Anterior half of ventral surface of genital double somite with similar protuberances as those on fifth pedigerous somite anterior to base of ovigerous spines. Ovigerous spines paired, relatively long (0.65 mm), unbroken, inserted in a protuberant base visible in lateral view (Fig. 2F), separated at base, equalling almost 43% of total body length; adhering eggs covered by gelatinous sheath. Tips of both spines separated from each other, with slight but distinct subterminal narrowing (Fig. 1G).

Caudal rami subrectangular, widely divergent, approximately 1.5 times longer than wide, each bearing 3 well developed setae, all of almost the same length (0.23–0.30 mm) and width.

Male.—unknown.

Remarks.—The absence of a reliable way to associate females with conspecific males is one of the main problems with the taxonomy of the Monstrilloida, a result of the complex life cycle of these parasitic copepods (see Suárez-Morales 2001b). As is the case of many other monstrilloids (see Suárez-Morales 1993, Suárez-Morales & Dias 2001), *C. concepcionae* is known only from

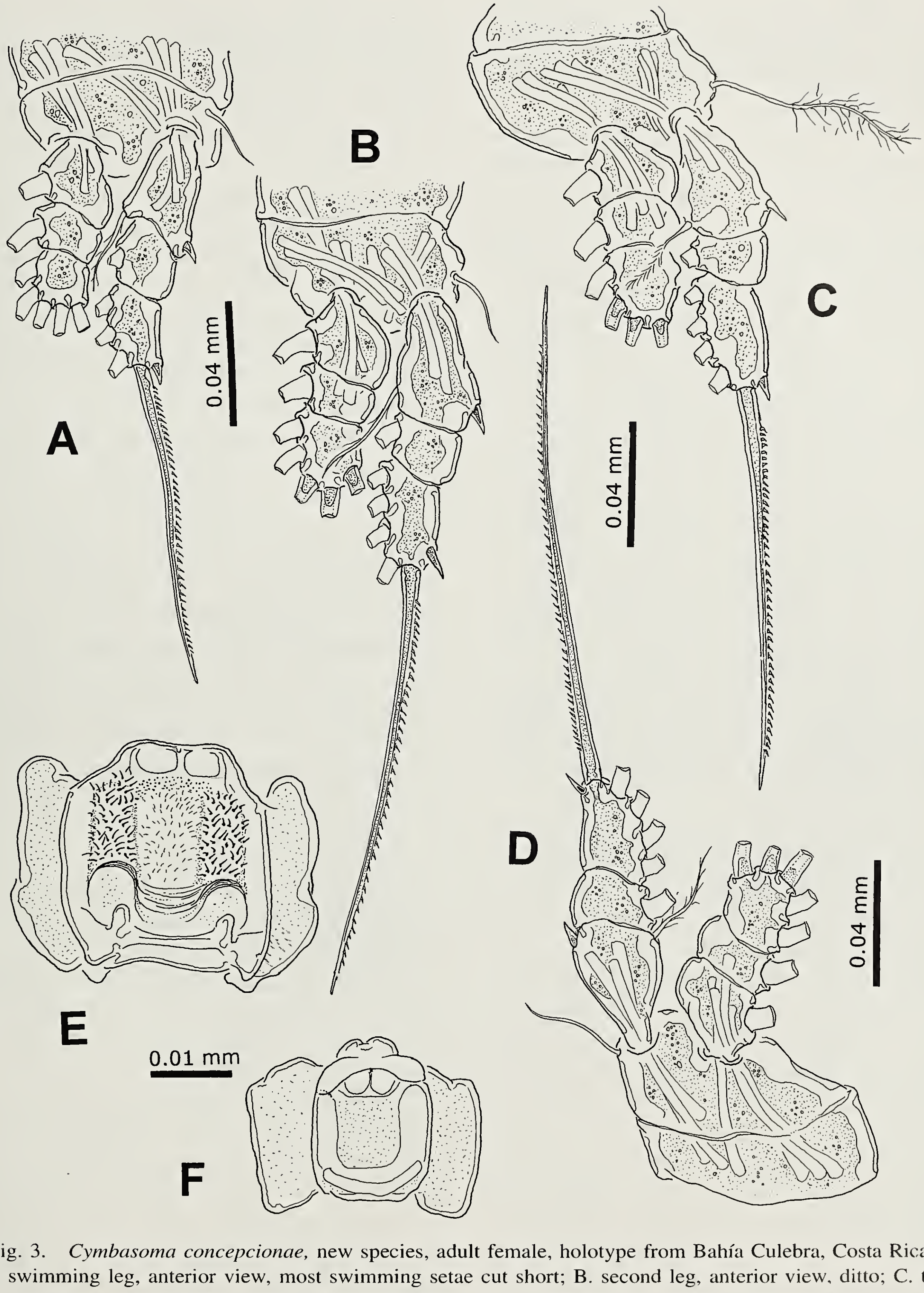

Fig. 3. *Cymbasoma concepcionae,* new species, adult female, holotype from Bahía Culebra, Costa Rica. A. first swimming leg, anterior view, most swimming setae cut short; B. second leg, anterior view, ditto; C. third swimming leg, anterior view, ditto; D. fourth swimming leg, anterior view, ditto; E. intercoxal sclerite, first swimming legs; F. intercoxal sclerite, fourth swimming legs.

the female, and from a single specimen, the common case with monstrilloids (Suárez-Morales and Palomares-García 1995, Suárez-Morales 2000).

The new species described here is placed in the genus *Cymbasoma* because of the presence of two urosomites, or only one free somite posterior to the genital double somite, in the female (Isaac 1975, Grygier 1994). Following the most widely used key to the species of this genus (Isaac 1975), and considering a non-striated cephalic segment option in the third couplet, the new species would match (in part) the female of either *C. tumorifrons* (Isaac, 1975) or *C. claparedi* (Giesbrecht, 1892), both found in the Eastern Atlantic. These two species also are members of a group of *Cymbasoma* with a single-lobed fifth leg armed with three setae; the group includes *C. striatum* (Isaac, 1974), *C. frondipes* Scott, 1904, *C. reticulatum* (Giesbrecht, 1892), *C. bali* Desai and Krishnaswamy, 1962, *C. bowmani* Suárez-Morales, 1998 (see Suárez-Morales & Gasca 1998), *C. boxshalli* (Suárez-Morales, 1993), and *C. quintanarooense* (Suárez-Morales, 1994).

The presence of rounded protuberances on the ventral surface of the fifth pedigerous somite and genital double somite of *Cymbasoma concepcionae* separates it from all other members of this group. *Cymbasoma concepcionae* shares with *C. striatum, C. quintanarooense,* and *C. tumorifrons* cephalic cuticular striations and a similar structure and armature of the fifth legs. Although *C. concepcionae* and *C. tumorifrons* are similar in the structure and armature of fifth legs and transverse striations of the cephalic area (see Table 2), they differ in the body proportions, the shape of the cephalothorax, the length of the ovigerous spines, and the shape of the genital double somite, which is strongly globose in *C. tumorifrons* (Table 2 and see Suárez-Morales and Alvarez-Silva 2001). Other important differences include the respective cuticular ornamentation patterns and the distinctive ventral rounded processes present in the urosome of the new species. The new species can be distinguished from *C. quintanarooense* by the ocelli which are very well-developed and intensely pigmented in the latter (see complementary description by Suárez-Morales and Escamilla 2001) vs. normally developed in *C. concepcionae.* The antennules are relatively longer in *C. quintanarooense* than in *C. concepcionae,* and the oral papilla is in a more posterior position. The three setae of the fifth legs are equal in length and breadth in *C. quintanarooense* vs. a short innermost seta in the new species (see Table 2).

Cymbasoma concepcionae differs from *C. striatum* by the latter's peculiar cuticular striation pattern covering almost half the length of its cephalothorax, as redescribed by Suárez-Morales (2000); a strongly globose shaped genital double somite vs. a slightly expanded shape in the new species; an oral papilla 18% along cephalic somite in *C. striatum* vs. 23% in the new species; "forehead" with medial protuberance formed by several irregularly arranged bumps; with a pair of sensillae in *C. striatum* vs. lower cuticular protuberances and no sensillae in the new species; ovigerous spines closely set distally and with subterminal rounded protuberances in *C. striatum* vs. distally separated spines with slight but distinct subterminal narrowing in *C. concepcionae*; and an outer, apical exopodal seta of swimming legs 1–4 with setules in *C. striatum* vs. naked in the new species (Suárez-Morales 2000).

Cymbasoma frondipes has a very long cephalothorax (over 66% of the total body length) and characteristically massive, short antennules (see Isaac 1975). *Cymbasoma concepcionae* differs from the remaining species shown in Table 2 by a combination of: an anteriorly weakly globose genital double somite; the inner seta of fifth leg shortest and outer seta longest; and transverse striations around the "neck" area. The taxonomic value of the morphology of the intercoxal sclerites has not been compared among these monstrilloids, although recent descriptions suggest a certain degree of ornamentation (Suárez-Morales and Dias 2001). The contours and setation of the first intercoxal sclerite in *C. concepcionae* is definitely the most complex pattern known for species in the group.

Cymbasoma concepcionae is the fourth confirmed species of the genus from waters of the Eastern Tropical Pacific (Suárez-Morales and Alvarez-Silva 2001). This also is the first record of a monstrilloid species in Costa Rica or along the Pacific coast of Central America. More records are to be expected from further examination of the zooplankton samples available from the region.

Acknowledgments

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Literature Cited

Desai, H. V., & S. Krishnaswamy. 1962. *Cymbasoma bali,* a new species of monstrilloid copepod from the Bombay plankton.—Proceedings of the Indian Academy of Sciences 55B:163–166.

Giesbrecht, W. 1892. Systematik und Faunistik der pelagischen Copepoden des Golfes von Neapel und der angrezenden Meeres-Abschnitte. Fauna und Flora des Golfes von Neapel und der angrezenden Meeres-Abschnitte herausgegeben von der Zoologischen Station zu Neapel. XIX. Monographie. Verlag von R. Friedländer & Sohn, Berlin, 1–831.

Glynn, P., E. Druffel, & R. Dunbar. 1983. A dead Central America coral reef tract: possible link with the Little Ice Age.—Science 203:47–49.

Grygier, M. J. 1994. Identity of *Thaumatoessa* (= *Thaumaleus*) *typica* Krøyer, the first described monstrilloid copepod.—Sarsia 78:235–242.

Grygier, M. J., & S. Ohtsuka. 1995. SEM observation of the nauplius of *Monstrilla hamatapex,* new species, from Japan and an example of upgraded descriptive standards for monstrilloid copepods.—Journal of Crustacean Biology 15:703–719.

Huys, R., & G. A. Boxshall. 1991. Copepod evolution. The Ray Society, London, 468 pp.

Isaac, M. J. 1974. Copepoda Monstrilloida from southwest Britain including six new species.—Journal of the Marine Biological Associaton of the United Kingdom 54:127–140.

Isaac, M. J. 1975. Copepoda, Suborder: Monstrilloida.—Fiches d'Identification du Zooplancton 144/145:1–10.

Jiménez, C. 1998. Arrecifes y comunidades coralinas de Bahía Culebra, Pacífico Norte de Costa Rica (Golfo de Papagayo). Unpublished M.Sc. thesis, Universidad de Costa Rica, San José, 218 pp.

Razouls, C. 1996. Diversité et répartition géographique chez les copépodes pélagiques. 2.—Platycopioida, Misophrioida, Mormonilloida, Cyclopoida, Poecilostomatoida, Siphonostomatoida, Harpacticoida, Monstrilloida.—Annales de l' Institut Océanographique Nouvelle Série 72:1–149.

Sars, G. O. 1903. An account of the Crustacea of Norway with short descriptions and figures of all species. Vol. IV. Copepoda Calanoida. The Bergen Museum, Bergen. 28 pp.

Suárez Morales, E. 1993. A new species of *Thaumaleus* (Copepoda, Monstrilloida) from the eastern coast of the Yucatan Peninsula, Mexico.—Crustaceana 64:85–89.

———. 1994. *Thaumaleus quintanarooensis,* a new monstrilloid copepod from the Mexican coasts of the Caribbean Sea.—Bulletin of Marine Science 54:381–384.

———. 2000. Redescription of two species of *Cymbasoma* from southwest Britain and from Indonesia (Copepoda: Monstrilloida), with notes on taxonomy.—Beaufortia 50:139–149.

———. 2001a. Redescription and first record of *Cymbasoma boxshalli* and *Monstrilla inserta* (Copepoda: Monstrilloida) from Curaçao, eastern Caribbean Sea.—Cahiers de Biologie Marine 42:243–254.

———. 2001b. An aggregation of monstrilloid copepods in a western Caribbean reef area: ecological and conceptual implications.—Crustaceana 74:689–696.

———, & C. Alvarez-Silva. 2001. *Cymbasoma tumorifrons* (Copepoda: Monstrilloida): an expanded description based on a new collection from the Eastern Tropical Pacific.—Pacific Science 55:183–189.

———, & C. Dias. 2001. Taxonomic report of some monstrilloids (Copepoda: Monstrilloida) from Brazil with description of four new species.—Bulletin de l' Institut Royal des Sciences Naturelles de Belgique. Biologie 71:65–81.

———, & J. B. Escamilla. 2001. Taxonomic report on some monstrilloids (Copepoda, Monstrilloida) from southeast Mexico with the description of a new species of *Monstrilla*.—Journal of Natural History 35:1433–1445.

———, & R. Gasca. 1998. *Cymbasoma bowmani* n.sp., a new monstrilloid (Copepoda: Monstrilloida) from a Caribbean reef, with notes on species variation.—Journal of Marine Systems 15(1–4):433–439.

———, & R. Palomares-García. 1995. A new species of *Monstrilla* (Copepoda: Monstrilloida) from a coastal system of the Baja California Peninsula, Mexico.—Journal of Plankton Research 17: 745–752.

Thompson, I. C. 1888. Copepoda of Madeira and the Canary Islands, with descriptions of new genera and species.—Journal of the Linnean Society of London (Zoology) 20:145–156.

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116(1):215–221. 2003.

Description of subadult *Pallisentis* (*Pallisentis*) *rexus* (Acanthocephala: Quadrigyridae) from the vertebrate intermediate host in Thailand with an examination of the species identity

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Abstract.—Subadults (considerably developed immatures) of the quadrigyrid acanthocephalan *Pallisentis rexus* Wongkham & Whitfield, 1999 are described from the swamp eel, *Monopterus albus* (Zieuw, 1793) in Thailand. The species is placed in the subgenus *Pallisentis.* Our specimens are compared with adults of the same species collected from the freshwater snakehead *Ophicephalus striata* Bloch also from Thailand. Discrepancies from the original description are noted, certain structures, e.g., proboscis hook roots and brain (cepahalic ganglion), are re-interpreted, and additional information provided.

The genus *Pallisentis* Van Cleave, 1928 was revised, three subgenera were erected, and a key to the valid species, and other taxonomic information were provided by Amin et al. (2000). About the same time, Wongkham & Whitfield (1999) described *Pallisentis rexus* from the freshwater snakehead, *Ophicephalus striata* Bloch, from the Chiang Mai Basin in Thailand. More recently, we have collected subadults of *P. rexus* from the swamp eel, *Monopterus albus* (Zieuw, 1793) from Bangkok, Thailand. Our specimens and type material examined by us shed considerably more light on the morphology and status of *P. rexus* which the present study reports in a comparative context.

Materials and Methods

Ten 40–80 cm long swamp eels, *M. albus,* were examined for parasites on 20 March 2001. The fish, obtained from a fish market in Bangkok, Thailand, had been collected from local streams. The 10 fish were infected with a total of 257 (range 5–74 per fish) ovoid whitish nodules in the body cavity especially at the external surface of the hind gut. The encapsulated worms were mostly alive when liberated from their cysts in fish physiological solution. Forty-two worms (16 males, 26 females) were refrigerated in tap water overnight then fixed and shipped in 5% formalin. They were subsequently transferred to 70% ethanol, stained in Mayer's acid carmine overnight then briefly destained, dehydrated in ascending concentrations of ethanol, cleared in graduated concentrations of terpineol in 100% ethanol, and whole mounted in Canada balsam.

Measurements are in µm unless otherwise stated. The range is followed by mean values (in parentheses). Width measurements refer to maximum width. Trunk length does not include proboscis, neck, or male bursa. The term subadults is used to describe the highly developed immature forms. They are practically identical to adults; all males and females were distended with sperm and ovarian balls, respectively. Specimens were deposited in the United States National Parasite Collection (USNPC) no. 91753. Beltsville, Maryland, U.S.A. Seven adult paratypes (3 males, 4 females) from the British Museum of Natural History (BMNH) (no. 1997.6.3.2-13) were also studied.

Results and Discussion

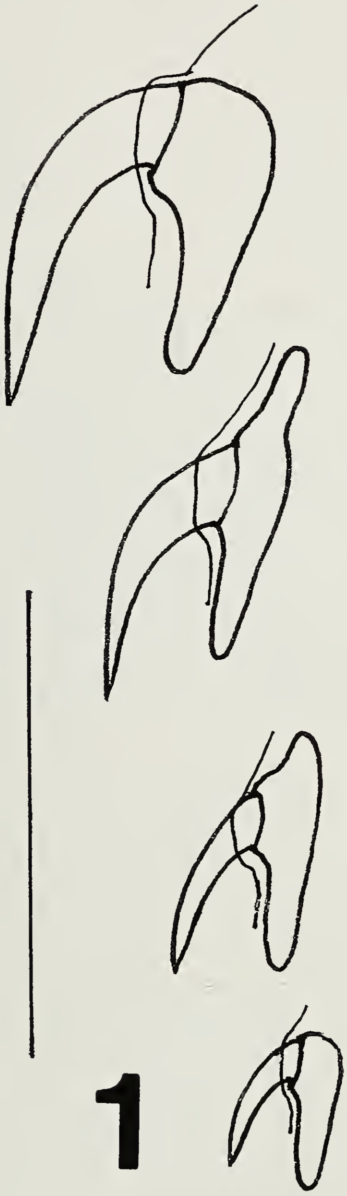
It is important to note that all characteristics of our *P.* (*P.*) *rexus* subadults listed in Table 1 and illustrated in Figures 1–3 match those observed in the adult paratypes borrowed from BMNH. The anatomy of the subadults is generally similar to that of the adults as described by Wongkham & Whitfield (1999). However, misinterpretations and omissions exist in the original description which otherwise was adequate. The quality of staining of paratypes produced faded and often indistinguishable structures, e.g., proboscis hook roots and cephalic ganglia, which readily explains Wongkham & Whitfield's (1999) version of worm anatomy. We shall report these discrepancies in the following section in an attempt to provide an accurate and complete description of the species.

Pallisentis rexus is placed in the subgenus *Pallisentis* according to Amin et al. (2000) because the proboscis hooks gradually decline in size posteriorly and the cement glands are long and with many giant nuclei.

Qualitative and quantitive traits of *P.* (*P.*) *rexus* subadults are provided and compared with those of adults, when available (Table 1). Measurements of subadults largely fell within the range of those reported for adults by Wongkham & Whitfield (1999). On the average, subadults, especially females, were relatively smaller than adults in only one character, trunk length. However, mean size of proboscis, proboscis hooks, proboscis receptacle, and lemnisci were somewhat greater in subadults than in adults. This observation is attributed to two factors: the apparent precocious state of development of subadult *P.* (*P.*) *rexus* (with sperm and ovarian balls) in their vertebrate intermediate host *M. albus*; this phenomenon has been observed in other acanthocephalans (Amin 1982); and the early development of attachment organs to ensure establishment of new recruits in the gut of the definitive host (see Amin 1986, 1987 for other examples).

Omissions in the original description include accounts of the giant nuclei of the hypodermis, lemnisci, and proboscis/neck, as well as some details of the male reproductive system and hook and spine insertion. We noted that one dorsal and one ventral elongate giant hypodermal nuclei were normally present. They were rarely absent on either side. Two similarly elongate giant nuclei were also noted within the proboscis retractor muscles in the proboscis/neck area. These nuclei are rarely reported in the genus *Pallisentis* but have been recently observed in *Pallisentis* (*Brevitritospinus*) *vietnamensis* Amin, Heckmann, Ha, Luc & Doanh, 2000. Each lemniscus had one large oval giant nucleus located at the level of the posterior half of the proboscis receptacle. Wongkham & Whitfield (1999) made no reference to the two large nuclei in the wall of Saefftigen's pouch which was properly described posterior to the cement reservoir (Fig. 1B) but not "at the posterior margin of cement gland" as stated in the Abstract (Wongkham & Whitfield 1999). No reference was made to the prominent sperm duct which ran parallel to the cement gland or the large common sperm duct which ran parallel to and overlapped Saefftigen's pouch and the posterior half of the cement reservoir. Proboscis hooks had variably elevated cuticular rims that were often prominent and body spines consistently had distinct cone-shaped cuticular sleeves that left only spine tips naked.

Misinterpretation in the original description includes accounts of the proboscis hook roots, brain (cephalic ganglion), collar and trunk spines, and position of the female gonopore. Each of these characteristics has important taxonomic significance that can not be overlooked. Three aspects of proboscis hook roots need to be addressed. All hook roots extend laterally for a short distance then loop back posteriorly in a direc-



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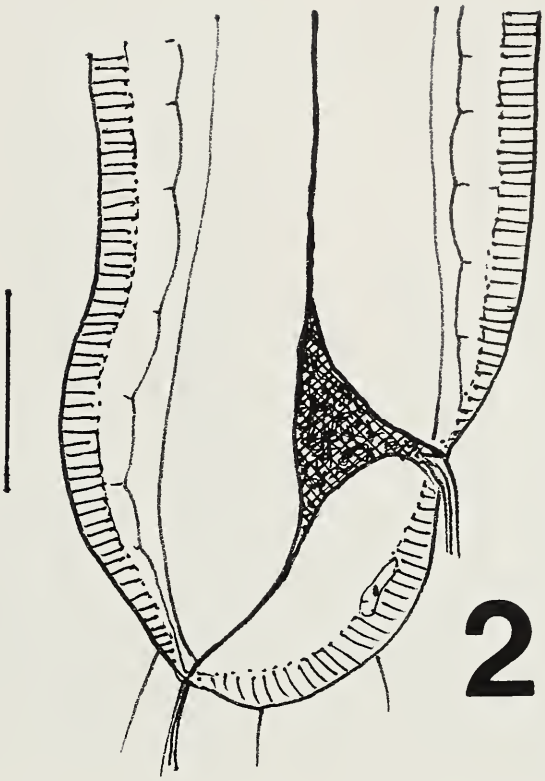

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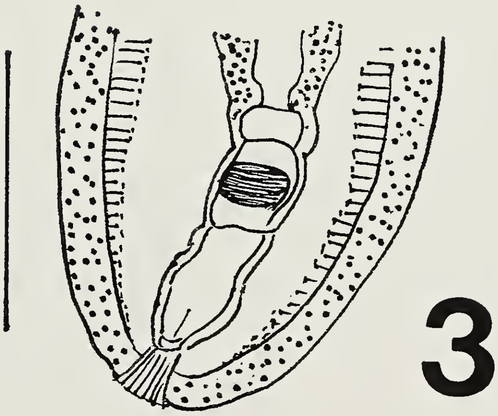

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Figs. 1–3. Diagnostic features of *Pallisentis* (*P.*) *rexus*. 1. One row of proboscis hooks and roots of female. 2. Posterior part of female proboscis receptacle showing triangular brain (cephalic ganglion) and ventro-lateral nerve cord passage through indented part of proboscis receptacle. 3. Posterior end of female showing slightly subterminal position (near terminal on ventral site) of gonopore. Scale bars = 100 μm.

tion paralleling that of the blade thus forming an inverted U-shaped structure (Fig. 1). In the original description, the angle between hook and root was shown to be about 120–140° inaccurately creating an inverted open V-shaped blade-root complex (Fig. 2A). Roots were only slightly shorter than blades in all circles with a ratio of 1:1.0–1.2, 1:1.4–1.5, 1:1.3–1.4, and 1:1.1–1.2 from anterior (Fig. 1). In the original description, roots were shown to be considerably shorter than blades in all circles with an unrepresentative ratio of 1:2, 1:2, 1:2, and 1:3 from anterior (Fig. 2A). In the same figure, Wongkham & Whitfield (1999) show the roots to be simple and with rounded corners. Actually, the roots do not have rounded corners and are not all simple. Hook roots in the second circle have conspicuously long anteriorly directed manubria and those in the third circle have prominent but shorter anteriorly directed manubria (Fig. 1).

The brain was not mentioned in the orig-

Table 1.—Diagnostic characteristics of *Pallisentis* (*Pallisentis*) *rexus* adults and subadults (measurements in μm unless otherwise stated).

	Adults (Wongkham & Whitfield 1999) (30 males, 30 females)	Subadults (this paper) (15 males, 17 females)
Trunk	Elongate, cylindrical	Cylindrical, enlarged anteriorly, curved ventrad posteriorly
Giant nuclei		Thin, elongate
Hypodermal	Not given	1 (rarely 2) dorsal, 1 ventral; rarely absent
Lemniscal	Not given	1 in each lemniscus
Proboscis/neck	Not given	2 (in retractor muscles)
Proboscis roots: hooks	1: 2–3 (Fig. 2A), inverted open V-shaped	1: 1.5, inverted U-shaped
Hook insertion simple	Simple	With variably elevated cuticular rims
Hook roots	Simple	Roots of second and third hooks with manubria
Brain	Oval, in mid-posterior part of proboscis receptacle (Fig. 1A); a misinterpretation of giant nucleus of lemniscus	Triangular, in indented ventro-posterior part of proboscis receptacle
Spines	"Most" with "broader roots"	Broadest at base, with cone-shaped cuticular sleeves
Collar	"Spear-shaped," split anteriorly (Fig. 2B)	Broad triangular, split longitudinally separated anteriorly, but tips fused
Trunk	"Spear-shaped," not split (Fig. 2C, D)	Thin triangular, split distally
Males		
Trunk (mm)	1.9–12.5 (6.02) by 0.20–0.55 (0.39)*	3.56–5.20 (4.97) by 0.29–0.49 (0.38)
Proboscis	100–150 (120) by 90–230 (200)	112–145 (130) by 175–220 (203)
First circle hooks	60–79 (68); 12 hooks	70–82 (77); 12 hooks
Second circle hooks	49–66 (57); 12 hooks	54–67 (61); 12 hooks
Third circle hooks	36–50 (43); 12 hooks	35–47 (42); 12 hooks
Fourth circle hooks	24–33 (28); 12 hooks	27–34 (31); 12 hooks
Proboscis receptacle	250–1,500 (550) by 90–220 (160)	572–738 (664) by 177–208 (200)
Lemniscus		
Long (mm)	0.15–3.05 (1.21) by 0.02–0.07 (0.05)	1.55–2.60 (2.19) by 0.05–0.07 (0.06)
Short	0.12–2.87 (1.02) by 0.02–0.07 (0.05)	1.41–2.24 (1.78) by 0.04–0.07 (0.06)
Collar spines		
Circles/no. per circle	12–17/6–18	14–16 (14.8)/7–20 (13.7)
Length	1–40 (24)	20–28 (23) (ant.); 20–28 (26) (post.)

Table 1.—Continued.

	Adults (Wongkham & Whitfield 1999) (30 males, 30 females)	Subadults (this paper) (15 males, 17 females)
Trunk spines	May reach anterior testis	May reach posterior testis
Circles/no. per circle	17–32/2–14	17–32 (25.4)/6–12 (ant.), 1–3 (post.)
Length	12–50 (28)	22–30 (26) (ant.); 20–25 (23) (post.)
Anterior testis	120–1,250 (500) by 40–220 (120)	347–572 (465) by 73–125 (100)
Posterior testis	110–1,140 (500) by 40–260 (110)	343–541 (433) by 83–135 (114)
Cement gland	140–1,600 (740) by 20–220 (100)	541–811 (671) by 62–104 (88)
No. nuclei	16–25	19–30
Females		
Trunk (mm)	2.3–33.0 (12.07) by 0.02–0.67 (0.41)	5.41–8.94 (7.57) by 0.28–0.48 (0.41)
Proboscis	120–160 (140) by 90–270 (200)	137–175 (155) by 183–240 (219)
First circle hooks	66–90 (78); 12 hooks	75–93 (83); 12 hooks
Second circle hooks	58–74 (66); 12 hooks	62–75 (69); 12 hooks
Third circle hooks	40–56 (48); 12 hooks	42–55 (49); 12 hooks
Fourth circle hooks	24–40 (32); 12 hooks	30–39 (34); 12 hooks
Proboscis receptacle	220–980 (590) by 110–240 (170)	520–801 (681) by 156–249 (206)
Lemniscus		
Long (mm)	0.48–4.05 (1.71) by 0.03–0.08 (0.06)	2.45–3.05 (2.70) by 0.05–0.06 (0.06)
Short (mm)	0.40–3.92 (1.41) by 0.03–0.08 (0.06)	1.73–2.55 (2.20) by 0.04–0.06 (0.06)
Collar spines		
Circles/no. per circle	12–19/8–18	12–17 (14.3)/2–20 (14.3)
Length	12–43 (29)	20–29 (22) (ant.); 25–30 (28) (post.)
Trunk spines		
Circles/no. per circle	29–59/9–17	41–63 (47.8)/5–14 (ant.), 1–3 (post.)
Length	12–64 (34)	25–31 (28) (ant.); 18–27 (21) (post.)
Gonopore	"Slightly subterminal"; ventral (Fig. 1C)	Slightly subterminal; not ventral
Eggs	95–116 (107) by 36–45 (42)	Not available

* Range (mean). Wongkham & Whitfield (1999) did not provide a separate measurement for trunk length but used "total body length" which also included the length of "elevated proboscis."

inal description but was drawn as an oval structure at the center of posterior part of the proboscis receptacle (Fig. 1A). Clearly this is a misinterpretation of the lemniscal giant nucleus which usually overlaps the proboscis receptacle in the same location. The brain is actually triangular in shape and is situated near the posterior part of the proboscis receptacle on the ventral side where the passage of the ventro-lateral nerve creates an indentation in its wall. No corresponding dorso-lateral nerve was observed. Only two other major nerves are evident, the anterior median and posterior median nerves (Fig. 2).

Collar and trunk spines were longest in the middle of the trunk then decreased in size towards both extremities. In males, anterior collar spines were 20–28 (23) long increasing to 20–28 (26) long in posterior most circle and anterior trunk spines were 20–30 (26) long decreasing to 20–25 (23) long in posteriormost circles. Corresponding measurements in females are 20–29 (22), 25–30 (28), 25–31 (28), and 18–27 (21), in the same order. All collar and trunk spines have cuticular cone-shaped sleeves encircling the whole spines except for their distal tip. The morphology of spines is revised as follows. Collar spines triangular, broadest at base, split longitudinally, fused at tips but separated into 2 or 3 branches anteriorly. Trunk spines are also triangular in shape but are split only posteriorly.

Some measurements in the original descriptions (Table 1) relating to some organs are questioned: maximum length of proboscis receptacle in males; minimum length of long and short lemnisci in males; minimum length of collar spines in males; minimum trunk width in females (at widest point); minimum proboscis width in both males and females; See Table 1 for details. One of these proboscis measurements is in error since the proboscis is consistently markedly wider than long.

The position of the female gonopore was described as "slightly subterminal" but illustrated in Fig. 1C of Wongkham & Whitfield (1999) in a completely ventral position some distance anterior to the posterior tip of the trunk. In our subadults, it was slightly subterminal (Fig. 3). In paratypes, it was in the same position as observed in our specimens and not as illustrated in Fig. 1C of Wongkham & Whitfield (1999).

Conclusions

The taxonomic implications of inadequacies in the original description of *P.* (*P.*) *rexus* are noted. The description of that species as revised in the present report is considered accurate and complete. It increases the number of species of the genus to 30. Twenty-six valid species were reviewed and keyed by Amin et al. (2000). The remaining three species are *Pallisentis chongqingensis* Liu & Zhang, 1993, *P. fotedari* Gupta & Sinha, 1991, and *P. jagani* Koul, Raina, Bambroo & Koul, 1991. The first of these three species belongs in the subgenus *Pallisentis* Van Cleave, 1928 and the latter two in the subgenus *Brevitritospinus* Amin, Heckmann, Ha, Luc & Doanh, 2000 according to Amin et al. (2000).

While Wongkham & Whitfield (1999) were correct in stating that the "invariable 12 proboscis hooks per circle . . . is the primary basis for considering the acanthocephalan under study as a new species," we add two other unique characteristics that distinguish *P.* (*P.*) *rexus* from all other species of the genus. These are the unique shape and location of the brain and the split nature of collar and trunk spines. The anatomy of proboscis hook roots is also unusual for the genus *Pallisentis* and represents an important distinguishing characteristic.

Literature Cited

Amin, O. M. 1982. Description of larval *Acanthocephalus parksidei* Amin, 1975 (Acanthocephala: Echinorhynchidae) from its isopod intermediate host.—Proceedings of the Helminthological Society of Washington 49:235–245.

———. 1986. Acanthocephala from lake fishes in Wisconsin: Morphometric growth of *Neoechinorhynchus cyclindtratus* (Neoechinorhynchidae) and taxonomic implications.—Transactions of the American Microscopical Society 105: 375–380.

———. 1987. Acanthocephala from lake fishes in Wisconsin: Morphometric growth of *Pomphorhynchus bulbocolli* (Pomphoorhynchidae).—Journal of Parasitology 73:806–810.

———. R. A. Heckman, N. V. Ha, P. V. Luc, & P. N. Doanh. 2000. Revision of the genus *Pallisentis* (Acanthocephala: Quadrigyridae) with the erection of three new subgenera, the description of *Pallisentis* (*Brevitritospinus*) *vietnamensis* subgen. et sp. n., a key to species of *Pallisentis*, and the description of a new Quadrigyrid genus, *Pararaosentis* gen. n.—Comparative Parasitology 67:40–50.

Gupta, V., & G. Sinha. 1991. On a new acanthocepalan parasite *Pallisentis fotedari* sp. nov. from the intestine of a marine fish *Clupea longiceps* Gunther from Puri Coast, Orissa.—Indian Journal of Helminthology 43:19–26.

Koul, P. L., M. K. Raina, P. Bambroo, & U. Koul. 1991. *Pallisentis jagani* sp. nov. from *Channa channa* in Jammu.—Indian Journal of Helminthology 43:124–128.

Liu, D., & Z. K. Zhang. 1993. A new species of the genus *Pallisentis* Van Cleave (Neoechinorhynchidea: Quadrigyridae).—Acta Zootaxonomica Sinica 18:5–9.

Van Cleave, H. J. 1928. Acanthocephala from China. I. New species and new genera from Chinese fishes.—Parasitology 20:1–9.

Wongkham, W., & P. J. Whitfield. 1999. *Pallisentis rexus* n. sp. (Eocanthocephala: Quadrigyridae) from snakehead fish, *Channa striata* Bloch, from Chiang Mai Basin, Thailand.—Thai Journal of Agricultural Sciences 32:241–261.

Zieuw, B. 1793. Biga Muraenarum, novae species.—Nova Acta Academiae Scientiarum Imperialis Petropolitanae 7:296–301.

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A new genus of the scleraxonian family Coralliidae (Octocorallia: Gorgonacea)

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Abstract.—A new genus of the family Coralliidae is established for seven species having longitudinally grooved axes and autozooids seated in distinctive axial pits with beaded margins.

During the preparation of a projected review of the family Coralliidae it became clear that the species currently assigned to the single genus *Corallium* Cuvier can be grouped in two morphological categories, (1) those having the autozooids seated in deep axial pits with margins conspicuously beaded especially near the tips of twigs, and (2) those without axial pits beneath the autozooids, although a depression without beaded margins may be present as in *C. rubrum.*

As constituted at the present time, the octocoral family Coralliidae consists of a single genus, *Corallium* Cuvier, 1797. Gray (1867) assigned the three species then known to three genera: *Corallium* Cuvier, 1797 for *C. rubrum* (Linnaeus, 1758); *Pleurocorallium* Gray, 1867 for *C. secundum* Dana, 1846; and *Hemicorallium* Gray, 1867 for *Corallium johnsoni* Gray, 1860. Ridley (1882:222) reviewed this arrangement and rejected *Hemicorallium* as a synonym of *Pleurocorallium.* Kükenthal (1924:47) considered both genera to be synonyms of *Corallium.*

Kükenthal (1924:47, 52) accepted the genus *Pleurocoralloides* Moroff 1902 from Japan, which was accepted also by Bayer (1956:70; later with reservations, 1964: 466). The original illustrations of *Pleurocoralloides formosum* and *P. confusum,* established by Moroff (1902:405, pl. 17, fig. 10, pl. 18, fig. 20; 404, pl. 17, fig. 8, pl. 18, fig. 19), clearly show that both species, as well as the genus *Pleurocoralloides,* can be referred to the family Melithaeidae. Although Moroff did not mention axial nodes and internodes, such features are suggested in the photograph of *P. confusum* on his plate 17, fig. 8. Moreover, the sclerites of both species as drawn are strongly suggestive of *Acabaria.* The polyps of *Pleurocorallium confusum* were said to have a fully retractile upper part and a low, projecting, wart-like calicular part; those of *Pleurocoralloides formosum* consisted of tentacular and projecting calicular parts with spindles forming triangular teeth projecting above the calyx margin. These characters do not occur in any coralliid, but are consistent with melithaeids. Consequently, *Pleurocorallium* sensu Moroff, 1902 (not Gray, 1867) becomes a probable synonym of *Acabaria* Gray, 1859. The correct identification of both species remains to be determined.

Seven species of *Corallium* share a skeletal character setting them unambiguously apart from all other species of the genus: the hard axis beneath each autozooid is marked by a distinct pit with a prominently beaded rim (Fig. 1), so there is no condition intermediate between axes with beaded pits and those without beaded pits. There is no ambiguity whatever about placing species in one group or the other, making the genus-group taxa within the Coralliidae more distinctive than many that are accepted in other families without question. The diagnostic character of the beading rim is also

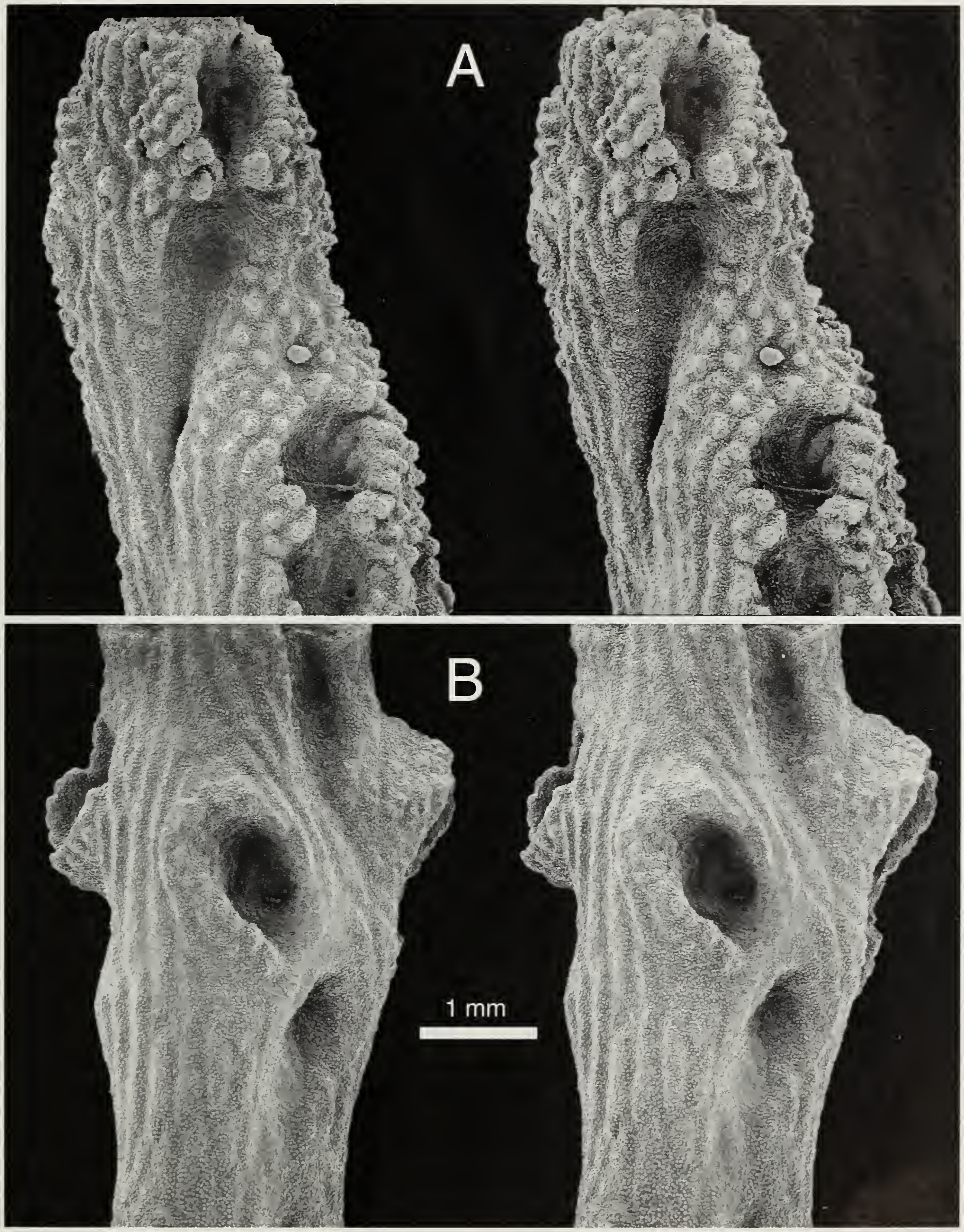

Fig. 1. Two stereo pairs illustrating the deep autozooid pits that are surrounded by beaded margins, and longitudinal grooves on the axis: Upper pair: *Paracorallium thrinax,* paratype, USNM 96511 (SEM 1331): lower pair: *Paracorallium nix,* part of holotype, SEM stub 1334. Both figures ×20.

illustrated for the species *B. tortuosum* by Bayer (1956: figs. 5b, 6c; 1993, pl. 16), for *C. thrinax* by Bayer (1996: figs. 2–3), and for *C. nix* by Bayer (1996: fig. 8).

Removal of the seven species from the genus, results in 19 species remaining in *Corallium*: *C. abyssale* Bayer, 1956 (Hawaii); *C. borneense* Bayer, 1950 (Borneo); *C. ducale* Bayer, 1955 (e. Pacific Mexico); *C. elatius* Ridley, 1882 (Mauritius and Japan); *C. halmaheirense* Hickson, 1907 (Indonesia); *C. imperiale* Bayer, 1955 (e. Pacific Mexico); *C. johnsoni* Gray, 1860 (northeast Atlantic); *C. kishinouyei* Bayer, 1996 (e. Pacific); *C. konjoi* Kishinouye, 1903 (Japan); *C. laanense* Bayer, 1956 (Hawaii); *C. maderense* Johnson, 1898 (e. Atlantic); *C. medea* Bayer, 1964 (w. Atlantic); *C. niobe* Bayer, 1964 (w. Atlantic); *C. regale* Bayer, 1956 (Hawaii); *C. reginae* Hickson, 1905 (Indonesia); *C. rubrum* (Linnaeus, 1758) e. Atlantic; *C. secundum* Dana, 1846 (Hawaii); *C. sulcatum* Kishinouye, 1903 (Japan); and *C. tricolor* Johnson, 1898 (e. Atlantic).

Paracorallium, new genus

Type species.—Corallium tortuosum Bayer 1956.

Seven species of *Corallium* characterized by axial pits with beaded rims are here recognized as members of a new genus morphologically distinct from *Corallium,* here called *Paracorallium*: *P. stylasteroides* (Ridley, 1882), *P. japonicum* (Kishinouye, 1903), *P. inutile* (Kishinouye, 1903), *P. salomonense* (Thomson & Mackinnon, 1910), *P. tortuosum* (Bayer, 1956), *P. thrinax* (Bayer & Stefani *in* Bayer, 1996), and *P. nix* (Bayer, 1996).

Diagnosis.–Coralliidae with autozooids seated in deep pits in the solid axis, pits with prominently beaded margins especially near branch tips; axis with strong longitudinal grooves. Sclerites including crosses, 6- and 8-radiate capstans that may be more or less asymmetrically developed, forming double clubs in some species. Long spindles have not been found in the autozooids of any species of *Paracorallium,* but otherwise the range of sclerites is the same as in species of *Corallium.*

Etymology.—Para, from Greek para = near + *Corallium,* from Greek *korallion* = coral. Neuter noun.

Distribution.—Indo-west Pacific, from Hawaii west to Japan and south to New Caledonia in the Pacific, and west to Mauritius and the Chagos Archipelago in the Indian Ocean. At moderate depths, all known records between 136 and 273 m.

In the following summary of nominal species at present referable to *Paracorallium,* the species are arranged according to their significant morphological characters.

I.—Species with smooth double clubs (double carafes, operaglasses) predominating in the coenenchymal sclerites, which also include 6-radiates, sometimes 7-radiates, and crosses; stubby rods in anthocodiae.

A.—Colonies branched on all sides, often anastomosing, major stems tend to remain in one plane, reaching a height of 12 cm. Cortex light red, axis white with pink tints.

Paracorallium inutile (Kishinouye, 1903), new combination

Corallium inutile Kishinouye, 1903:626; 1904:28, pl. 5, figs. 1, 2; pl. 7, fig. 7; pl. 9, fig. 18 (in Japanese); 1905:27, pl. 5, figs. 1, 2; pl. 7, fig. 7; pl. 9, fig. 18 (in English).

Distribution.—Japan: Shikoku, Kashiwajima, Tosa, 100–150 m.

B.—Colonies branched dichotomously, in one plane, reaching a height of 6 cm. Cortex white, axis white.

Paracorallium thrinax (Bayer & Stefani *in* Bayer 1996), new combination

Corallium thrinax Bayer & Stefani *in* Bayer 1996:206, figs. 1–6.

Distribution.—New Caledonia, 23°06.50′S, 167°53.74′E, 240 m.

II.—Species with no smooth double clubs in coenenchyme; predominant sclerites are 8-radiate forms but a few radiates may be somewhat asymmetrical, 6- and 7-radiates and crosses more or less abundant.

A.—Largest coenenchymal 8-radiates are 0.07 mm in length.

i.—Species with solid axis white.

a.—Cortex pale orange, calyces of autozooids yellow; many 6- and 8-radiates asymmetrical, tubercles of one side somewhat enlarged but not as smooth spheroids.

Paracorallium stylasteroides (Ridley, 1882), new combination

Corallium stylasteroides Ridley, 1882:225, pl. 9, figs. 1–4.—Bayer 1996:17, pl. 17.

Distribution.—Mauritius, 136 m.

b.—Cortex white, autozooids white; radiates symmetrical.

Paracorallium nix (Bayer, 1996), new combination

Corallium nix Bayer, 1996:213, figs. 7–10.

Distribution.—New Caledonia, 23°06.50′S, 167°53.74′E, 240 m.

ii.—Species with solid axis colored pink or red.

a.—Axis dark red with white center, becoming paler distally, branch tips nearly white. Colonies abundantly branched in one plane, with small prickle-like twigs on front and sides of branches; sclerites are 8-radiates and crosses.

Paracorallium japonicum (Kishinouye, 1903), new combination

Corallium japonicum Kishinouye, 1903: 623; 1904:22, pl. 1, figs. 1, 2; pl. 2; pl. 4, fig. 3; pl. 7, fig. 1; pl. 8, figs. 1–6 (in Japanese); 1905:21, pl. 1, figs. 1, 2; pl. 2; pl. 4, fig. 3; pl. 7, fig. 1; pl. 8, figs. 1–6 (in English).

Distribution.—Japan: Kiushu; off Tosa, Shikoku, 100–150 m.

b.—Axis pale pink, becoming darker distally; cortex pink or salmon-colored, polyps darker. Colonies branched irregularly in one plane, twigs crooked and tortuous. Coenenchymal sclerites are 8-radiates and crosses; anthocodiae with small rods and crosses.

Paracorallium tortuosum (Bayer, 1956), new combination

Corallium tortuosum Bayer, 1956:82, figs. 5b, 6c, 8e–g.

Corallium salomonense tortuosum.—Bayer, 1993:16, pls. 10, 14–16.

Distribution.—Hawaii: Pailolo Channel, 153–273 m.

B.—Largest coenenchymal radiates reach a length of 0.1 mm or more. Fully developed branching unknown; coenenchyme yellowish, anthocodiae orange, axis presumably white or pale pink in color.

Paracorallium salomonense (Thomson & Mackinnon, 1910), new combination

Sympodium salomonense Thomson & Mackinnon, 1910:168, pl. 12, figs. 11, 12; pl. 13, fig. 15a, b.

Corallium salomonense.—Bayer, 1993:14, pls. 10–13.

Distribution.—Salomon, Chagos Archipelago, Indian Ocean, 217–272 m.

Remarks

Authentic specimens of *P. japonicum* and *P. inutile* received from K. Kishinouye, and Ridley's slide of the sclerites of *P. stylasteroides* were available for examination. Other than *P. tortuosum,* which is represented by numerous specimens from five stations made in the Hawaiian Islands by the U.S. Fish Commission steamer *Albatross,* no species of *Paracorallium* is represented by specimens from more than a single locality. Consequently, nothing can be said about possible individual and geographical variation. All colonies of *P. tortuosum* from Hawaii (see Bayer 1993: pl. 10, lower figures) are consistent in growth form, and bear a strong resemblance to the unique type specimen of *P. stylasteroides* from Mauritius, now lost (see Ridley 1882: pl. 9, fig. 1), but sclerites of Ridley's slide (see Bayer 1993: pl. 17) are sufficiently distinct from those of *P. tortuosum* (see Bayer 1956:85, fig. 8e–g; 1993, pls. 14, 15) to justify specific separation. However, the sclerites of original material of *P. salomonense* (see Bayer 1993: pls. 11–13, and compare Thomson & Mackinnon 1910: pl. 13, fig. 15a, b) are morphologically so similar to those of *P. tortuosum* that the latter was treated as a geographical subspecies of *P. salomonense,* in spite of the lack of fully developed colonies of the latter. Furthermore, the growth form of *P. nix* from New Caledonia resembles in some ways that of *P. tortuosum* and *P. stylasteroides,* and the sclerites of all three are generally similar. Pending the discovery of additional specimens, these nominal species are maintained as distinct but might in future be treated as a single variable species widely distributed from Hawaii to New Caledonia in the Pacific and Mauritius and the Chagos Archipelago in the Indian Ocean.

Structure of the solid axis.—Investigations of *Corallium rubrum* (Linnaeus) by Grillo et al. (1993), summarized by Allemand (1993), definitively refuted the generally accepted theory of axis formation in *Corallium* proposed by Lacaze-Duthiers (1864), which also had been rejected by Hickson (1907:2), who stated that "It is clearly incorrect, from these [Hickson's] observations, to describe the axis of the Coralliidae as the 'result of spicules fused together' " by cement substance. Hickson held that "the evidence of comparative anatomy suggests very forcibly that [the cement substance] is not formed by the activity of the scleroblasts but by a modification of the chemical character of the mesogloea."

However, the theory of Lacaze-Duthiers subsequently was accepted by authors as late as Weinberg (1976:99, pl. 20; 1993:51, fig. 11), who published scanning electron micrographs of the axial surface showing presumed sclerites embedded in the calcareous mass.

Lawniczak (1987) presented evidence that in *C. johnsoni* the axis is composed initially of "fibrous" calcite crystals followed by "lamellar" secondary thickening, without participation of sclerites. On the other hand, Grillo et al. showed that in *C. rubrum* the axis is initially composed of coenenchymal sclerites that form a core subsequently overgrown by secondary thickening consisting of sheets of rectilinear calcite crystals produced by an axis epithelium cytologically indistinguishable from the multicellular scleroblasts that produce the free mesogloeal sclerites. They "suggest that the axis epithelium treats the incipient skeleton as if it were the core of a single sclerite" and that the scleroblasts are a fragmented axis epithelium.

The discrepancy between the results of Lawniczak's investigation of *C. johnsoni* and those of Grillo et al. of *C. rubrum* led the latter authors to conclude that "the family Coralliidae may exhibit a broad spectrum of octocoral skeletal structures, including those that are independent of sclerites [sic] formation . . ." (1993:127). They conclude that ". . . the further study of this species [i.e., *C. rubrum*] and other coralliids has merit for both systematics and the general process of carbonate skeleton formation in marine invertebrates."

No fully formed sclerites more or less completely incorporated in the axial mass were found on the axial surface, as has been observed in *Corallium kishinoueyi* (Bayer 1996: 218, figs. 16, 17), were seen in any species of *Paracorallium.* The tubercles on the axial surface at the summit of terminal branches of *P. thrinax* and *P. tortuosum* resemble the tubercles of sclerites more closely than axial protuberances. Roughly transverse fractures of axis of *P. inutile* and *P. tortuosum* exposed former surface features but no morphological features that could be interpreted unequivocally as parts of sclerites even at the center of the axis. Numerous circular structures could as reasonably be interpreted as fragments of axial protuberances as the broken ends of the primary axis of sclerites. Consequently, it is probable that sclerites have an insignificant or even nonexistent role in axis formation in *Paracorallium,* possibly with scleroblasts more integrated and functioning as a fragmented axis epithelium forming the axis as if it were one large sclerite. The bulk of the axial mass consists of fascicles of rectilinear calcite crystal oriented in various directions and commonly appearing "cross bedded."

Acknowledgments

This study was based upon examination of specimens assembled over many years. K. Kishinouye presented specimens used in the preparation of his classic work on Japanese precious corals. Material from Hawaii was obtained by operations of the U.S. Fish Commission steamer *Albatross* during the Hawaiian cruise in 1902. Ridley's slide preparation of sclerites of the holotype of *Corallium stylasteroides* were provided by the Natural History Museum, London. Specimens from New Caledonia collected during expeditions of MUSORSTOM were made available by Alain Crosnier of the Muséum National d'Histoire Naturelle, Paris. Thomson & Mackinnon's type material of *Sympodium salomonense* was made available by the Natural History Museum, London, and the Zoological Museum of Cambridge University. Sincere appreciation is expressed to all of those past and present who provided this essential material for research.

Literature Cited

Allemand, D. 1993. The biology and skeletogenesis of the Mediterranean red coral, a review.—Precious Corals & Octocoral Research 2:19–39, frontisp. 1; figs. 1–18.

Bayer, F. M. 1950. A new precious coral from North Borneo.—Journal of the Washington Academy of Sciences 40(2):59–61.

———. 1955. Contributions to the nomenclature, systematics, and morphology of the Octocorallia.—Proceedings of the United States National Museum 105:207–220.

———. 1956. Descriptions and redescriptions of the Hawaiian octocorals collected by the U.S. Fish Commission steamer "Albatross" (2. Gorgonacea: Scleraxonia).—Pacific Science 10(1):67–95, 11 figs.

———. 1964. The genus *Corallium* (Gorgonacea: Scleraxonia) in the western North Atlantic Ocean.—Bulletin of Marine Science of the Gulf and Caribbean 14(3):465–478, figs. 1–7.

———. 1993. Generic reassignment and affinities of *Sympodium salomonense* Thomson & Mackinnon (Coelenterata: Octocorallia).—Precious Corals & Octocoral Research [Tokyo] 1:14–19, pls. 10–17.

———. 1996. Three new species of precious coral (Anthozoa: Gorgonacea, genus *Corallium*) from Pacific waters.—Proceedings of the Biological Society of Washington 109(2):205–228, figs. 1–19.

Cuvier, G. [1797]. Tableau élémentaire de l'histoire naturelle des animaux. Paris, Baudouin. Pp. i–xvi + 1–710, pls. 1–14.

Dana, J. D. 1846. Zoophytes.—United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. Vol. 7. i–vi + 1–740 pp., 45 text figs. Philadelphia: Lea and Blanchard. Atlas, Zoophytes. 61 pls., 1849.

Gray, J. E. 1859. Description of some new genera of lithophytes or stony zoophytes.—Proceedings of the Zoological Society of London 1859:479–486.

———. 1860. Description of a new coral (*Corallium johnsoni*) from Madeira.—Proceedings of the Zoological Society of London 1860:393–394, pl. 18.

———. 1867. Additional note on *Corallium johnsoni.*—Proceedings of the Zoological Society of London 1867:125–127.

Grillo, M.-C., W. M. Goldberg, & D. Allemand. 1993. Skeleton and sclerite formation in the precious red coral *Corallium rubrum.*—Marine Biology 117:119–128, figs. 1–5.

Hickson, S. J. 1905. On a new species of *Corallium* from Timor.—Proceedings, Koninklijke Academie van Wetenschappen, Amsterdam 8:268–271.

———. 1907. Die Alcyoniden der Siboga-Expedition I. Coralliidae.—Siboga-Expeditie Monogr. 13c: 1–8, pl. 1.

Johnson, J. Y. 1898. Short diagnoses of two new species of Coralliidae from Madeira.—Annals and Magazine of Natural History (7)2:421–422.

Kishinouye, K. 1903. Preliminary note on the Coralliidae of Japan.—Zoologischer Anzeiger 26(705):623–626. (27 July).

———. 1904. Sango no kenkyu.—Suisan chosa hokoku 14(1):1–31, pls. 1–9. (25 August).

———. 1905. Notes on the natural history of corals.—Journal of the Imperial Fisheries Bureau 14(1): 1–32, pls. 1–9. (28 Jan 1905).

Kükenthal, W. 1924. Gorgonaria.—Das Tierreich 47: i–xxviii + 1–478, 209 figs. Berlin and Leipzig, Walter de Gruyter & Co.

Lacaze-Duthiers, H. de. 1864. Histoire naturelle du corail. Pp. i–xxv + 1–371, pls. 1–20. Paris, J.B. Bailliere et Fils.

Lawniczak, A. 1987. Les modalités de croissance de l'axe calcaire chez *Corallium johnsoni* (Cnidaria: Gorgonaria: Scleraxonia).—Senckenbergiana maritima 19(3/4):149–161, ill.

Linnaeus, C. 1758. Systema naturae. Editio decima, reformata. 1. Pp. i–iv + 1–824. Holmiae: Impensis Direct. Laurentii Salvii.

Moroff, T. 1902. Studien über Octocorallien.—Zoologische Jahrbücher (Syst.) 17:363–410, pls. 14–17.

Ridley, S. O. 1882. On the arrangement of the Coralliidae, with descriptions of new or rare species.—Proceedings of the Zoological Society of London 1882:221–233, pl. 9.

Thomson, J. A., & D. L. Mackinnon. 1910. Alcyonarians collected on the Percy Sladen Trust Expedition by Mr. J. Stanley Gardiner. Part 2, the Stolonifera, Alcyonacea, Pseudaxonia, and Stelechotokea.—Transactions of the Linnean Society of London (2) 13(2):165–211, pls. 6–14.

Weinberg, S. 1976. Revision of the common Octocorallia of the Mediterranean circalittoral. I. Gorgonacea.—Beaufortia 24(313):63–104, pls. 1–20.

———. 1993. Il corallo rosso e la ricerca scientifica nei secoli. Pp. 37–60 *in* F. Cicogna and R. Cattaneo-Vietti, eds., Il corallo rosso in Mediterraneo: Arte, Storia e Scienza. Roma. Ministero delle Risorse Agricole, Alimentarie Forestoli.

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New taxa and combinations of *Ageratina* from Ecuador, Colombia, and Venezuela (Eupatorieae: Oxylobinae)

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Abstract.—Thirteen new species, one new combination, and one new forma of *Ageratina* are validated, mostly from from Ecuador, some from Colombia and Venezuela. The new taxa in subg. *Ageratina* are *Ageratina adenophoroides, A. campii, A. cumbensis, A. cumbensis* f. *glandulifera, A. ewanii, A. parviceps, A. pseudogracilis, A. rosei, A. serrulata, A. villonacoensis,* and *A. websteri,* with a new combination for *A. rhodopappa* f. *glandularis.* New species in subg. *Andinia* are *A. harlingii, A. maranonii,* and *A. regalis.*

Efforts to complete the tribe Eupatorieae for the Flora of Ecuador have necessitated a review of species of *Ageratina* in and near Ecuador. The result has been the recognition of 26 species in Ecuador, including 17 of subg. *Ageratina* and 9 of subg. *Andinia.* Ecuadorian species include the common *A. pichinchensis* (H.B.K.) R.M.King & H.Rob., *A. sodiroi* (Hieron.) R.M.King & H.Rob., some primarily more northern species, such as *A. glyptophlebia* (B.L.Rob.) R.M.King & H.Rob. and *A. tinifolia* (H.B.K.) R.M.King & H.Rob. and a specimen of the primarily more southern species, *A. glechonophylla* (Less.) R.M.King & H.Rob. One name that has been used in previous studies now falls into synonymy, *A. exerto-venosa* (Klatt) R.M.King & H.Rob. proves to be the same as *A. fastigiata* (H.B.K.) R.M.King & H.Rob.

For useful references on *Ageratina* see King and Robinson (1970, 1990) and Turner (1997).

Ten of the new species are known from Ecuador, *Ageratina pseudogracilis* only from Venezuela and two species, *A. ewanii* and *A. serrulata* only from Colombia. The latter three species all have similar small shrubby habits and glabrous to nearly glabrous achenes. The differences are discussed most completely under *Ageratina serrulata.*

Measurements of heights of heads in the following descriptions include involucres, corollas, and pappus, but exclude emergent styles.

Ageratina (*Ageratina*) *adenophoroides* H.Rob., sp. nov.
Fig. 1

Type: Ecuador. Bolivar: Carretera Chillanes—Tiquibuso, en restos de vegetación y sembríos en vegetación de borde de carratero, en el sector de San José de Guayabal, 01°55′S, 79°05′W, 2100 m, 3 Sep 1987, *Zak & Jaramillo 2701* (holotype US, isotype MO).

Ad *A. adenophora* in glandulis stipitatis numerosis similis sed in laminis foliorum apice acuminatis et in floribus e bracteis involucri vix excedentibus differt.

Subshrub to 6 dm high, vegetative branches not seen; stems brownish, terete, densely covered with minute stipitate glandular hairs; internodes 7–10 cm long. Leaves opposite, petioles 1.0–2.5 cm long, slightly broadened distally; blades membranaceous, broadly ovate, 5–8 cm long, 3–5 cm wide, base broadly obtuse to subtruncate, acuminate at petiole, margins serrate with 15–20 short teeth, apex abruptly acuminate, surfaces concolorous, dark dull green, adaxial surface evenly pilosulous,

Ageratina adenophoroides H.Rob.
Holotype

det. H. Robinson, U. S. National Herbarium, 2001

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ASTERACEAE
Eupatorium
Ageratina glandulifera (Hieron.) K.&R.

Prov. BOLIVAR: carretera Chillanes-Tiouibuso. En restos de vegetación y sembrios en vegetación de borde de carretero, en el sector de San José de Guayabal.
01°55'S 79°05'W 2100 m

Sufrutex de 60 cm, capitulos cremas.

3 septiembre 1987
Vlastimil Zak & Jaime Jaramillo 2701
MISSOURI BOTANICAL GARDEN HERBARIUM (MO)

Fig. 1. *Ageratina adenophoroides* H.Rob., holotype, *Zak & Jaramillo 2701* (US).

densely puberulous on main veins, abaxial surface pilosulous on larger veins, puberulous on veinlets; (3–)5–plinervate from 1–2 mm above base, with main secondary veins spreading at ca. a 30° angle. Inflorescences terminal and from distal axils, branches spreading at an angle of 40–45°, covered with minute stipitate glands, ending in rather dense broadly corymbiform clusters of heads; peduncles 4–8 mm long. Heads 5–6 mm high, involucral bracts ca. 15, mostly subequal, elliptical-lanceolate, 4.5–5.5 mm long, ca. 1 mm wide, with immediate tips thinly membranaceous and somewhat acute, mostly yellowish-green, puberulous and narrowly bicostate outside. Florets ca. 25–30 in a head; corollas whitish, ca. 3.3 mm long, basal tube slender, ca. 1.5 mm long, distal part of throat and lobes pilosulous, throat narrowly campanulate, ca. 1.5 mm long, lobes narrowly triangular, ca. 0.4 mm long; anther thecae ca. 0.8 mm long, white. Achenes 1.8–2.2 mm long, fusiform, with short setulae along ribs, many short setulae clustered at carpopodium; carpopodium annuliform; pappus whitish, of ca. 20 capillary bristles ca. 3.5 mm long, slightly but distinctly broadened distally.

Ageratina adenophoroides is known only from the type collection from 2100 m elevation in south-central Ecuador. The numerous stipitate glands and the long petioles broadened toward the blade are somewhat reminiscent of *A. adenophora* (Spreng.) R.M.King & H.Rob. of Mexico and Central America, which has become weedy in Hawaii and Australia. The Ecuadorian species is easily distinguished by the abruptly acuminate leaf tips and the florets of the heads scarcely exceeding the involucral bracts. The carpopodium is unusually short for a member of subg. *Ageratina*.

Ageratina* (*Ageratina*) *campii H.Rob., sp. nov.

Fig. 2

Type: Ecuador. Cañar: North rim of valley of Río de Cañar, between Suscal and Chontamarca, 25 Apr 1945, *Camp (Gilar) E-2869* (holotype US, isotype NY).

In foliis primariis valde cordatis late divericate triplinervatis et in inflorescentiis cymiformibis et in floribus in capitulo 50 vel ultra distincta.

Perennial herbs, woody at base, to 5 dm high, with 1 or 2 pairs of ascending branches; stems brownish to reddish, terete, puberulous with reddish hairs; internodes mostly 2–8 cm long, in some parts fistulose. Leaves opposite, petioles 0.5–2.0 cm long; blades broadly ovate, thinly papyraceous, bright green with purplish tinge, 2.5–6.0 cm long, 2–5 cm wide, base cordate, with deep narrow sinus on larger leaves, margins with 8–10(–20) blunt teeth, coarse and often double from sinus to near tip in larger leaves, apex short-acute, adaxial surface sparsely pilosulous, abaxial surface somewhat paler, with hairs mostly along veins; triplinerved from sinus at base of blade, secondary veins usually spreading at a 45–50° angle, reaching only midleaf, veins sometimes reddish. Inflorescences terminal on leafy stems, rather laxly cymiform, with 8–15 heads; branches puberulous; peduncles 4–14 mm long. Heads 5–7 mm high; involucral bracts 23–25, oblong-lanceolate, ca. 6 mm long, 1.0–1.2 mm wide, outer bracts green, inner stramineous, apices short-acute, inner membranaceous, fringed with many fine hairs, outside sparsely puberulous. Florets 50–70 in a head; corollas whitish, ca. 4 mm long, pilosulous on lobes, few hairs on throat, basal tube ca. 1.5 mm long, throat ca. 2 mm long, lobes 0.5–0.6 mm long; anther thecae ca. 0.9 mm long, whitish. Achenes ca. 2.3 mm long, fusiform, with many setulae on ribs and sides; pappus whitish to pinkish or reddish, of ca. 22 capillary bristles, to 4 mm long, not broadened distally.

Ageratina campii is known only from the type collection from south-central Ecuador. The species seems most distinct in the deeply cordate leaves of the main stems with a widely spreading triplinerved main veins and the 50–70? florets in the heads.

Fig. 2. *Ageratina campii* H.Rob., holotype, *Camp E-2869* (US).

The inflorescence also seems more cymiform than in other species. The collection data mention the purplish tinge of the leaves, and the deep pink to reddish pappus, the reddish condition being correlated with a deeper colored, reddish, stem and leaf veins. However, in the dried material, only the pinkish color of some of the pappus bristles is evident.

Ageratina* (*Ageratina*) *cumbensis H.Rob., sp. nov.

Fig. 3

Type: Ecuador. Azuay: 30 km S of Cumbe on road to Saraguro, 9800 ft, 26 Jan 1979, *King & Almeda 7806* (holotype US, isotypes CAS, MO).

In plantis fruticosis in ramis virgatis plerumque 3–4 dm altis et in petiolis brevibus distincta.

Wiry often subscandent shrubs 3–4(–10) dm tall, moderately to rather densely branched; stems brownish, terete, puberulous with mostly reddish hairs; internodes 1–6 cm long. Leaves opposite, petioles 1–3(–6) mm long; blades broadly ovate, mostly 1–2 cm long, 7–18 mm wide, base subcordate, margins serrulate with 4 or 5 small blunt teeth, apex obtuse to broadly acute, adaxial surface dark green, glabrous or sparsely pilosulous, abaxial surface paler green to reddish, pilose mostly on veins; triplinervate from base of blade, secondary veins spreading at a 35–40° angle. Inflorescences terminal on leafy stems, with ascending branches ending in few loosely cymosely disposed heads; peduncles 6–30 mm long, puberulous with reddish hairs, with minute stipitate glands in forma *glandulifera*. Heads 7–8 mm long; involucral bracts ca. 15, eximbricate, narrowly elliptical to lanceolate, 4–6 mm long, 0.8–1.0 mm wide, apices acute, firm, puberulous with sparse reddish hairs externally. Florets 30–40 in a head; corollas whitish, 3.5–4.5 mm long, basal tube slender, ca. 1.5 mm long, throat narrowly campanulate, 1–2 mm long, lobes ca. 0.5 mm long, with few to many hairs outside; anther thecae ca. 0.9 mm long, whitish. Achenes ca. 1.5 mm long, fusiform, sparsely to rather densely setulose along ribs; carpopodium cylindrical; pappus often rather pink, 3.5–4.5 mm long, fragile at base, not or scarcely broadened distally.

Ageratina cumbensis occurs in southern Ecuador in páramo habitats (mostly above 3000 m). The shrubby habit with slender stems and small, subsessile leaves is distinctive. Specimens have been determined in the past as *Ageratina cutervensis* (Hieron.) R.M.King & H.Rob.; that Peruvian species differs by the tendency of dried leaves to blacken and by the coarse yellowish hairs of the stems.

Ageratina cumbensis f. *cumbensis*

Peduncles puberulous with reddish hairs, without glands.

Paratypes: Ecuador. Chimborazo: Road/trail from campsite above Río Algo (85 km from Guardiana Alais by road from Alao), NNE to pass/continental divide (via old route to Huamboya), 3350–3550 m, 20 May 1990, *King & Judziewicz 10168* (MO, US). Azuay: vicinity of Nabón, 25–26 Sep 1918, *Rose, Pachano & Rose 23014* (US). "Oriente Border," Parámo del Castillo and surrounding forested areas, crest of eastern cordillera on trail between Sevilla de Oro and Méndez, 9000–10,000 ft, 18 Aug 1945, *Camp E-4822* (NY, US). Along road to Loja, ca. 13 km generally S of Cumbe, ca. 10,900 ft, 4 Feb 1974, *King 6713* (MO, US). Along road to Loja, ca. 25 km S of Cumbe, ca. 10,800 ft, 5 Feb 1974, *King 6728* (MO, US). Muletrack Sevilla de Oro–Méndez, at pass and adjacent slopes, Páramo de Castillo, 02°48′S, 78°36′W, 3250–3500 m, 16 Sep 1976, *Øllgaard & Balslev 9584* (AAU, US). About 7 km SE of Jima on road towards San Miguel de Cuyes, 3100 m, 27 Apr 1985, *Harling & Andersson 24688* (GB, US). Loja: Parque Nacional Podocarpus, at pass on road Loja–Zamora, 03°58′S, 79°07′W, 2850–2960 m, 11 June 1984, *Øllgaard & Madsen 74731*

Ageratina cumbensis H.Rob.
det. Harold Robinson (US), July 2001

K & A

7806

PLANTS OF ECUADOR

Cytological and/or Biochemical Vouchers

ROBERT MERRILL KING 26 January 1979
AND FRANK ALMEDA, NO 7806

Ageratina cutervensis (Hieron.) K & R

Azuay: 30 km S of Cumbe on the road to Saraguro at an elevation of 9800 ft.

wiry herb to 1 ft. tall. Local.

Specimens collected for the United States National Herbarium, Smithsonian Institution and the Herbarium of the California Academy of Sciences

Fig. 3. *Ageratina cumbensis* H.Rob., holotype, *King & Almeda 7806* (US).

(AAU, QCA, US). Parque Nacional Podocarpus, pass on road Yangana Valladolid (Nudo de Sabanilla), 04°27′S, 79°08′W, 2750–2900 m, 28 Feb 1985, *Øllgaard, Laegaard, Thomsen, Korning & Illum 58392, 58402* (AAU, QCA, US). Nudo de Sabanilla, W slope ca. 10 km above Yangana on road to Valladolid, 2500 m, 3 Apr 1985, *Harling & Andersson 23582* (GB, US). In páramo of "el Tiro," Northern terminus of Podocarpus National Park, 500 m from Loja–Zamora highway, 03°59′S, 79°08′W, 2940–2970 m, 9 June 1993, *Keating 141* (US). Páramo above refugio de Cajanuma (Centro de Informacion), Podocarpus National Park, 04°07′S, 79°30′W, 3250–3404 m, 31 Jul 1993, *Keating 402* (US). Cordillera de Las Lagunitas, Amaluza–Jimbura–Zumba, km 41, 04°44′55″S, 79°25′13″W, 3270 m, 22 Nov 1994, *Jørgensen, Ulloa, León, Vargas & Lozano 782* (LOJA, MO, QCA, QCNE, US). Páramo above Refugio de Cajanuma (Centro de Información), Podocarpus National Park, 04°07′S, 79°09′30″W, 3200–3400 m, 2 Jul 1996, *Keating 511* (US). Morona-Santiago: Trail Alao–Huamboya, E slopes above and around La Magdalena, 01°47′S, 78°24′W, 3550–3700 m, 7 May 1982, *Øllgaard, Holm-Nielsen, Andreasen, Larsen, Kvist & Jensen 38310* (AAU, QCA, QNA, US).

Ageratina cumbensis f. ***glandulifera*** H.Rob., forma nov.

Type: Ecuador. Azuay: 8–10 km S of Cumbe on road to Loja, 9050–9400 ft, 22 Jan 1979, *King & Almeda 7756* (holotype US, isotypes CAS, MO).

A varietatis typicis similis sed in pedunculis stipitate glanduliferis differt.

Peduncles with minute stipitate glands mixed with puberulence.

Paratype: Ecuador. Azuay: Along road to Loja, ca. 6 km generally SE of Cumbe, ca. 9600 ft, 4 Feb 1974, *King 6693* (MO, US).

Ageratina (***Ageratina***) ***ewanii*** H.Rob., sp. nov.

Fig. 4

Type: Colombia. Nariño: Cordillera Oriental, W slide of Volcán Doña Juana, 3000 m, rare small herbaceous sp. about 30 cm high, among soil pockets of boulder slide, 16 Dec 1944, *Ewan 16618* (holotype US; isotype US).

In habitis ad *A. gracilem* similis sed in foliis pilosis et in acheniis subglabrous et in bracteis involucri exterioribus brevioribus distincta.

Subshrub ca. 30 cm high, to 20 cm wide, densely branched; stems brownish, densely pilose with strongly ascending hairs; internodes 4–13 mm long. Leaves opposite, petioles 2–3 mm long; blades stiffly herbacous, ovate, mostly 7–15 mm long, 3–9 mm wide, base rounded, margins with 5–7 minute appressed teeth, apex acute, adaxial surface puberulous along insculpate main veins, smaller hairs between veins and near margins, abaxial surface densely puberulous with coarse often pale hairs along exsculpate larger veins; triplinervate near base, secondary veins ascending at ca. a 30° angle. Inflorescences densely corymbiform, branches strongly ascending; peduncles 3–8(–12) mm long, densely puberulous with dark hairs. Heads 5–6 mm high; involucral bracts ca. 15, narrowly oblong, 2–4 mm long, apices broadly to narrowly acute, outer 7 or 8 bracts shorter, thicker, puberulous externally, inner bracts with smooth, glabrous, membranaceous tips exserted. Florets 25–30 in a head; corollas white, 3.0–3.2 mm long, basal tube ca. 1.2 mm long, throat ca. 1.2 mm long, lobes ca. 0.8 mm long, pilosulous outside; anther thecae ca. 0.8 mm long, whitish. Achenes ca. 1.8 mm long, nearly glabrous, sometimes with few minute setulae distally on ribs; carpopodium cylindrical; pappus whitish, 2.7–3.0 mm long, of ca. 25 fragile capillary bristles, not or slightly broadened distally.

Ageratina ewanii is known only from the type collection. The specimen was previously identified as *A. gracilis,* a common Colombian species with a similar habit but a more decumbent base and glabrous leaves. The new species is most distinctive in the many outer involucral bracts usually distinctly shorter than the inner bracts.

Fig. 4. *Ageratina ewanii* H.Rob., holotype, *Ewan 16618* (US).

Ageratina (*Andinia*) *harlingii* H.Rob., sp. nov.
Fig. 5

Type: Ecuador. Loja: 15 km S of Loxa, 2450 m, 12 Jul 1959, *Harling 5822* (holotype S).

A speciebus pluribus subgeneribus Andiniis in caulibus glandulis stipitatis dense obtectis distincta.

Subshrubs or shrubs 0.2–0.5 m high, with often dense branching in distal subverticillate clusters; stems dark brown, densely covered with short, stout, yellowish, stipitate glands; internodes mostly 1–3 cm long. Leaves opposite, nearly sessile, petioles 1–2 mm long; blades thinly coriaceous, oblong-ovate, mostly 15–32 mm long, 10–25 mm wide, base rounded, margins serrulate with 6–15 teeth, apex short-obtuse, adaxial surface glabrous, smooth or somewhat glossy, with prominulous veins and veinlets, with few or no glandular dots, abaxial surface with prominent veins and prominulous veinlets, densely gland-dotted; triplinervate from 1–2 mm above base of blade, veins ascending at ca. a 35° angle from midrib, with 1 or 2 pairs of weak widely spreading distal secondary veins. Inflorescences terminal on branches, in corymbiform clusters mostly 4–5 cm wide, sometimes with clusters clustered; branches with stout stipitate glands; foliiform bracts and bracteoles subimbricate, 5–10 mm long, 3–7 mm wide; peduncles 1–2 mm long above uppermost bracteole. Heads ca. 10 mm high, 6 mm wide; involucral bracts 12–14 in ca. 2 series, 5–6 mm long, outer bracts thinly herbaceous, oblong-elliptical, ca. 5 mm long, subacute, with glandular dots outside, small stipitate glands nearer base, inner bracts reddish-tinged distally and marginally, membranaceous, lanceolate, 6.0–6.5 mm long, acute, margins with fringe of fine hairs, with glandular dots outside. Florets 12–15; corollas whitish, 5.5–6.0 mm long, with glandular dots on tube and lobes, basal tube 1.5 mm long, throat campanulate at base, cylindrical distally, 3.0–3.5 mm long, lobes 0.7–0.9 mm long; anther thecae ca. 1.2 mm long, slightly reddish to brownish. Achenes narrowly prismatic, ca. 3.5 mm long, scabrid with short setulae on ribs and upper sides; pappus of 35–45 slender bristles, 4.5–5.0 mm long, reddish at base, not or scarcely broadened near tips.

Loja: 15 km S of Loja, 2600 m, 12 Jul 1959, *Harling 5804* (S); 2400 m, 12 July 1959, *Harling 5816* (S).

Ageratina harlingii can easily be distinguished by the habit, with distal clusters of subverticillate branches and the stems rather densely foliate and densely covered with stout, stipitate glands. Only the three 1959 collections of Gunnar Harling have been seen. Subsequent deterioration of the environment in Loja may mean this the localized species is extinct.

Ageratina (*Andinia*) *maranonii* H.Rob., sp. nov.
Fig. 6

Type: Peru. Amazonas: Prov. Bongará, Jalca zone 3 km south of Pomacocha, E of Shipasbamba, 2400 m, 20 June 1962, *Wurdack 975* (holotype US, isotypes NY, USM).

Ad *A. macbridei* in foliis papyraceis late lanceolatis et stricte pinnate nervosis similis sed in foliis abaxialiter subglabris et in bracteis involucri apice rotundatis vel obtusis differt.

Shrubs 1.5–3.0 m high, branching at a 30–40° angle; stems slightly hexagonal, becoming terete, viscid, with numerous glandular dots; internodes 2.0–6.5 cm long. Leaves opposite, petioles 1.0–2.3 cm long; blades papyraceous, broadly lanceolate, mostly 10–16 cm long, 2–6 cm wide, base obtuse to broadly acute, margins entire in basal fourth, mostly serrulate to serrate with 20–40 teeth, apex narrowly acute to slightly acuminate, surfaces with prominulous reticulum of veinlets, with glandular dots obscure, appearing glabrous, adaxial surface dark green, with pale veins and veinlets,

Fig. 5. *Ageratina harlingii* H.Rob., holotype, *Harling 5822* (S).

Fig. 6. *Ageratina maranonii* H.Rob., holotype, *Wurdack 975* (US).

sometimes few hairs on midvein, abaxial surface paler green, with few small sparse hairs on veins; secondary veins pinnate, with 10–12 veins on each side. Inflorescences terminal on leafy stems, broadly fastigiate, shallowly rounded-corymbiform; branches and bracts viscid, puberulous to pilosulous; peduncles 1–5 mm long. Heads 7–9 mm long; involucre with ca. 10 green weakly subimbricate bracts, narrowly oblong, 3–5 mm long, apices rounded to obtuse, thinly scarious, weakly bicostate and viscid outside. Florets 5–8 in a head; corollas white, 4.5–5.0 mm long, basal tube ca. 1 mm long, with glandular dots, limb glabrous, throat ca. 3 mm long, lobes ca. 0.5 mm long; anther thecae ca. 1.2 mm long, reddish. Achenes 2.0–2.5 mm long, ribs not pale, with glandular dots on ribs and distally on sides; pappus white or with pink bases, of 30–35 slender unflattened bristles 3–4 mm long.

Paratype: Ecuador. Loja: Cerro Toledo, road to "La Torre," ca. 7 km SE Yangana, 2500 m, 7 Apr 1985, *Harling & Andersson 23819* (GB, US).

Ageratina maranonii occurs in northern Peru near Chachapoyas and from one locality in southern Ecuador. The habit in Ecuador is forest and old clearings. The species is closely related to *A. macbridei* B.L.Rob. of central Peru; specimens have been previously identified as that species. The latter has the same large leaf blades with 20–40 teeth and 10–12 pairs of strictly pinnate secondary veins. However, the latter also has distinctive spider-like clusters of hairs on the abaxial leaf surface beside the midvein, its involucral bracts have acute tips, and its corolla lobes are narrower and ca. 1 mm long.

Ageratina* (*Ageratina*) *parviceps H.Rob., sp. nov.
Fig. 7

Type: Ecuador. Carchi: 4 km NE of Mira on road toward El Angel, roadside near cornfield, 2500 m, 12 May 1990, *King, Peterson & Judziewicz 10069* (holotype US, isotype MO).

In habitis herbaceis vel suffruticosis et in laminis foliorum 15–30 mm longis et in captulis aliquantum diminutivis et in pedunculis non glanduliferis et in bracteis involucri 3–4 mm longis distincta.

Herbs or subshrubs 35–90 cm tall, sparsely to densely branched; stems brownish or reddish, puberulous or pilosulous with reddish hairs; internodes 1.5–9.0 cm long. Leaves opposite, petioles 2–8 mm long; blades ovate, mostly 15–30 mm long, 9–22 mm wide, base truncate to broadly obtuse, often with broad acumination at petiole, margins serrate with 5–10 ascending rather blunt teeth on each side, apex short-acute, adaxial surface dark green, drying blackish, sparsely pilosulous, sometimes appearing glabrous, abaxial surface usually paler green, puberulous or pilosulous with pale hairs mostly on veins; triplinervate from base of blade, secondary veins spreading at ca. a 30° angle. Inflorescences terminal on leafy stems, with ascending branches ending in rather flat corymbiform cluster of heads; peduncles 5–18 mm long, puberulous to hirtellous with reddish hairs. Heads 5–6 mm high; involucral bracts ca. 15, in ca. 2 series, greenish or reddish, oblong-elliptical, 3–4 mm long, to 1 mm wide, apices acute, margins ciliate, bicostate and puberulous outside. Florets 30–35; corollas whitish, ca. 3 mm long, basal tube ca. 1.3 mm long, throat 1.3–1.5 mm long, lobes 0.3–0.5 mm long, with few small hairs outside; anther thecae ca. 0.8 mm long, white. Achenes ca. 2 mm long, with short setulae on ribs; pappus whitish, rarely slightly reddish, ca. 3 mm long, of ca. 30 capillary bristles, very fragile at base, scarcely wider distally, often densely scabridulous. $n = 17_{II}\ 2_{I}$ or round frag., *K6974* (King et al. 1977, as *A. azangaroensis*).

Paratypes: Ecuador. Carchi: La Rinconada, a ranch between Ibarra and Tulcán, 3000 m, 10–11 Aug 1923, *Hitchcock 20796* (US). Wooded hills about 5 miles S of Tulcán, 10 Aug 1923, *Hitchcock 20996* (US).

Fig. 7. *Ageratina parviceps* H.Rob., holotype, *King, Peterson & Judziewicz 10069* (US).

Road Tulcán–San Gabriel, km 19, S of Tulcán, 3000–3100 m, 22 Feb 1974, *Harling & Andersson 12055* (GB, US). Scrub at edge of Páramo, 10–11 km NE of El Angel, 00°40′N, 77°53′W, ca. 11,000 ft, 8 Aug 1978, *Webster 23073* (DAV, US). 10 km SW of Tulcán, on road to El Angel, 3140 m, 14 May 1990, *King, Peterson & Judziewicz 10118* (MO, US). Imbabura: Lago Cuicocha, ca. 00°20′N, 78°20′W, 3000 m, 10 Dec 1966, *Sparre 13353* (S). Mojanda, ca. 10 km SSW Otavalo, ca. 00°10′N, 78°18′W, 2900–3150 m, 12 Dec 1966, *Sparre 13501* (S). Laguna Cuicocha, crater lake 30 km W of Ibarra, 00°18′N, 78°22′W, ca. 3100 m, 24 May 1973, *Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 6300* (AAU, S). Vía Nueva América–Tambo–Palmira–Mariano Acosta, zona húmeda, 10,000–10,400–11,800–10,400 ft, 30 Dec 1979, *Jaramillo, Coello & Sarmiento 1754* (AAU, QCA); Otavalo–Hcda. Perugachi, sitio de colecciones Quichinche–Faldas Nor–Oeste de Penas blancas, frente a fábrica de Cemento Solvalogre, zona húmeda, bosque secundario, 2670–2910 m, 5 Jan 1980, *Jaramillo, Coello & Young 1886* (AAU, QCA). Cotacachi Cantón, Reserva Ecológica Cotacachi–Cayapas, Laguna de Cuicocha, Sendero alrededor de la Laguna, Suelo Volcánico, 00°18′N, 78°22′W, 3100–3300 m, 23 Dec 1991, *Peñafiel, Bersosa, Gaibor & Toasa 664* (MO, QCNE, US); Sendero de la Laguna, entre Cotacachi–Loma y la Quebrada de Chumabí, Suelo Volcánico, 00°18′N, 78°22′W, 3000–3300 m, 28 Dec 1991, *Peñafiel, Tamayo & Toasa 776* (MO, QCNE, US). Pichincha: Prope Quito pass. 15 Mar 1871, *Sodiro 29* (S). Rio Machangara pr. urb. Quito, ad Marg. viae., 16 Apr 1920, *Holmgren 519* (S). Ad declivitates montis Pichincha pr. Quito, 30 Sep 1937, *Sydow 170* (S). Iliniza, Hacienda en Ortuno, 3650 m, 26 Nov 1956, *Weydahl 39* (S); Iliniza, Hacienda en Ortuno, 3590 m, 28 Nov 1956, *Weydahl 88, 119* (S). Quebrada Violetas, ca. 4 km W Aloag–Sto Domingo, 3000 m, 25 Mar 1967, *Sparre 14966* (S). Pululahua Crater about 22 km N of Quito, 2950 m, 5 Apr 1973, *Humbles 6258* (AAU, US). Hacienda de San Xavier, ca. 3 km SW of Chillogallo, ca. 10,800 ft, 17 Jan 1974, *King 6503* (MO, US). W of Calicalí, W slopes of Cordillera Occidental, km 12 on road from Calicalí, mountain scrub along road, 0°01′N, 78°33′W, ca. 2800 m, 24 May 1979, *Løjtnant & Molau 13619* (AAU). Vía Chillogallo–San Juan, partidero desde la población de San Juan hacia faldas del Atacazo "antenas militares," colección en border del carretero y pajonal, terreno humifero, zona húmeda, 13 Jul 1980, *Jaramillo & Lascano 3128* (AAU, QCA). Carretera de la Hacienda "Mi Cielo," faldas NW del Volcán Pichincha, 00°10′S, 78°30′W, 3400–3600 m, 24 Apr 1987, *Zak & Jaramillo 2014* (MO, US). Chimborazo: Along Pan-American Highway (route 1), ca. 6 km generally S of Mocha, ca. 11,200 ft, 24 Jan 1974, *King 6580* in part (MO, US). Along road to Riobamba, ca. 45 km SW of Riobamba, ca. 7900 ft, 31 Jan 1976, *King & Garvey 6974* (MO, US). Sucumbios: 8 km E of Pan American Hwy on road to La Bonita, S at Cocha Seca 1.2 km, 00°38′N, 77°41′W, 3000 m, 1 Mar 1992, *Funk & Gavilanes 11060* (US). Napo: Quijos Cantón, Reserva Ecológica Antisana, carretera Pifo–Papallacta, 3 km W de La Virgen, Laguna Miguacocha–Río Tumiguina, 00°23′S, 78°09′W, 3420 m, 25 Jul 1998, *Vargas, Narváez et al. 1984* (MO, US). Tena Cantón, Parque Nacional Llanganates, Vía Salcedo–Tena, km 55–60, Río Anatenorio, 00°58′S, 78°15′W, 3015 m, 17 Sep 1998, *Vargas, Narváez & Orellana 2531* (MO).

Colombia: Cundinamarca: Páramo de Palacio, *Cleef & Uribe 6729* (US).

Ageratina parviceps occurs only in northern Ecuador at elevations above 3000 m. A few specimens with the characteristics of the species seem to represent occurrences as far south as Chimborazo. Habitats include roadsides beside cultivated fields, scrub at edge of paramo, shrubby vegetation on old lava flows, and very humid montane forest on metamorphic rock substrate. Specimens have been identified in the past as *A. azangaroensis* (Sch.Bip. ex Wedd.) R.M.King & H.Rob., *A. sodiroi* or cf. *A. gracilis* (H.B.K.) R.M.King & H.Rob. The size is small, most like the Colombian *A. gracilis,* but the latter has essentially sessile, glabrous leaves. The present species differs from both *A. azangaroensis* and *A. sodiroi* by having smaller heads with much shorter involucral bracts.

Ageratina (Ageratina) pseudogracilis H.Rob., sp. nov.

Fig. 8

Type: Venezuela. Tachira Páramo de El Colorado (continuacion de El Zumbador), cumbre del páramo, 3200–3300 m, 20 Jan 1973, *Cuatrecasas, Ruiz-Terán & López-Figueras 28381* (holotype US, isotypes US).

In habitis ad *A. gracilem* similis sed in foliis pilosis et in acheniis glabris vel subglabris differt.

Subshrub or shrub 2–3 dm high, to 1.7 dm wide, with many branches; stems brownish, hirsutulous; internodes 1–2 cm long. Leaves opposite, subsessile, petioles 1–2 mm long; blades ovate, membranaceous, mostly 12–18 mm long, 5–12 mm wide, base rounded or obtuse, margins with 4–6 low blunt teeth, apex short-acute, adaxial surface sparsely pilose, abaxial surface pilose on veins; triplinervate from very near base of blade, with slender secondary veins spreading at ca. a 35° angle, reaching near distal third, weaker spreading basal veins close to basal margin. Inflorescences corymbiform, with branches strongly ascending, hirtellous; peduncles 2–7 mm long. Heads 5–6 mm high; involucral bracts ca. 15, mostly ca. 4 mm long, 1.2 mm wide, with margins and tips broadly membranaceous, 2 or 3 outer ca. 3 mm long, ca. 0.7 mm wide, without thin margins, apices shortly acute. Florets 30–35 in a head; corollas white, ca. 3 mm long, basal tube ca. 1.2 mm long, throat ca. 1.7 mm long, lobes ca. 0.5 mm long, densely pilosulous outside; anther thecae ca. 0.7 mm long, whitish. Achenes ca. 1.7 mm long, nearly glabrous, with few short setulae on distal ribs; carpopodia short-cylindrical; pappus whitish, ca. 3 mm long, of ca. 25 fragile capillary bristles, slightly broadened distally.

Ageratina pseudogracilis is known only from the type collection. It resembles *A. gracilis* (H.B.K.) R.M.King & H.Rob. in habit, with its small size and the small, subsessile leaves. The species is evidently more erect, the stems and leaves are pubescent, and the achenes are glabrous or nearly glabrous.

Ageratina (Andinia) regalis H.Rob., sp. nov.

Fig. 9

Type: Ecuador. Azuay: 8–10 km S of Cumbe on road to Loja, 9050–9400 ft, 22 Jan 1979, *King & Almeda 7754* (holotype US, isotypes CAS, MO).

Ad *A. pseudochilcam* in laminis foliorum coriaceis et subquinquenervosis similis sed in axilis venosi abaxialibus piliferis distincta.

Shrubs or small trees 1–4 m tall, moderately branched, branches ascending at ca. a 45° angle or less, not or scarcely viscid on stems, leaves and branches of inflorescence, with sparse minute puberulence; stems brownish, terete with slight costae; internodes mostly 1.0–5.5 cm long. Leaves opposite, somewhat persistent along distal branches, petioles 5–15 mm long; blades thinly coriaceous, narrowly ovate to ovate-elliptical, mostly 4.0–6.5 cm long, 1.2–3.0 cm wide, base rounded or obtuse to broadly acute, margins with usually 10–22 teeth distal to the basal fifth, apex obtuse to acute, adaxial surface dark green, nitid, with prominulous larger veinlets, slightly insculpate smaller veinlets, glandular dots scattered, abaxial surface subnitid, with close reticulum of prominulous veinlets, smaller veinlets usually dark, minute glandular dots scattered, not restricted to veinlets, pilose with pale hairs along sides of

Fig. 8. *Ageratina pseudogracilis* H.Rob., holotype, *Cuatrecasas, Ruiz-Terán & López-Figueiras 28381* (US).

UNITED STATES

2850328

NATIONAL HERBARIUM

Ageratina regalis H.Rob.
det. Harold Robinson (US), July 2001

PLANTS OF ECUADOR
Cytological and/or Biochemical Vouchers

ROBERT MERRILL KING
AND FRANK ALMEDA, NO 7754
22 January 1979

Ageratina pseudochilca (Benth.) K&R.

Azuay: 8-10 km S of Cumbe on the road to Loja.
Elevation 9050-9400 ft.

slender shrub 1.5 m tall. Florets white but linged with pink. Common.

Specimens collected for the United States National Herbarium, Smithsonian Institution and the Herbarium of the California Academy of Sciences.

Fig. 9. *Ageratina regalis* H.Rob., holotype, *King & Almeda 7754* (US).

midvein and on bases of secondary veins, especially obvious in axils of large secondary veins; two pairs of strongly ascending secondary veins near base of blade, pair nearest base weak, near margin, distal pair more ascending, spreading at a 30–40° angle, usually straight or with convex curve from base. Inflorescences terminal on leafy stems, fastigiate with ascending branches, forming rather dense slightly rounded corymbiform clusters of heads; peduncles 0–1 mm long, with heads mostly in sessile subgroups of 2 or 3. Heads 7–8 mm long; involucral bracts weakly subimbricate, with ca. 7 subequal bracts, pale green, oblong to elliptical, mostly ca. 4 mm long, apices subacute, scarious, scarcely bicostate outside at base, with many glandular dots. Florets 5–7; corollas white to pale pink or with pink lines, ca. 5.0 mm long, basal tube 1.5–1.8 mm long, with scattered minute glandular dots, throat ca. 2.5 mm long, glabrous, lobes ca. 0.7 mm long, glabrous; anther thecae 1.2–1.5 mm long, reddish. Achenes ca. 2.5 mm long, with minute setulae or glandular dots along ribs, glands on sides near pappus; pappus rather persistent, whitish or base pale pink, 3–4 mm long, of 30–35 bristles, slightly flattened, not broadened distally. n = ca. 42, *K6891* (King et al. 1977, as *A. pseudochilca*).

Paratypes: Ecuador. Cañar: Region of San Marcos, ca. 10 km NE of Azogues, 9500 ft, 25 Sep 1944, *Prieto P-69* (NY, US). El Oro: Cerro de Chilla, 03°30′S, 79°38′W, 3595 m, 3 May 1997, *Vargas & Canaday 1423* (MO, QCNE, US). Chimborazo/Cañar: Western escarpment, near, El Tambo, 10,000–11,500 ft, 6–9 Jul 1945, *Camp E-4099* (NY, S). Cañar: Between Biblián and Cañar, ca. 3200 m, 21 Sep 1955, *Asplund 17683* (S); ca. 2900 m, *Asplund 17710* (S). Páramo between Biblián and Cañar, 3350 m, 5 Aug 1959, *Harling 6285* (S). Partidero El Corte–San Miguel de Porotos–Parcialidad Jatupamba–Cerro La Comuna, zona húmeda, 9400–10,000 ft, 26 May 1979, *Jaramillo 985, 1032* (AAU, QCA). Azuay: Cruz Pamba region above Baños (ca. 15 km SW of Cuenca), 9000–10,000 ft, 29–30 June 1945, *Camp E-3921* (NY, S, US). Cumbe, 3000 m, 9 May 1947, *Harling 824* (S). 10 km S of Cumbe, 3000 m, 8 Jul 1959, *Harling 5660* (S). Sayausid, ca. 3000 m, 1 Apr 1968, *Harling, Storm & Ström 7930* (GB). Road Cuenca–Girón (ca. 10 km N of Girón), ca. 2700 m, 2 Apr 1968, *Harling, Storm & Ström 7949* (GB, US). Cumbe, S of Cumbe, ca. 2700 m, 22–24 Apr 1968, *Harling, Storm & Ström 8703* (GB, US). Along road to Limón, ca. 17 km E of Gualaceo, ca. 8900 ft, 31 Jan 1974, *King 6631* (MO, US). Along road to Loja, ca. 6 km generally SE of Cumbe, ca. 9600 ft, 4 Feb 1974, *King 6695* (MO, US). Portete del Tarqui, Cuenca–Girón, 2700–2900 m, 5 Apr 1974, *Harling & Andersson 13193* (GB, US). Road Cuenca–Loja, upper northern slopes of Valle del Río León and southern parts of Páramo de Tinajillas, ca. 2800 m, 9 May 1974, *Harling & Andersson 14518* (GB, US). Baños, SW of Cuenca, cultivated ground, ca. 2700 m, 12 May 1974, *Harling & Andersson 14572* (GB). Along road to Loja, ca. 17 km S of Cumbe, ca. 9700 ft, 24 Jan 1976, *King & Garvey 6891* (MO, US). Partidero Llantera–Chiquintad–Saucay–Guandum, zona húmeda, 9200 ft, 27 May 1979, *Jaramillo 1051* (AAU, QCA). Tarqui, near the monument, 2600 m, 5 Feb 1982, *Harling, Bohlin, Lindstrom & Roth 20243* (GB, US). Loja: Jera 10 km NE of Saraguro, 03°24′S, 79°14′W, 2 Mar 1989, *Ellemann 91651* (AAU, QCA, US).

Common name: "urcu chilca" (Quechua). Use: for bath, a decoction of whole plant is used.

Ageratina regalis seems endemic to the area of Azuay and nearby parts of Cañar, El Oro, and Loja. The species occurs in parámo or subparámo vegetation. Specimens have been consistently identifed in the past as the more northern *A. pseudochilca.* The present species is instantly distinguishable by the abaxial leaf hairs along the midvein and bases of the secondary veins, which are particularly evident in the axils of the secondary veins. The stems are also more terete, the leaf blades generally thinner, and the corollas often pink.

The species is named after the collector of a number of the specimens and specialist in the Eupatorieae, Robert Merrill King.

Ageratina rhodopappa f. ***glandularis*** (B.L.Rob.) H.Rob., comb. nov.

Basionym: *Eupatorium pichinchense* f. *glandulare* B.L.Rob., Contrib. Gray Herb., n.s. 61:10. 1920. Type: Ecuador. Chimborazo: vicinity of Huigra, mostly on Hacienda de Licay, Aug 1918, *Rose & Rose 22210* (holotype GH, isotypes NY, US).

Ageratina (***Ageratina***) ***rosei*** H.Rob., sp. nov.

Fig. 10

Type: Ecuador. Chimborazo: Vicinity of Huigra, mostly on Hacienda de Licay, 21 Aug 1918, *Rose & Rose 24078* (holotype US).

Ad *A. rhodopappam* f. *glandularum* in setis pappi roseis et pedunculis glanduliferis similis sed in laminis foliorum base triplinervatis differt.

Herbs 5–10 dm tall, scarcely to moderately branched, often with many proliferations from axils; stems slender, brownish to purplish, terete, usually puberulous to hirtellous; internodes 1.5–6.5(–14.0) cm long. Leaves opposite, petioles 4–16 mm long; blades thinly papyraceous, ovate, mostly 1.2–5.0 cm long, 0.6–3.0 cm wide, widest near basal 5th, base subtruncate or shallowly cordate to rounded, margins crenate or serrate with 5–12 blunt teeth on each side, apex acute, rarely slightly acuminate; adaxial surface sparsely and evenly pilosulous, abaxial surface slightly paler, pilosulous mostly on veins; triplinervate from base of blade at petiole, rarely just distal to base. Inflorescences terminal on leafy stems, broadly and usually rather flatly corymbiform; branches ascending, usually with many minute stipitate glands; peduncles 5–17 mm long. Heads 6–8 mm high; involucral bracts ca. 18, greenish or brownish-green with purplish tips, oblong-lanceolate, mostly subequal, 4–6 mm long, 1.0–1.3 mm wide, apices acute, inner bracts with paler membranaceous often erose tips, scarcely ciliate, outside minutely puberulous with usually reddish hairs, narrowly bicostate. Florets ca. 35–45 in a head; corollas whitish, 3.5–4.0 mm long, basal tube slender, 1.0–1.5 mm long, throat 1.5–2.0 mm long, lobes 0.5–0.8 mm long, with few hairs outside; anther thecae 0.6–0.9 mm long, white. Achenes ca. 2 mm long, fusiform, with many short setulae along ribs from carpopodium to pappus, very rarely glabrous; carpopodium cylindrical; pappus of ca. 20 whitish to mostly reddish bristles, fragile at base, 3.5–4.0 mm long, scarcely to distinctly broadened distally. n = 17 + 1, *K6532*; n = 17 + 2 frag., *K6587* (King et al. 1977, as *A. azangaroensis*).

Paratypes: Ecuador. Locality uncertain: In locis herbidis subandinis, *Sodiro 549* (US). And. Quitenorum, s.d., *Jameson s.n.* (S). El Oro: Railway station Cotopaxi, 3550 m, 26 May 1939, *Asplund 6498* (S). Pichincha: Pichincha, a little above Quito, 3200–3500 m, 1952?, *Fagerlind & Wibom 2035* (S). Antisanilla, 11,500 ft, Oct 1923, *Anthony & Tate 337* (US). Cerca de la estación de Chiriaco, 2820 m, 2 Apr 1928, *Firmin 421* (US). Quito, Panecillo, 2900 m, 16 May 1939, *Asplund 6078* (S). Saloya (W of Quito), 2000 m, 28 June 1939, *Asplund 7360* (S). Dauli (flag stop) on railroad SE of Corazon Volcano, 00°34′S, 78°36′W, 3300 m, 31 May 1947, *Fosberg 27638* (US). Cordillera Occidental, los Vertientes de Pichincha, 11 Jul 1959, *Barclay, Juajibioy & Tinajero 7819* (US). Cordillera Occidental, Páramo de Trujillo, border of Prov. Cotopaxi, between peaks Illiniza to W and Cotopaxi to E, ca. 3450 m, 15 Jul 1959, *Barclay & Juajibioy 7933* (US). Quebrada Yanahuaico, ca. 3 km W Conocoto, 2700–2800 m, 3 Dec 1966, *Sparre 13292* (S). Road St Domingo–Quito, Cornejo Astorga (Tandapi), ca. 1600 m, 7–10 May 1968, *Harling, Storm & Ström 9393* (GB). Cerro

Fig. 10. *Ageratina rosei* H.Rob., holotype, *Rose & Rose 24078* (US).

Pichincha, above Quito, 3500–5000 m, 2 Nov 1974, *Gentry 12381* (MO). Along route from Quito to Santo Domingo de los Colorados between San Juan and La Palma via Chiriboga, 15 km NE of Chiriboga, 2480 m, 2 Sep 1976, *Croat 38725* (MO). Along road between Quito and Nanegal, via Cotocollao and Nono, 18–21 km NW of Quito, 3100–3200 m, 4 Sep 1976, *Croat 38802* (MO). Páramo and shrub vegetation on the eastern slopes of Cerro Pichincha, 3600–4000 m, 26 Jan 1977, *Harling, Eliasson & Andersson 14834* (GB). W slopes of Cordillera Occidental, W of Calicalí, 00°01′N, 78°32′W, ca. 2700 m, 25 Mar 1979, *Løjtnant & Molau 11358* (AAU, GB). W of Calicalí, W slopes of Cordillera Occidental, km 12 on road from Calicalí, 00°01′N, 78°33′W, 24 May 1979, *Løjtnant & Molau 13619* (AAU, GB). Quito, Parraoquia El Salvador–Toctiuco–Chorrera–Faldas del Pichincha, zona húmeda, pendiente, 11,000–11,400 ft, 24 Jun 1979, *Jaramillo & Jaramillo 1206* (AAU, QCA); Hcda. Mi Cielo–Faldas del Pichincha, zona húmeda, 11,000 ft, 20 Jul 1979, *Jaramillo 1260* (AAU, QCA); vía Toctiuco–Chorrera–Pirámide (Antena de Televisión) Faldas del Ruccu–Pichincha, zona húmeda, 11,600 ft, 11 Aug 1979, *Jaramillo & Lascano 1328* (AAU, QCA); Pasochoa–Localidad Sur Oriente, colecciones en bosque de Coja Andina y pajonal, zona humeda, 3500–3650 m, 17 Nov 1979, *Jaramillo, Coello, Narvaes, Elisabeth, Bravo & Rasa 1567* (AAU, QCA). Carretera Chillogallo–San Juan–Chiriboga–Empalme, colecciones en alrededores de San Juan, 00°18′S, 78°39′W, 3100–3260 m, 8 Sep 1985, *Zak & Jaramillo 621* (MO, US). Carretera Quito–San Juan–San José de la Victoria, en la cercanía de San José, 2900–3400 m, 24 Dec 1987, *Zak & Jaramillo 3280* (MO, US). Cotopaxi: Volcán Cotopaxi, above Limpio Pamba, 00°37′S, 78°26′W, 3781 m, 10 Jul 1963, *Ugent & Albornoz 5662* (US). Volcán Cotopaxi WNW slopes (NE Ami Grande) 4000 m, 26 Apr 1967, *Sparre 15777* (S). Road Salcedo–Napo, km 21, 3800 m, 5 Sep 1967, *Sparre 18420* (S). Road Quevedo–Latacunga, Zumbagua, W of Zumbagua, ca. 3200 m, 2 May 1968, *Harling, Storm & Ström 8942* (GB, US). Tungurahua: Along road to Baños, ca. 1 km SE of Ambato, ca. 8700 ft, 20 Jan 1974, *King 6532* (MO, US). Mocha, alrededores del Pueblo, 01°27′S, 78°40′W, 2900 m, 30 Sep 1995, *Villacres 257* (F, US). Bolívar: Railway station Cotopaxi, 3550 m, 26 May 1939, *Asplund 6498* (S, US). Along road to Guaranda (route 7), ca. 28 km generally SW of Ambato, ca. 11,000 ft, 25 Jan 1974, *King 6587* (MO, US). Chimborazo: Vicinity of Huigra, mostly on Hacienda de Licay, 28 Aug 1918, *Rose & Rose 24078a* (US); 6 Sep 1918, *Rose & Rose 24078b* (US). Cañon of Río Chanchan near Huigra, 4000–4500 ft, 7–14 May 1945, *Camp E-3148* (NY, S, US). Between San Andrés and Cuatro Esquinas, Oct 1952, *Fagerlind & Wibom 881* (S). El Retén (20 km south of Cebadas, 31 Jan 1968, *Harling, Storm & Ström 6793* (GB). Carretera Riobamba–Licto–Pungalá–Alao–Huamboya, en la quebrada Supaychuan, 01°50′S, 78°30′W, 3570–3620 m, 26 Dec 1987, *Zak & Jaramillo 3304* (MO, US). Cañar: between Biblián and Cañar, edge of thicket, ca. 3200 m, 21 Sep 1955, *Asplund 17682* (S). Azuay: Cerro Soldados (W of Sayausid), below Quinoas, ca. 3400 m, 25 Apr 1968, *Harling, Storm & Ström 8748* (GB). Napo: Alrededores de la Cordillera de Los Llanganati, Chihuila Sacha o Ainchilibí, 25–29 Aug 1959, *Barclay & Juajibioy 9004* (US). Morona-Santiago: Parque Nacional Sangay, Peace Corps Sangay Mountaineering Expedition, between Plazapamba and Yanayacu, 02°02′S, 78°25′W, 3200–3600 m, 23–31 Dec 1995, *Clark, Harris, Sulser, Teizeira & Baño 1829* (MO, QCNE, US).

Three additional paratypes are triplinervate slightly above base of the blade:

Ecuador: Pichincha: Crescit prope Quito, 1864, *Jameson s.n.* (US). Puingasí (cul.) en um cerco, ca. 3000 m, 18 Apr 1927, *Firmin 46* (US, achenes without setulae). Quito Cantón, carretera Quito–Nono–Tandayapa, 00°01′N, 78°40′W, 1500–1800 m, 5 Sep 1991, *Rubio 2083* (MO, QCNE).

Peru: Dept. Lambayeque: Prov. Ferrenafe: Sinchigual–Laguna Tembladera, Distrito Incahuasi, 3100 m, 13 Sep 1985, *Sagástegui, Skillman, Mostacero & Ramírez 12859* (F, HUT, US).

Ageratina rosei occurs mostly in central Ecuador at middle and higher elevations. Habitats cited include páramo on dry rocks of high cliff above grassy slope, on ridges in montane forest area, bunch-grass association, under shrubs along ditch between cultivated fields, and roadside. The combination of often reddish pappus and glanduliferous inflorescence branches tends to distinguish the species. It is named for the collector of some of the earlier specimens, Joseph Nelson Rose, and its pappus color was also taken into consideration in the choice of the name. Some of the early collections of the species were identified by B. L. Robinson as his *Eupatorium pichinchensis* f. *glandulare,* the type of which has the triplinervation of the leaf far distal to the base of the blade, and it is placed now in *A. rhodopappa.* Both *A. rosei* and *A. rhodopappa* lack the long stem hairs of *A. pichinchensis,* although some specimens of that species have glands on the inflorescence branches and reddish pappus bristles. More recent collections of *A. rosei* have often been determined as *A. azangaroensis* (Sch.Bip. ex Wedd.) R.M.King & H.Rob., an apparent synonym of *A. glechonophylla* (Less.) R.M.King & H.Rob. that has generally larger heads, corolla throats much longer in comparison to their lobes, and achenes with coarser setulae on the ribs and distal lateral surfaces. The Peruvian specimen has generally longer peduncles, 2.5 cm long.

Ageratina* (*Ageratina*) *serrulata H.Rob., n.sp.

Fig. 11

Type: Colombia. Antioquia: Ituango, camino entre El Retiro y Cerro Paramillo, 3200–3600 m, 25 Feb 1993, *Cuadros 5003* (holotype HUA, isotypes MO, US).

In habitus ad *A. gracilem* similis sed in foliis flaccide pilosis in foliis erecto-patentiter multiserrulatis et in acheniis glabris distincta.

Subshrubs 15–20 cm high, sparsely branched below, distal parts densely branched; stems dark brown when dry, densely hirsute with flaccid hairs; internodes mostly 4–8 mm long, to 25 mm long on young shoots. Leaves opposite, petioles 2–4 mm long; blades papyraceous, ovate, 10–22 mm long, 5–12 mm wide, base rounded to broadly obtuse, margins with 5–11 small sharp teeth, apex acute, adaxial surface pilosulous with sparse hairs, abaxial surface with long flaccid hairs spreading from midvein and larger secondary veins, triplinervate at the base of blade, secondary veins spreading at a 30–35° angle. Inflorescences terminal on leafy stems, often overtopped by lateral leafy shoots, branches slender, few, sparsely hirtellous, peduncles 4–17 mm long. Heads ca. 5 mm high; involucral bracts 15–17, lanceolate, subequal, ca. 4.5 mm long, 0.7 mm wide, narrowly acute, glabrous outside, inner bracts thinner, paler, bicostate. Florets ca. 30 in a head; corollas white, ca. 3.5 mm long, basal tube ca. 1.5 mm long, throat ca. 1.3 mm long, lobes ca. 0.6 mm long, with few or no hairs; anther thecae whitish, ca. 0.7 mm long. Achenes ca. 2 mm long, glabrous; carpopodium narrowly cylindrical; pappus whitish, ca. 3 mm long, of ca. 20 fragile bristles, scarcely broadened distally.

Ageratina serrulata is known only from the type collection. The species is one of four described in this paper that have at times been identified as *A. gracilis* (H.B.K.) R.M.King & H.Rob. All are from above 3000 m and differ from the Colombian *A. gracilis* by the more erect habits and the pubescence on the leaf blades. The Ecuadorian species, *A. parviceps,* is usually a larger plant with much longer petioles, and it has definitely setuliferous achenes. The western Venezuelan *A. pseudogracilis* and

Fig. 11. *Ageratina serrulata* H.Rob., isotype, *Cuadros 5003* (US).

southern Colombian *A. ewanii* differ by the broader more membranaceous tips on the involucral bracts, the very short internodes of the stems, and nearly but usually not completely glabrous achenes. Also, *A. ewanii* has a series of outer involucral bracts usually distinctly shorter than the inner ones. The present *A. serrulata* is most distinct in the many sharper more jutting small teeth of the leaves and by the lanceolate essentially glabrous bracts of the involucre.

***Ageratina* (*Ageratina*) *villonacoensis* H.Rob., n.sp.**

Fig. 12

Type: Ecuador. Loja: Eastern slopes of Cerro Villonaco, grassland or dense shrub vegetation, 2500–2600 m, 12 Apr 1974, *Harling & Andersson 13439* (holotype US, isotype GB).

Ad *A. pichinchensem* in caulibus villosis et in inflorescentiis compactis similis sed in laminis foliorum base cordatis margine acute dentatis et apice valde acuminatis et in bracteis involucri longe acuminatis distincta.

Subshrubs to ca. 1 m tall, sparsely branched; stems scrambling, terete, densely villous with often violet septate hairs over 1 mm long; internodes 6–9 cm long. Leaves opposite, petioles 5–18 mm long; blades broadly ovate, 2.5–5.0 cm long, 2–4 cm wide, papyraceous, base rounded to shallowly cordate, margins coarsely serrate, with 7–10 teeth on each side, apex distinctly acuminate, adaxial surface pilose, abaxial surface pilose on veins; triplinervate from base, often from basal acumination, with secondary veins spreading at ca. a 45° angle. Inflorescences terminal on leafy stems, with branches spreading at a 30–45° angle, densely villous; ending in rather dense corymbiform clusters of heads; peduncles 3–6 mm long. Heads 7–8 mm long; involucral bracts 20–22, in ca. 2 series, papyraceous, subequal, lanceolate, 6–7 mm long, 0.8–1.0 mm wide, outer bracts purplish, inner bracts stramineous, tips narrowly acute to long-acuminate, outside pilose with violet hairs. Florets ca. 30–35 in a head; corollas white, 4.0–4.3 mm long, pilosulous on distal part of throat and on lobes, basal tube slender, ca. 2 mm long, throat ampliate, becoming cylindrical, ca. 1.7 mm long, lobes ca. 0.7 mm long, pilosulous with fine hairs; anther thecae ca. 1 mm long, whitish. Achenes ca. 2 mm long, fusiform, setuliferous on distal part of ribs and on sides near pappus; pappus whitish, of ca. 25 capillary bristles ca. 3.5 mm long, fragile at base, slightly broadened distally.

Paratype: Peru. Cajamarca: Prov. Cajamarca, Cerro Chupacotoy, 2800 m, 2 June 1992, *Ochoa & Salas 16139* (US).

Ageratina villonacoensis is known only from the type collection in southern Ecuador and a single similar but smaller-headed and less pubescent specimen from Cajamarca, Peru. It is similar to *A. pichinchensis* and *A. sodiroi.* It has the longer pubescence of the former, without any trace of stipitate glands sometimes found in that species. It has the larger more acute teeth of the leaf margins as in *A. sodiroi,* but the latter has shorter pubescence. The present species differs from both the related species by the more strongly cordate bases of the leaf blades and by the narrow often long-acuminate tips of the involucral bracts.

***Ageratina* (*Ageratina*) *websteri* H.Rob., sp. nov.**

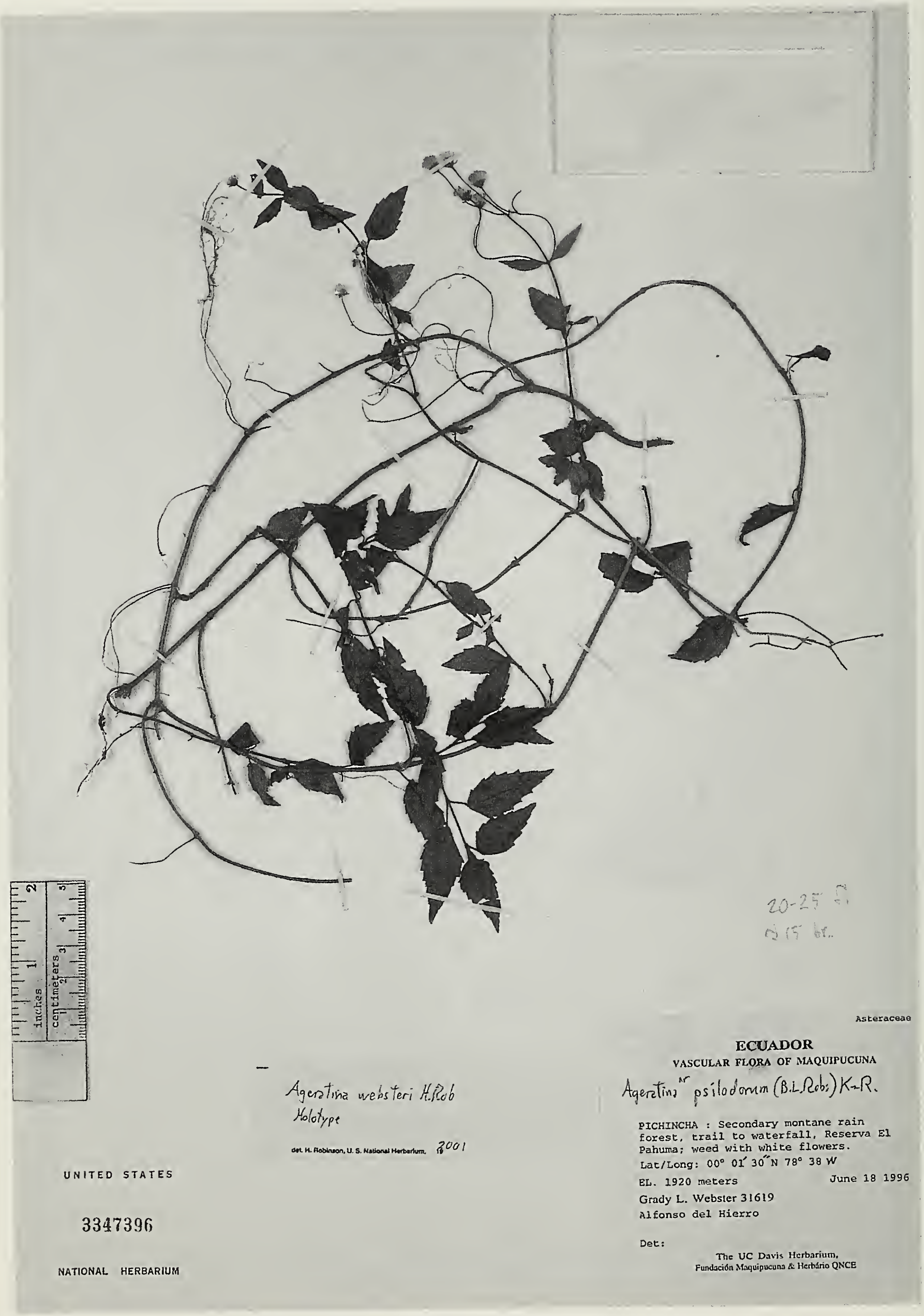
Fig. 13

Type: Ecuador. Pichincha: Secondary montane rain forest, trail to waterfall, Reserva El Pahuma, weed with white flowers, 00°01′N, 78°38′W, 1920 m, 18 June 1996, *Webster 31619* (DAV, US).

In habitis decumbentibus et in caulibus rubri-puberulis et in laminis foliorum 20–32 mm longis et margine argute serratis et in capitulis laxe dispositis et in bracteis involucri e acheniis vix longioribus et in floribus in capitulo 20–25 et in tubis corollarum sparsim minute pilosulis distincta.

Herbs with long decumbent rooting

Fig. 12. *Ageratina villonacoensis* H.Rob., holotype, *Harling & Andersson 13439* (US).



Asteraceae

ECUADOR
VASCULAR FLORA OF MAQUIPUCUNA
Ageratina nr psilodorum (B.L.Rob.) K.&R.

PICHINCHA : Secondary montane rain forest, trail to waterfall, Reserva El Pahuma; weed with white flowers.
Lat/Long: 00° 01′ 30″ N 78° 38 W
EL. 1920 meters June 18 1996
Grady L. Webster 31619
Alfonso del Hierro

Det:

The UC Davis Herbarium,
Fundación Maquipucuna & Herbário QNCE

Ageratina websteri H.Rob
Holotype

det. H. Robinson, U. S. National Herbarium, 2001

UNITED STATES
3347396
NATIONAL HERBARIUM

Fig. 13. *Ageratina websteri* H.Rob., holotype, *Webster & Hierro 31619* (US).

stems and projecting leafy branches 4–5 dm long, branching at ca. a 45° angle; stems brownish to dark reddish, densely puberulous with reddish hairs; internodes mostly 1.5–4.0 cm long. Leaves opposite, petioles 4–7 mm long; blades membranaceous, ovate, 20–32 mm long, 8–14 mm wide, base obtuse, margins serrate with 4–6 sharp teeth, apex acute, adaxial surface dark green, nearly glabrous, with scattered minute hairs, more puberulous on veins near base, abaxial surface slightly paler, with few hairs along veins; triplinervate 1.0–1.5 mm distal to base of blade, secondary veins spreading at ca. a 25–30° angle. Inflorescences terminal on leafy branches, with 1–7 laxly disposed heads; branches puberulous with reddish hairs; peduncles slender, 12–25 mm long. Heads 5–6 mm high; involucral bracts ca. 15, in 1–2 series, membranaceous, few outer bracts darker green, narrowly oblong, subequal, 2.0–2.5 mm long, ca. 0.5 mm wide, apices obtuse, densely ciliate with fine hairs, outside puberulous with sparse minute hairs, costae not obvious. Florets 20–25 in a head; corollas whitish, ca. 2.8 mm long, with fine pale hairs on basal tube, basal part of throat and on lobes, basal tube slender, ca. 1.5 mm long, throat ca. 1 mm long, lobes ca. 0.3 mm long; anther thecae ca. 0.5 mm long, whitish. Achenes ca. 2 mm long, with minute setulae often biseriate along ribs, sparse distally on sides; carpopodium cylindrical; pappus ca. 2.8 mm long, whitish or pinkish, of ca. 25 slender bristles, not or scarcely broadened distally.

Ageratina websteri is known only from the type collection. It was originally determined as possibly *A. psilodorum,* a Colombian species, but it does not have the glabrous stems of that species. Relationship is regarded here as closest to *A. parviceps,* which has a more erect habit with more heads on shorter peduncles, over 30 florets in the heads, corolla tubes and throats without hairs, larger more overlapping involucral bracts distinctly longer than the mature achenes, an almost strictly whitish pappus, and which occurs at elevations usually at least 1000 m higher.

Acknowledgments

The extensive technical help of Marjorie Knowles is acknowledged. The scans of the U.S. type specimens were prepared by Susan Hunter of the Department of Botany.

Literature Cited

King, R. M., & H. Robinson. 1970. Studies in the Eupatorieae (Compositae). XIX. New combinations in *Ageratina.*—Phytologia 19:208–229.

———, & ———. 1990. Notes on *Ageratina* in Mesoamerica (Eupatorieae: Asteraceae).—Phytologia 69:61–86.

———, D. W. Kyhos, A. M. Powell, P. H. Raven, & H. Robinson. 1977. Chromosome numbers in Compositae, XIII. Eupatorieae.—Ann. Missouri Bot. Gard. 63:862–888.

Turner, B. L. 1997. The Comps of Mexico, a systematic account of the family Asteraceae. I. Eupatorieae.—Phytologia Mem. 2:i–iv, 1–272.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(1):256–261. 2003.

ERRATUM

Erratum regarding.—Marcus, J. and S. Hourdez. 2002. A new species of scaleworm (Polychaeta: Polynoidae) from Axial Volcano, Juan de Fuca Ridge, northeast Pacific. Proceedings of the Biological Society of Washington 115(2):341–349.

Statement.—Higher printing quality of the figures illustrating the new species *Vampiropolynoe embleyi* (Polychaeta; Polynoidae) are presented here. Due to printing problems the figures issued with the original publication did not satisfactorily illustrate the morphological detail described in the text.

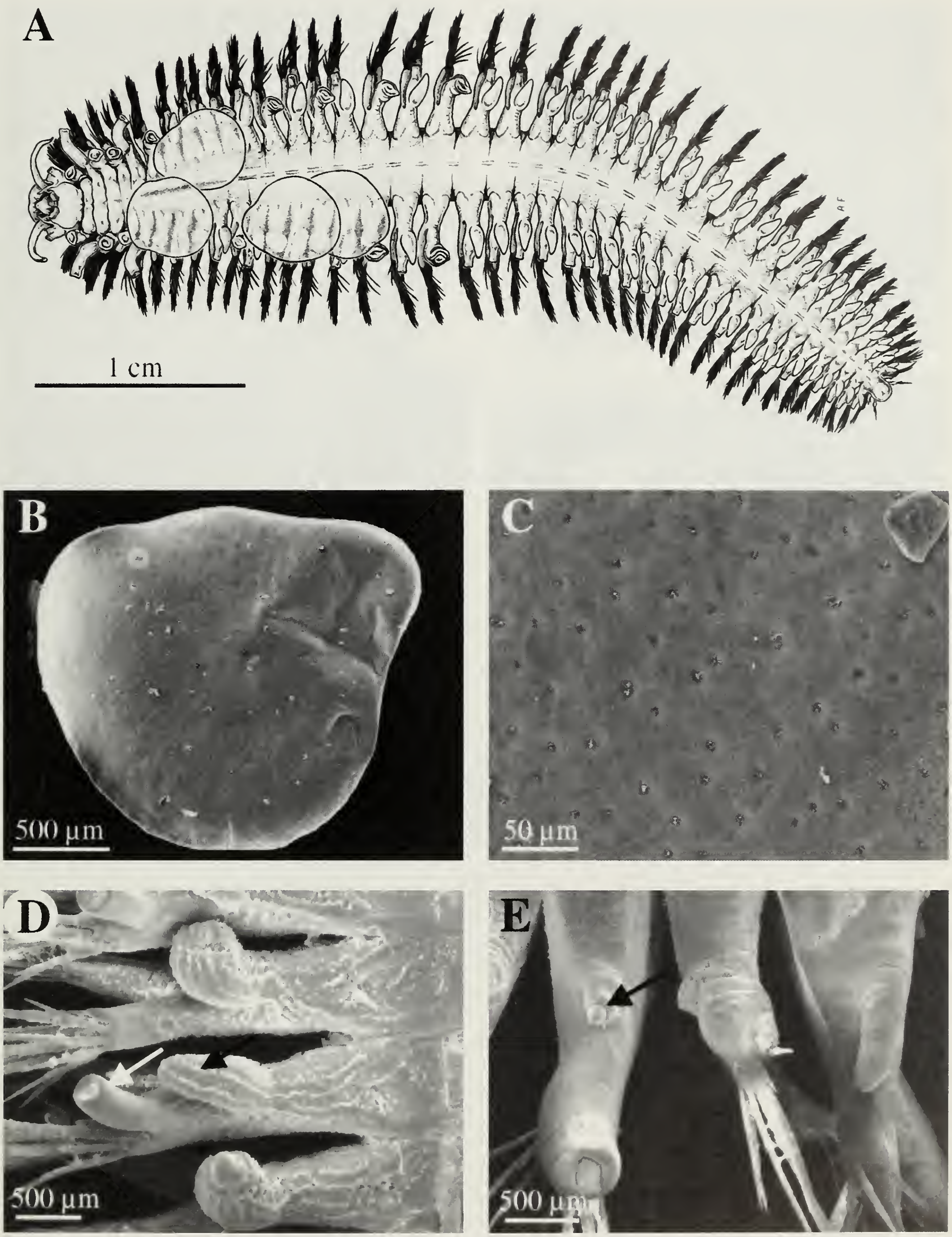


Fig. 1. A. Drawing of paratype (R473-6096), dorsal view of whole specimen. Dorsal cirri have broken off. B–E, SEM views. B. Elytron from the mid-section, dorsal view. C. Detail of elytral surface. D. Dorsal view of segments 11 (bottom)–14 (top). White arrow points to cirrophore on segment 12, black arrow points to digitiform dorsal tubercle on the same segment. E. Detail of first dorsal tubercle on segment 6 (black arrow).

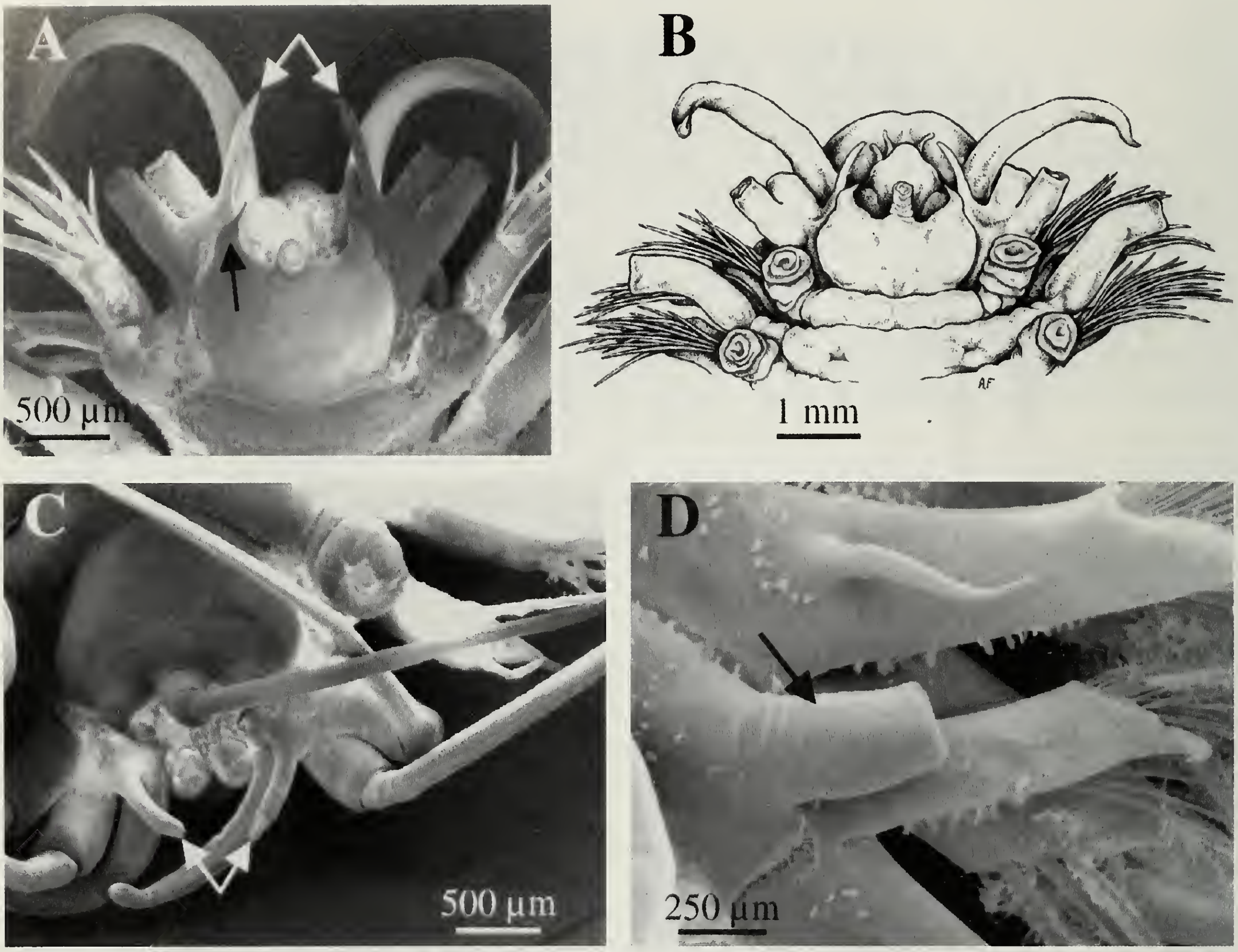


Fig. 2. A, C, and D, SEM views. A. Dorsal view of anterior part of worm. White arrows point to the strong aciculae protruding from the 1st segment. Black arrow points to the left hooked frontal filament. B. Drawing of the anterior part of paratype (R473-6096), pharynx partially everted. C. Frontal view of prostomium showing median antenna, tentacular cirri, aciculae (white arrows). D. Detail of the buccal cirrophore (black arrow), and second ventral cirrus (3rd segment).

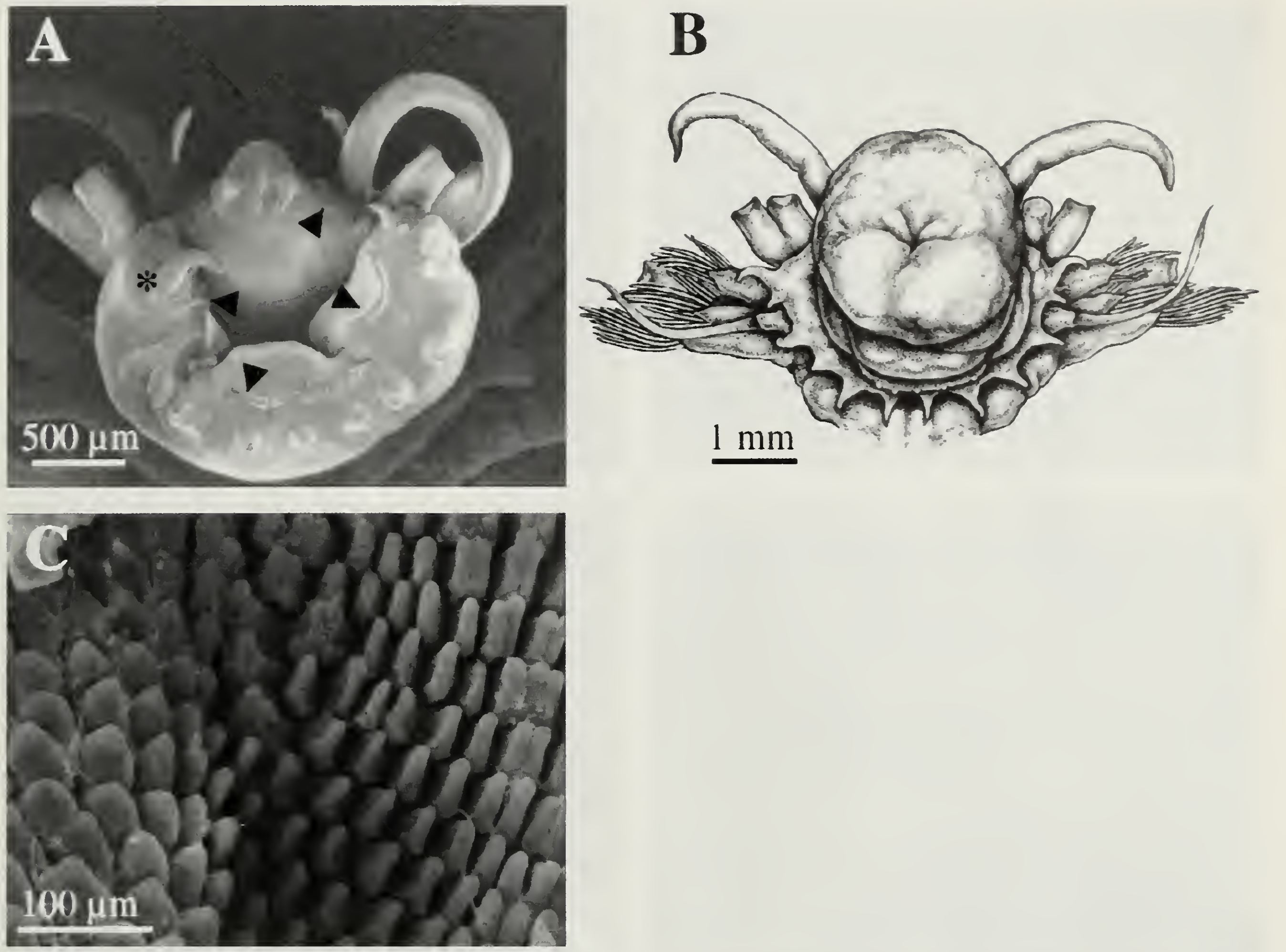


Fig. 3. A and C, SEM views. A. Ventral view of a partially everted pharynx showing upper, lateral and ventral lips with their papillae and ridges. Black arrowheads point to lip ridges, asterisk points to shared bulbous base of the two median papillae on the lateral lip. B. Drawing of paratype (R473-6096), ventral view of a more everted pharynx, with the buccal papillae forming a crown at the base of the pharynx. C. Keratinized teeth at the junction between the mouth opening and the pharynx.

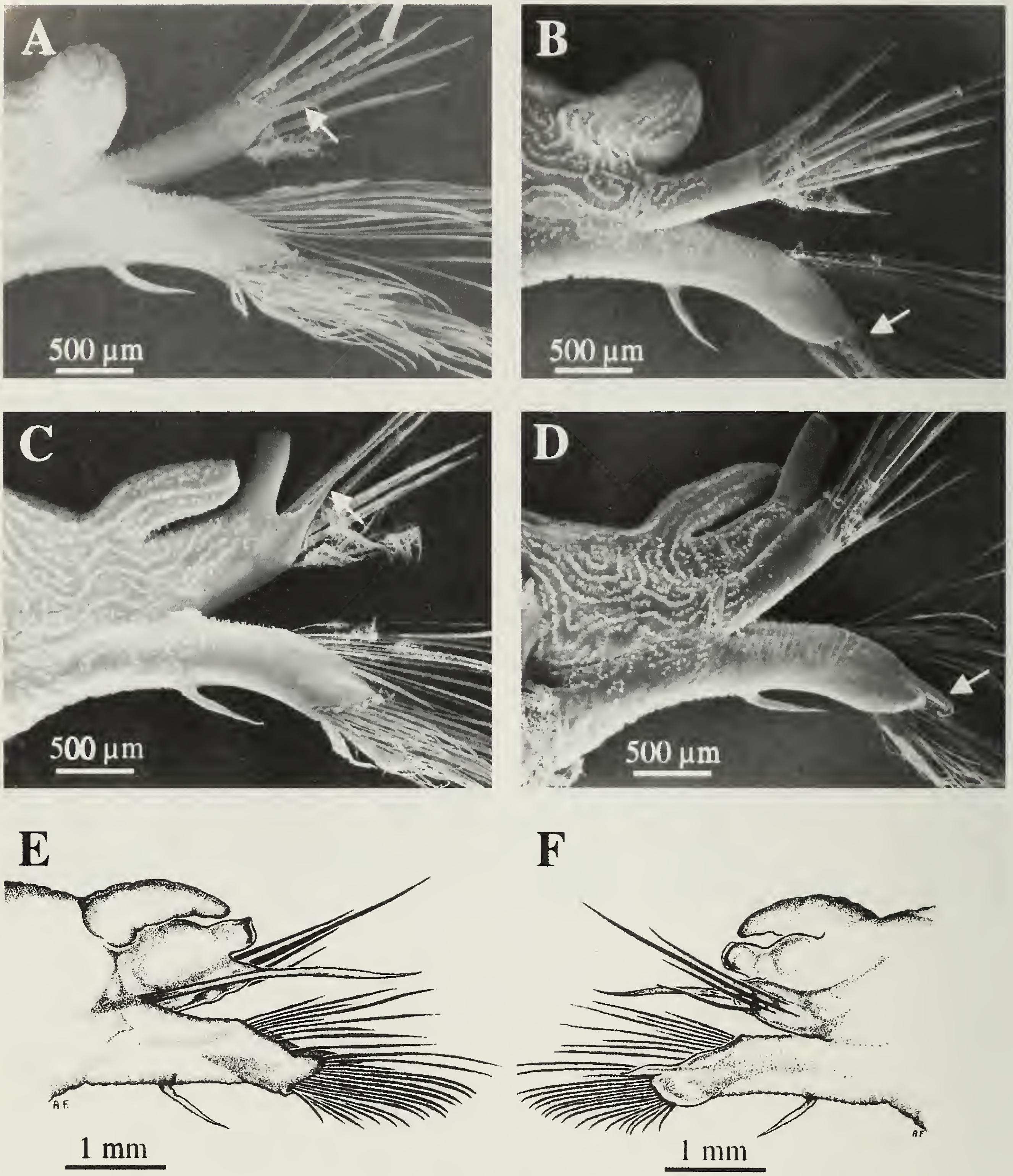


Fig. 4. A–D, SEM views; E and F, drawings. A. Posterior view of elytrigerous parapodium (segment 15). Arrow points to the ligule of the notopodium. B. Anterior view of the parapodium from the same segment. Arrow points to the ligule of the neuropodium. C. Posterior view of cirrigerous parapodium (segment 14). Arrow points to the ligule of the notopodium. D. Anterior view of the parapodium from the same segment. Arrow points to the ligule of the neuropodium. E. Posterior view of cirrigerous parapodium of segment 24, note the protruding acicula. F. Anterior view of the same parapodium depicted in E.

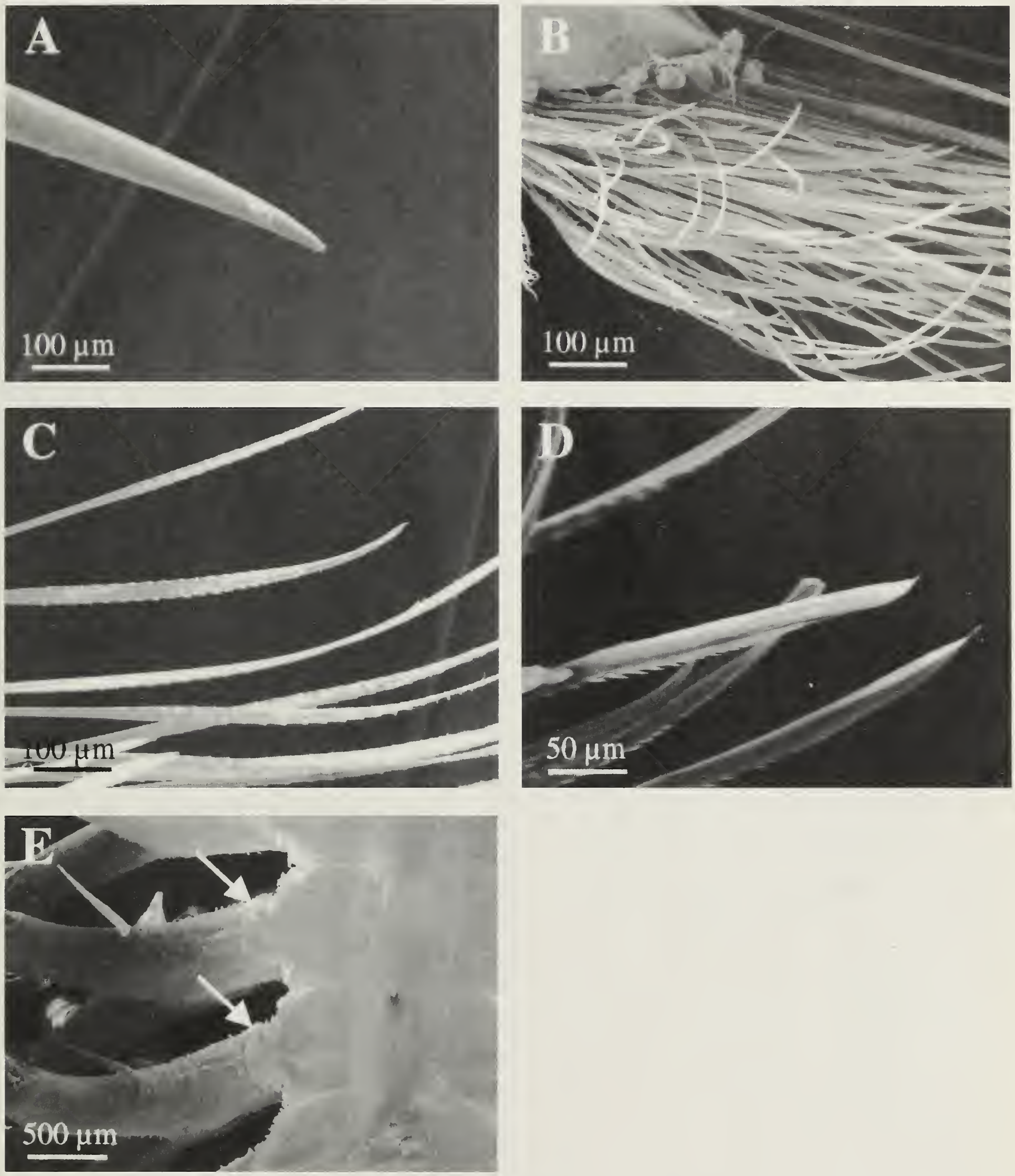


Fig. 5. A–E, SEM views. A. Tip of a notoseta. B. Feather-like neurosetae on the lower side of the neuropodium. C. Upper neurosetae. D. Detail of neurosetae tips. E. Ventral view of segments 11–14 showing inconspicuous nephridial papillae (white arrows).

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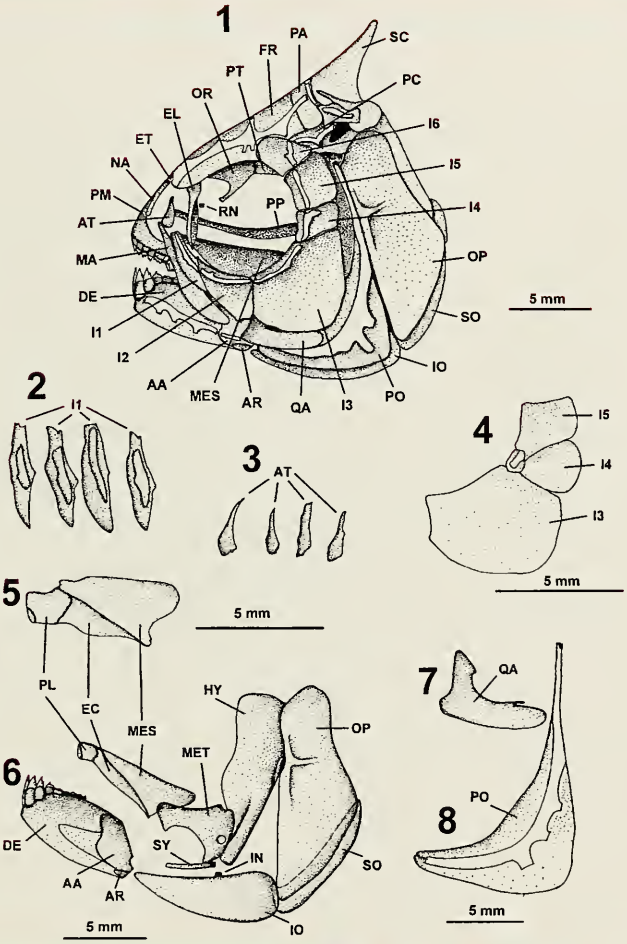

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Notes on the genus *Ruellia* (Acanthaceae) in Bolivia, Peru and Brazil

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Abstract.—Taxonomic notes on *Ruellia* are presented in preparation for the authors' forthcoming annotated checklist of Bolivian Acanthaceae. Four new species (*R. antiquorum, R. beckii, R. dolichosiphon* and *R. exserta*) are described and illustrated, two new combinations are made and variation in *R. haenkeana* is discussed leading to the recognition of two varieties and two forms in the species. The little-known *R. pearcei* is described, illustrated and discussed in relation to the widespread *R. brevifolia.*

Ruellia is the second largest genus of Acanthaceae in the flora of Bolivia with 27 species in the annotated checklist of Bolivian Acanthaceae (Wasshausen and Wood, in prep.). Most species are quite well defined and there are relatively few novelties, perhaps a reflection of the fact that *Ruellia* is not primarily Andean in distribution. The following notes update our taxonomic knowledge of the genus in Bolivia preliminary to the publication of our checklist.

1. Infra-specific Variation

Two species are especially variable but differ in the nature of their variation. *Ruellia puri* (Nees) Mart. ex Jackson varies greatly in the size of its corolla and the form of its inflorescence but detailed study of this widespread species is needed before the nature of this variation can be determined. However, *R. haenkeana* (Nees) Wassh. is restricted to a relatively small area of Bolivia and Peru and we have been able to recognize one very distinctive variety and two forms below, based mainly on striking color variations.

Ruellia haenkeana (Nees) Wassh.

Ruellia haenkeana (Nees) Wassh., Beitr. Biol. Pflanzen 63: 423 (1988). Type: Peru, *T. Haenke s.n.* (isotypes PR, GZU!).

var. *haenkeana*

This is the common morphotype of the species found throughout its range in Peru and Bolivia. It is characterized by its glabrous or puberulous leaves and crimson corollas.

var. **pilosa** Wasshausen & J. R. I. Wood, *var. nov.*

Fig. 1A–C

Ruellia haenkeana var. *pilosa* Wasshausen & J. R. I. Wood, *var. nov.* Type.—BOLIVIA: La Paz, Sud Yungas, Río Bopi, San Bartolomé (near Calisaya), 750–900 m, 1–22 Jul 1939, *B. A. Krukoff 10502* (holotype US!; isotypes NY!, K!).

Varietas nova corolla rosea et foliis pilosis distincta.

Additional specimens examined.—BOLIVIA: La Paz, Sud Yungas, Cerro Pelado, Puerto Linares-Yacumo, 1050 m, 14 Jul 1979, *Beck 1756* (US, LPB); Larecaja, San Carlos, Mapiri, 850 m, 11 May 1927, *Buchtien 1372* (US); ibid, 5 May 1927, *Buchtien 1373* (US); ibid, 16 Apr 1927, *Buchtien*

Fig. 1. A–C, *Ruellia haenkeana* var. *pilosa* (*Krukoff 10502*). A, Habit; B, Bracteole and calyx lobes; C, Corolla, stamens and stigma.

1378 (US); Caranavi, 19 km from Caranavi towards Bella Vista, 1240 m, 8 Jun 1996, *Wasshausen et al. 2109* (LPB, US); ibid, *Wasshausen et al. 2111* (CAS, LPB, US).

Leonard had annotated a number of duplicate *Krukoff 10502* collections as "*Ruellia nobilis* Leonard, type". Since he never published this epithet it simply remains a *nomen nudum.*

f. **lutea** Wasshausen & J. R. I. Wood, *forma nov.*

Fig. 2A–D

Ruellia haenkeana var. *haenkeana* forma *lutea* Wasshausen & J. R. I. Wood, *f. nov.* Type.—BOLIVIA: La Paz, Murillo, Valle de Zongo, 1300 m, 14 Jun 1980, *Beck 3681* (holotype US!; isotype LPB!).

Fig. 2. A–D, *Ruellia haenkeana* var. *haenkeana* f. *lutea* (*Beck 3681*); E–G, *Ruellia haenkeana* var. *haenkeana* f. *purpurea* (*Wasshausen & Wood 2144*). A, Habit; B, Bracts, bracteoles and calyx lobes; C, Bracteoles, calyx lobes, corolla, stamens, style and stigma; D, Corolla expanded; E, Habit; F, Bract, bracteoles and calyx lobes; G, Bracteoles, calyx lobes, corolla, stamens, style and stigma.

Forma nova corolla lutea et foliis glabris distincta.

Additional specimen examined.—BOLIVIA: La Paz, Murillo, Valle de Zongo, 1400–1600 m, 22 Apr 1982, *Solomon 7535* (MO, US).

f. **purpurea** Wasshausen & J. R. I. Wood, *forma nov.*
Fig. 2E–G

Ruellia haenkeana var. *haenkeana* forma *purpurea* Wasshausen & J. R. I. Wood, *f. nov.* Type.—BOLIVIA: La Paz, Caranavi, by road ascending serrania E of Caranavi towards Bolinda, 1200 m, 27 Jul 1998, *Wood & Wasshausen 13768* (holotype US!; isotypes K!, LPB).

Forma nova corolla purpurea et foliis puberulis distincta.

Additional specimens examined.—BOLIVIA: La Paz, Caranavi, Bolinda above Caranavi, 1300 m, 27 Jul 1998, *Wasshausen & Wood 2144* (US, LPB); Caranavi, 5 km from Serrania de Bella Vista on road to Caranavi, 1100 m, 8 Jun 1996, *Wasshausen et al. 2104* (CAS, GOET, LPB, K, US); Caranavi, Serrania de Bella Vista, 17.6 km N of the bridge at Carrasco, 1600 m, 11 Jun 1985, *Solomon 13984* (MO, US); Caranavi, N of Caranavi towards Linares, 17 km from Carrasco, 1700 m, 30 Jun 1983, *Beck 9242* (LPB, US); Caranavi, 10 km N of Bolinda, 1450 m, 2 Jun 1991, *Rea & Rea 10* (LPB, US).

The new variety and forms are restricted to moist hill forest in the area NE of La Paz, occurring very locally amongst typical *R. haenkeana*. Forma *lutea* is apparently restricted to the Zongo Valley whereas the other variety and form have their centers of distribution on the mountains north and east of Caranavi. Variety *pilosa* is the most distinct, as it has pilose leaves in addition to the distinctive pink corolla.

2. Species Clusters

Ruellia geminiflora Kunth and *R. brevifolia* (Pohl) Ezcurra are the best known and most widespread representatives of two species clusters, which require detailed study throughout South America. The group centered on *R. geminiflora* comprises blue-flowered perennial herbs of open savannas and cerrados. Most species have some kind of thickened rootstock, which enables the plant to survive burning, something that often stimulates the plants to flower. Apart from *R. geminiflora* there are only two representatives of this group in Bolivia, *R. bulbifera* Lindau and *R. brachysiphon* (Nees) Benth. & Hook. f. The three species differ from each other in indumentum and corolla size but are probably good species, although no final decision about their status and relationships can be made without detailed studies of the whole species complex, which is centered in Brazil.

R. brevifolia is part of a cluster of species, which includes *R. pearcei* Rusby, *R. gracilis* Rusby and *R. ruiziana* (Nees) Lindau. These are bushy perennials of forest regions and are more diverse in the Andes than in the lowland regions. The four species in Bolivia are reasonably well defined although a few specimens can be difficult to assign. One of them, *R. pearcei*, has been universally neglected since its description and so we include a description of its main characters below, together with the citations of a range of specimens:

Ruellia pearcei Rusby
Fig. 3A–D

Ruellia pearcei Rusby, Bull. New York Bot. Gard. 4: 429 (1907). Type.—BOLIVIA: Cochabamba, *Bang 2056* (lectotype NY!, here chosen; isolectotype US!)

Ruellia pearcei is related to *R. brevifolia* (Pohl) Ezcurra but can be distinguished from that species and all of its allies by its much longer corolla, which is 3.6–4.0 cm in length (up to 3.0 cm only in *R. brevifolia*) and differently shaped. The corolla tube has a very short cylindrical base and is then ventricose and gradually widened to the mouth whereas in *R. brevifolia* the basal cy-

Fig. 3. A–D, *Ruellia pearcei* (*Wasshausen et al. 2103*); E–H, *Ruellia brevifolia* (*Nee & Atha 50090*). A, Habit; B, Bracteoles and calyx lobes; C, Calyx lobes, corolla and stamens; D, Anther enlarged; E, Habit, F, Bracteoles and calyx lobes; G, Bracteoles, calyx lobes, corolla and stamens; H, Anther enlarged.

lindrical part is longer, the tube is then abruptly ventricose and even slightly contracted at the mouth (Fig. 3C, G). In habit, it is a perennial herb similar in general appearance to *R. brevifolia* but the leaves are always lanceolate or oblong-lanceolate, acuminate at the tip, glabrous and usually dark violet on the undersurface.

Habitat and distribution: R. pearcei is a local species of moist, tropical lowland forest along the eastern foothills of the Andes from the Santa Cruz area in Santa Cruz north through the Yungas of La Paz to southern Peru. Its distribution appears to be somewhat discontinuous, perhaps indicating that it has somewhat precise ecological demands. It is found between 600 and 1200 meters.

Additional specimens examined.—BOLIVIA: Beni, Ballivián, bridge Río Quibquibey, 4 km towards San Borja, 700 m, 14 Jul 1979, *Beck 1691* (LPB, US); Beni, Ballivian, E side of Serrania de Pilon Lajas, 21 km from Yacumo [15°17′S, 67°40′W], 1035 m, 17 May 1989, *Smith, Quintana & Garcia 13200* (K, LPB, MO); La Paz, Iturralde, Río San Antonio, 46 km from Ixiamas to Alto Madidi, 300 m, 17 Aug 1997, *Kessler et al. 11204* (LPB, US); La Paz, Tamayo, Haciend Ubito, Río Ubito Valley, 800 m, 12 Jul 1993, *Kessler 3803* (LPB, US); ibid, *Kessler 3836* (LPB, US); La Paz, Larecaja, 5 km from Consata to Sorato, 1250 m, 31 May 1995, *Kessler et al. 4402* (LPB, US); La Paz, Sud Yungas, 5 km from Chamaca to La Asunta, 850 m, 6 Oct 1995, *Kessler et al. 5793* (LPB, US); Sud Yungas, ca. 1.5 km W of El Sillar on road from Sapecho to Yacumo, 600 m, 28 Jul 1998, *Wood & Wasshausen 13783* (K, LPB); La Paz, Caranavi, outskirts of Caranavi, along streambank, 680 m, 27 Jul 1998, *Wasshausen & Wood 2139* (CAS, GOET, LPB, US); Caranavi, 17 km from Caranavi along road to Coroico, 500 m, 7 Jun 1996, *Wasshausen et al. 2103* (CAS, GOET, K, LPB, US); Nor Yungas, ca. 25 km below Yolosa on road to Caranavi, near Chala, 900 m, 19 Feb 1999, *Wood & Mondaca 14530* (K, LPB); La Paz, without exact location, Río San Juan, 1100 m, 7 Apr 1902, *Williams 258* (K, NY); Cochabamba, Chapare, Espiritu Santo, 160 km NE of Cochabamba, 750 m, Jan 1909, *Buchtien 2239* (US); ibid, *Buchtien 2309* (US); Cochabamba, Tiraque, on escarpment above El Palmar, 1200 m, 6 Jun 1998, *Wood 13673* (K, LPB); Chaparé, Río Espirito Santo, at beginning of ascent to Cochabamba, 1000 m, 19 Jun 1994, *Wood 8537* (K, LPB, US); Río Espirito Santo, ca. 20–25 km E of Villa Tunari on road to Cochabamba, 700 m, 27 Jul 1995, *Wood 10081* (K, LPB); Cochabamba area without precise department, *Bang 1223* (K, NY, US); Santa Cruz, Ichilo, ca. 2 km below Campamiento Mataratu, Amboró Park, 300 m, 30 May 1997, *Wood 12212* (K, US); Ichilo, near San Rafael de Amboró, S of Buenavista, 500 m, 21 May 1995, *Wood 9843* (K, LPB, US); Ichilo, Campamiento Mucuñucu. Amboró Park, 500 m, 28 May 1996 *Wood et al. 11150* (LPB): Amboró, SW of Buena Vista, near Macuñucu Camp, 450–500 m, 28 May 1996, *Brummitt et al. 19320* (K, LPB, US); ibid, *Wasshausen et al. 2060* (CAS, GOET, K, LPB, US); ca. 2 km below Campamiento Mataratú, Amboró Park, 300 m, 30 May 1997, *Wood 1212* (K, LPB); Santa Cruz, Valle Grande, 10 km from Loma Larga to Masicuri, 1450 m, 26 May 1996, *Kessler et al. 6104* (LPB, US).—PERU: Puno, Sandia, between San Juan de Oro and San Ignacio, 1200 m, 7 Jun 1982, *Wasshausen & Salas 1205* (K, MO, NY, US, USM); ibid, 1100 m, *Wasshausen & Salas 1211* (G, K, MO, NY, US, USM); without precise locality, 1863, *Pearce 276* (K), *596* (K); Huánuco, Pachitea, Honoria, Iparia Nationál Forest, along Río Pachitea, 11 km above Tournavista Village, 3–400 m 19 Jul 1967, *Schunke 2128* (K, US); Cuzco, Quispicanchis, Inambari bridge, 530 m, 4 Mar 1965, *Vargas 16185* (CUZ, US); ibid, 580, m, 8 Dec 1967, *Vargas 18455* (CUZ, US).

3. New Combinations

The following is a widespread species in the SW Amazon region although hitherto unnamed in most herbaria:

Ruellia nitida (Nees) Wassh. & J. R. I. Wood, *comb. nov.*

Ruellia nitida (Nees) Wassh. & J. R. I. Wood, *comb. nov. Arrhostoxylum nitidum* Nees, in Mart., Fl. Bras. 9(7): 59 (1847). Type.—BRAZIL: Amazonas: Borba, *Riedel s.n.* (holotype LE!; isotype GZU!).

This species appears to be common in moist lowland forest and we have seen many collections from northern Bolivia in the departments of Pando, Beni and Santa Cruz, and in western Brazil in the territory of Rondônia [e.g. *Prance et al. 5603* (K, NY, US,), *5876* (K, NY, US)], and in the states of Amazonia and Mato Grosso.

Ruellia multisetosa Rusby is not, in fact, a *Ruellia* and should be transferred to the genus *Suessenguthia* as follows:

Suessenguthia multisetosa (Rusby) Wassh. & J. R. I. Wood, *comb. nov.*

Suessenguthia multisetosa (Rusby) Wassh. & J. R. I. Wood, *comb. nov. Ruellia multisetosa* Rusby, Mem. New York Bot. Gard. 7: 362 (1927). Type.—BOLIVIA: La Paz: Huachi (alto Beni), 13 Aug 1921, *White 547* (holotype NY!).

4. New Species

The following four species are new, with three being from Bolivia and one being from Brazil. The Brazilian species is included because of its obvious similarity to the Bolivian novelty, *R. beckii.*

Ruellia antiquorum Wassh. & J. R. I. Wood, *sp. nov.*

Fig. 4A–C

Species nova speciosa R. patula *Jacq. revocans sed corolla longipedunculata statim recedens et inter speciorum austro-americanarum corolla coerulea, longipedunculata, solitare, axilliare valde distincta.*

Low perennial herb from a woody rootstock; stems to 25 cm long, trailing, terete, pilose with spreading multicellular trichomes, becoming slightly woody when old, occasionally sending down adventitious roots from the leaf nodes; leaves shortly petiolate, the petioles 1–4 mm long, the blades ovate or elliptic, acute at apex, abruptly narrowed to the base, 1.4–3.0 cm long, 0.5–2.2 cm wide, sparsely to densely pilose with white, multicellular trichomes which are sometimes bulbous at the base, the margin entire; inflorescence of solitary pedunculate flowers borne in the axils of the upper leaves, in each leaf pair, one axil fertile and one sterile; peduncles slender, glabrous, 1.5–5 cm long; bracteoles paired, borne 1–2 mm below flower, linear-oblong, 9–10 mm long, 0.75–1.00 mm wide, sparsely ciliate; calyx 1.4–1.7 mm long, divided to ca. 1 mm above base, the lobes narrowly oblong-elliptic, acute, glabrous or with a few short, marginal trichomes; corolla funnel-shaped, 55–70 mm long, ca. 2 mm wide at base, cylindrical for 25–30 mm, then gradually widened to 18–28 mm at the mouth, the tube dirty whitish-brown, pubescent on the exterior, the lobes blue, glabrous, spreading, broadly ovate to suborbicular, rounded, 10–16 mm long, 15–20 mm wide; stamens 4, didynamous, inserted ca. 30 mm above base of corolla, immediately above narrow cylindrical part of the tube; filaments glabrous, 5–6 mm long, the outer one in each pair ca. 1 mm longer than the other; anthers included in corolla tube, ca. 3 mm long, glabrous; style 40 mm long, pubescent, persistent; ovary glabrous; capsule 10–15 mm long, 4 mm wide, narrowly obovoid, glabrous, gland-dotted; seeds lenticular, ca. 3 mm long and wide, flattened, glabrous, the margin white.

Type.—BOLIVIA: Santa Cruz: Florida, Samaipata, on hill by radio transmitter, 1700 m, 17 Feb 1995, *J. R. I. Wood 9419* (holotype K!; isotypes LPB, US!).

Additional specimens examined.—BOLIVIA: Santa Cruz: Florida, El Fuerte, Samaipata, 1800 m, 15 May 1994, *Wood 8376* (K, LPB); ibid, 11 Sep 1994, *Wood 8630* (K, LPB, US); ibid, 2 May 1994, *Rojas & Vargas 1994* (BOL); ibid, 1550–1650 m,

Fig. 4. A–C, *Ruellia antiquorum,* A, B, (*Wood 9419*) C, (*Beck 6769*); D, E, *Ruellia dolichosiphon* (*Balcazar, Montero & Alvarez 2422*). A, Habit; B, Bracteoles, calyx lobes and corolla; C, Corolla expanded; D, Habit; E, Bracteoles, calyx lobes and corolla.

23 Mar 1981, *Beck 6769* (LPB, US); Río Piraí Gorge between Las Cuevas and Bermejo, 1300 m, *Wood 10561* (K, LPB).

Ruellia beckii Wassh. & J. R. I. Wood, *sp. nov.*

Fig. 5A–D

Inter species generis Ruellia *habitu scandenti, ramis lignosis, corolla luteo-viridi et antheris valde exsertis bene distincta.*

Woody liana reaching 10 m in height; stems woody, weakly quadrangular, sparsely scurfy-pubescent when young, glabrescent; leaves shortly petiolate, the petioles 0.8–1.0 cm long, the blades 6–14 cm long, 3–6 cm wide, broadly oblong-elliptic, acute, tapering at both ends, slightly asymmetric at the base, the margin obscurely repand, glabrous except for a few trichomes on the veins, cystoliths common above; inflorescence a small, terminal subumbelliform cyme, the branches arising in opposite pairs, the branches scurfy-pubescent; bracteoles ovate-triangular, 4–8 mm long, 2–3 mm wide, glabrescent or with a few scurfy marginal trichomes; calyx 5-lobed to just above the base, lobes 12–14 mm long, 5–6 mm wide, oblanceolate to obovate, imbricate, glabrous or with a few scattered marginal trichomes; corolla ca. 38 mm long, tube ca. 7 mm wide at base, bulbous, then gradually narrowed to 4 mm at 13 mm above base, then abruptly widened to ca. 14 mm, shortly glandular pubescent on the exterior, lobes broadly oblong, 7 mm long, 6.5 mm wide, rounded, yellow-green; stamens 4, didynamous, inserted ca. 10 mm above base of corolla tube, the outer of each pair inserted ca. 1 mm below the inner; filaments 22 mm long, glabrous; anthers exserted 10–15 mm, 6 mm long, glabrous, sagittate at base; ovary glabrous except for the puberulent tip; style 45 mm long, pubescent, stigma bifurcate; capsule not known.

Type.—BOLIVIA: La Paz: Caranavi, 20 km along road from Caranavi to Carrasco, 1200 m, 1 Jul 1983, *S. G. Beck 9298* (holotype US!; isotype LPB).

Only known from the type locality where it was growing in hill forest.

Ruellia exserta Wassh. & J. R. I. Wood, *sp. nov.*

Fig. 5E–H

A R. beckii *inflorescentia spicata unilaterale et lobis calycis angustioribus, distantibus, corolla parviori diagnoscenda.*

Woody liana to 10 m, "climbing over trees"; stems woody, rounded, glabrous below, scurfy above; leaves petiolate, the petioles 0.6–2.0 cm long, the blades 6–23 cm long, 2.0–10.5 cm wide, lanceolate, ovate or oblong-elliptic, acuminate at apex, tapering to a sometimes asymmetric base, the margin obscurely crenate, glabrous except for a few scurfy trichomes on the veins, cystoliths common above; inflorescence of small, apparently one-sided spike-like cymes terminal on branches arising alternately from each leaf axil; pedicels 3–5 mm long with numerous cystoliths; bracteoles ovate-triangular, 2–6 mm long, 1.5–2.5 mm wide, pubescent on the margins; calyx 5-lobed to just above the base, lobes 8–9 mm long, 2 mm wide, oblong, obtuse, distant, glabrous above, puberulent or sometimes scurfy glandular-pubescent below; corolla ca. 28 mm long, tube at base 2.0–4.5 mm wide, cylindrical for ca. 10 mm, not or hardly narrowed, then gradually widened to 12 mm at mouth, the exterior pubescent and with scattered subsessile glands, the lobes ovate, 6 mm long and 5 mm wide, rounded, yellow-green or green; stamens 4, didynamous, inserted ca. 17 mm above base of corolla tube; filaments ca. 22 mm long, glabrous; anthers 5 mm long, glabrous, sagittate at base, exserted 10–13 mm; ovary pubescent; style 32–35 mm long, pubescent with a few glands, stigma bifurcate; capsule oblanceolate, apiculate, ca. 20 mm long, 8 mm wide, shortly and densely pubescent, 4-seeded; seeds suborbicular, 3.5 mm long, 3

Fig. 5. A–D, *Ruellia beckii* (*Beck 9298*); E–H, *Ruellia exserta* (*de Santos et al. 1798*). A, Habit; B, Calyx lobes; C, Calyx lobes, disc and ovary; D, Corolla, stamens, style and stigma; E, Habit; F, Calyx; G, Calyx lobes, disc and ovary; H, Corolla, stamens, style and stigma.

mm wide with a pale margin and scurfy surface.

Type.—BRAZIL: Mato Grosso: N of Xavantina on Xavantina-São Felix road, 40 km N of base camp at [12°54′S, 51°52′W], 14 Jun 1968, *R. R. de Santos, R. Souza & A. Ferreira 1798* (holotype K!; isotype US!).

Additional specimens examined.—BRAZIL: Pará: ca. 6 km on road NW of Camp 3-Alfa towards Camp 4-Alfa [5°47′S, 50°34′W], 250 m, 9 Jun 1982, *Sperling et al. 6013* (K, NY); Marabá, 24 May 1982, *Secco et al. 300* (MB, NY); Mato Grosso: Cuibá-Porto Velho, 15 km from frontier with Rondônia, Patronal District, Vila Bela de Santissima Trinidade [12°13′S, 60°59′W], 9 Jun 1984, *Cid et al. 4387* (K, NY, US); 16 km N of [12°51′S, 51°52′W], ca. 270 km N of Xavantina, 20 May 1968, *de Santos et al. 1483* (K, NY, US); Territory Rondônia: Mun. de Ariquemes, Mineração Mibrasa, Sector Alto Candeias, km 128, [10°35′S, 63°35′W], SE of Ariquemes, 14 May 1982, *Texeira 440* (INPA, NY); Mun. de Costa Marques, Chapada dos Parecís, Distrito de Alta Floresta, estrada P-56, km 17 [11°12′S, 62°63′W], 16 Jun 1984, *Cid 4581* (INPA, NY).

Habitat and distribution: Apparently an uncommon Brazilian endemic plant of Pará, Mato Grosso and Territory Rondônia, growing on roadsides, in disturbed primary forest and in swampy gallery forest around 250 m.

Ruellia beckii and *R. exserta* are closely related species, being similar in habit, leaf shape and flower color. After some hesitation, we felt confident in treating them as different species, since the calyx is very different in the two species and the corolla is somewhat so. Possibly more important is the inflorescence, ± umbellate in *R. beckii* but in apparently one-sided spikes in *R. exserta.* Although we have only seen one collection of *R. beckii,* there are various collections of *R. exserta,* all of which maintain the distinctive inflorescence, calyx and corolla character even though collected from different states in Brazil. Additionally, it is highly improbable that an Andean species such as *R. beckii* should be widespread in the Brazilian lowlands without any intermediate populations.

Ruellia dolichosiphon Wassh. & J. R. I. Wood, *sp. nov.*
Fig. 4D–E

Ob inflorescencia terminale et calyce quam bracteis bracteolisque longiore Ruellia glischrocalyx *Lindau tingit sed ramis albo-pilosis, foliis ovatis, corolla longituba, lobis roseis distincta.*

Stout herb to 50 cm; stem rounded, densely white-pilose; petioles 0.4–1.4 cm long, white pilose; blades 3.5–8.5 cm long, 2.0–3.5 cm wide, ovate, acute, base abruptly narrowed and then attenuate onto the petiole, sparsely white-pilose, the trichomes mostly on the upper surface, margins and veins, cystoliths very small, obscure, margin slightly undulate; inflorescence of short terminal racemes; pedicels 2–4 mm long, glandular-pilose; bracts at base of pedicel, 6–8 mm long, 1.0–1.5 mm wide, subpetiolate, linear-oblanceolate, rounded, pilose with large, brownish trichomes; bracteoles 5–6 mm long, 1.0–1.5 mm wide, linear-elliptic or linear-oblanceolate, weakly acute, pilose with large brownish trichomes; calyx much longer than the bracts, subequally 5-lobed to just above the base, lobes 20–22 mm long, 4 mm wide, oblong-lanceolate, obtuse, one slightly larger than the others, ciliate and with a thick line of brownish trichomes along the midrib, a few trichomes noticeably longer than the others; corolla funnel-shaped, the tube pubescent below, ca. 47 mm long, 4 mm wide at base, then narrowed to 1.5 mm after ca. 4 mm, before widening gradually to 6 mm at mouth, pale, probably dirty white, the lobes ca. 8 mm long, ca. 15 mm wide, broadly ovate, acute, pink, subglabrous outside; anthers not seen; style sparsely pilose; ovary minutely and densely pilose; capsule not seen.

Type.—BOLIVIA: Pando: Manuripi,

Communidad Lago, 17 km NE of Pursima on road to Chivé [05°0012′S, 57°3581′W] 220 m, 29 Jun 2001, *J. Balcazar, J. C. Montero & J. Alvarez 2422* (holotype USZ!).

Habitat and distribution: Only known from the type collection in Amazonian rainforest in northern Bolivia.

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Literature Cited

Ezcurra, C. 1993. Systematics of *Ruellia* (Acanthaceae) from South America.—Annals of the Missouri Botanical Garden 80:747–845.

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Phylogeography and systematic notes on two species of gracile mouse opossums, genus *Gracilinanus* (Marsupialia: Didelphidae) from Brazil

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Abstract.—Although they were described more than a century ago, *Gracilinanus agilis* and *Gracilinanus microtarsus* are still mistaken for each other and their status as valid species has been challenged. Morphological studies are rare and accounts of molecular characters are even scarcer. In this paper, we present the first phylogeographic analysis for these two species based on mitochondrial cytochrome *b* sequences and provide a morphological analysis and extended diagnosis for both species. We show that *G. agilis* and *G. microtarsus* are valid species, geographically bounded and distinguishable by morphological and molecular characters. *Gracilinanus agilis* is geographicaly widespread and genetically more homogenous, with low levels of divergence between three clades in central, northeastern and eastern Brazil. *Gracilinanus microtarsus* occurs in southeastern and southern Brazil, being comprised of two clades that show a considerable level of sequence divergence. Although at this time we regard these two clades as geographic units of *G. microtarsus*, it is possible that more samples will show that there is greater diversity in this group than the current taxonomy recognizes.

The genus *Gracilinanus* (Gardner and Creighton, 1989) comprises delicately built opossums, generally smaller than individuals of *Marmosops* and *Marmosa* with which they are often confused. The dorsal coloration varies considerably, from bright reddish-brown to pale grayish-brown; the ventral pelage is often cream or pale orange with gray-based hairs, but sometimes white or pure cream as in *G. emiliae*. The tail is moderately long to very long, with non-petiolate central hairs in each caudal-scale triplet. Among diagnostic cranial characters, the more trenchant are the highly fenestrated palate, with maxillary vacuities often present, and bullae with an anteromedian strut forming a secondary foramen ovale (R. S. Voss, in litt.). Other characters and detailed descriptions of the genus can be found in Tate (1933) and Creighton (1984) under the *microtarsus* section of the formerly inclusive genus *Marmosa*, and in Gardner & Creighton (1989) and Hershkovitz (1992). Costa (in press) discusses the phylogenetic affinities of *Gracilinanus* among the didelphids, based on cytochrome *b* (cyt *b*) sequences and morphological characters.

The genus ranges from the Guiana region, through Venezuela and Colombia, bordering the western limit of the Amazon basin with scattered localities in Peru, Bolivia and Paraguay, to the mouth of the Paraná river in Argentina, then northeast along the coast and interior tablelands of Brazil, reaching the southeastern border of Amazonia. It is apparently absent from all, or at least the majority of the lowland Amazon basin in Brazil as specimens recorded from this vast region were either misidentified (see Patton et al. 2000, Voss et al. 2001) or are of questionable occurrence (Patton and Costa 2003).

Tate (1933) provided the most comprehensive analysis of the taxa currently included in *Gracilinanus* under the "*microtarsus* section" of his monograph. Later, Gardner & Creighton (1989) established the genus *Gracilinanus* to include six species: *G. aceramarcae* (Tate, 1931), *G. agilis* (Burmeister, 1854), *G. dryas* (Thomas, 1898), *G. emiliae* (Thomas, 1909), *G. marica* (Thomas, 1898) and *G. microtarsus* (Wagner, 1842). Yet, the number of species within the genus remains debatable since Hershkovitz (1992), in his recent revision, recognized the same six species listed above but described three new ones from the Andean slopes of Colombia (*G. longicaudus* and *G. perijae*) and Peru (*G. kalinowskii*), and recorded what he considered an undescribed additional species from Ecuador. Voss et al. (2001) subsequently defined a new genus, *Hyladelphys,* for *G. kalinowiskii.* In addition, these authors regard *G. longicaudus* as a junior synonym of *G. emiliae,* and they pointed out that Hershkovitz's undescribed "*Gracilinanus*" from Ecuador is a *Marmosa* (sensu stricto).

In the present report we address two species: *G. agilis* and *G. microtarsus.* The range of *G. microtarsus* includes the mesic habitats of the Atlantic Forest in southeastern Brazil south to Rio Grande do Sul, while *G. agilis* is more widespread in Brazil, occurring primarily in dry and gallery forests of the interior plateau, isolated areas in the Northeast, and through the wet and dry forests of northeastern Argentina, Paraguay, and Bolivia (Emmons & Feer 1997, Eisenberg & Redford 1999). Although *G. agilis* and *G. microtarsus* were described nearly 150 years ago, the lack of adequate comparisons between them has raised doubts about their validity as species. Although both Hershkovitz (1992) and Gardner (1993) recognize *G. agilis* and *G. microtarsus,* the first author suggests that *G. microtarsus* could be "no more than a subspecies of *G. agilis*", while the second author states that "the forms *agilis* and *microtarsus* may prove to be conspecific". Here we provide a phylogeographic analysis of geographic samples of both *G. microtarsus* and *G. agilis,* and present morphological comparisons and systematic comments. We also include a third species (*G. aceramarcae,*' a rare opossum known only from the type locality in Bolivia [Tate 1931] and two localities in southern Peru [Eisenberg & Redford 1999; L. H. Emmons, in litt.]) in the molecular analysis to provide a more representative sampling of the taxonomic diversity within the genus.

Methods

Molecular analyses.—Our samples consist of a single specimen from Vilcabamba, Peru, tentatively identified as *G. aceramarcae,* and 34 individuals of *G. agilis* and *G. microtarsus* from 24 localities in Brazil (Fig. 1), including topotypes of *G. microtarsus* (from Ipanema, São Paulo; see Appendix). We also have samples from a locality in the same region where the type specimen of *G. agilis* was collected (Lagoa Santa, Minas Gerais).

We extracted DNA from frozen or ethanol-preserved liver tissue using the Chelex® method (Walsh et al. 1991) and amplified the cytochrome *b* (cyt *b*) gene by the Polymerase Chain Reaction (PCR), (Saiki et al. 1988) using primer pairs MVZ05 in combination with MVZ04 and/or MVZ 16. The double-strand PCR products were cleaned using the DNeasy™ Tissue Kit (QIAGEN, Inc.) and submitted to cycle sequencing reactions that utilized the dRhodamine Terminator Cycle Sequencing Kit and Protocol (PE Biosystems, Inc.), and primers MVZ05, MVZ04 and MVZ65. All sequencing was done in an ABI Prism 377 automated sequencer. Sequences were aligned by eye using Sequence Navigator (Version 1.0.1, Applied Biosystems, Inc.). The data set varied from 518 bp to 801 bp of the cyt *b* sequence, each sequence beginning with the start codon of the gene. A Nexus file of all sequences is available from the authors upon request.

Relationships among different haplotypes

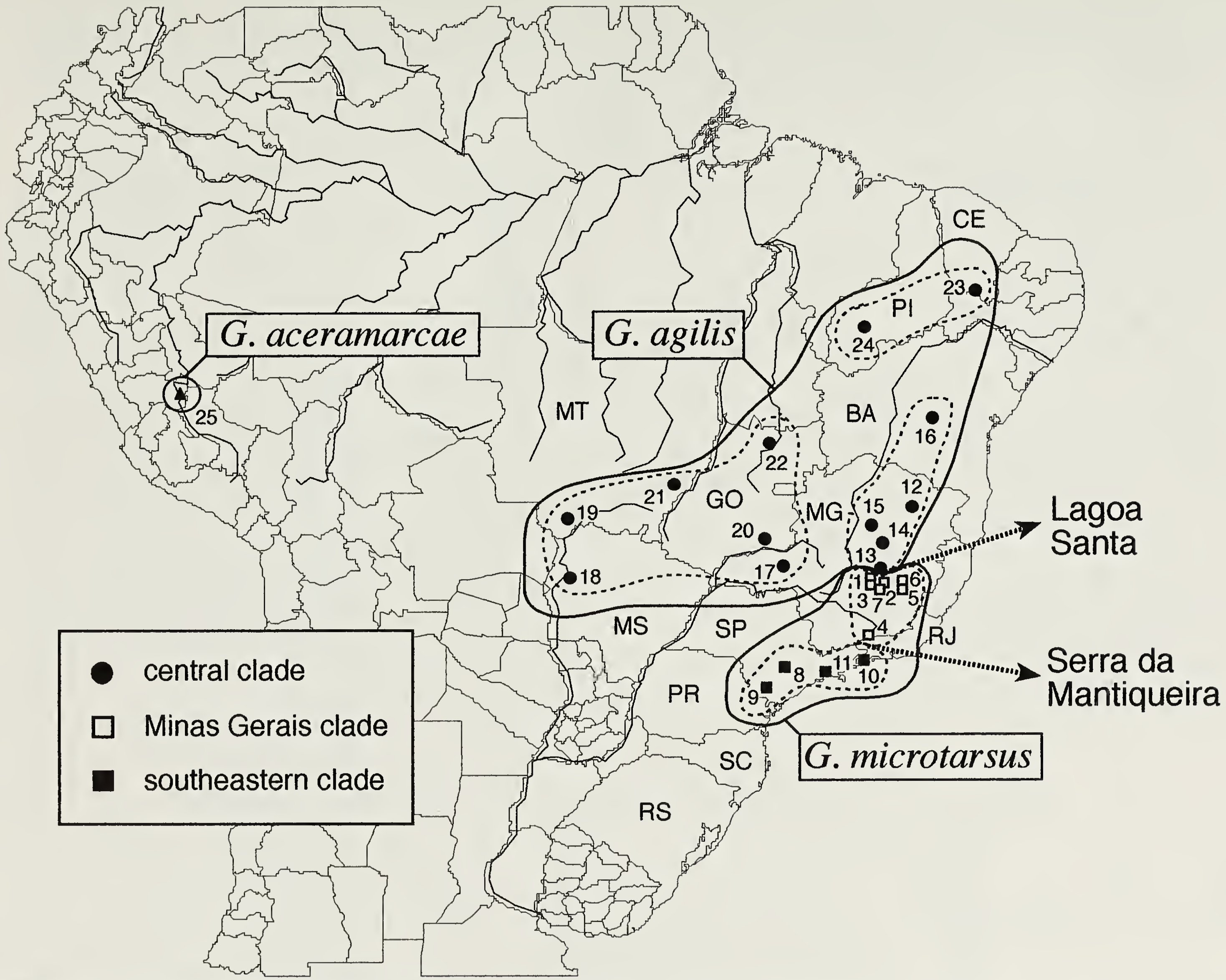

Fig. 1. Map showing the distribution of our samples and the taxa and geographic clades recognized in this report. The widespread species *Gracilinanus agilis* contacts *G. microtarsus* near Lagoa Santa, MG (locality 1; the type locality of *G. agilis*). The two clades of *G. microtarsus* are separated by the Serra da Mantiqueira mountain range. Solid lines delimit species boundaries and dashed lines indicate clades within species (see Fig. 3). Numbered localities are georeferenced in the Appendix and correspond to the same localities labeled in Fig. 3. Brazilian states are: Ceará (CE), Piauí (PI), Bahia (BA), Minas Gerais (MG), Goiás (GO), Mato Grosso (MT), Mato Grosso do Sul (MS), São Paulo (SP), Rio de Janeiro (RJ), Paraná (PR), Santa Catarina (SC), and Rio Grande do Sul (RS).

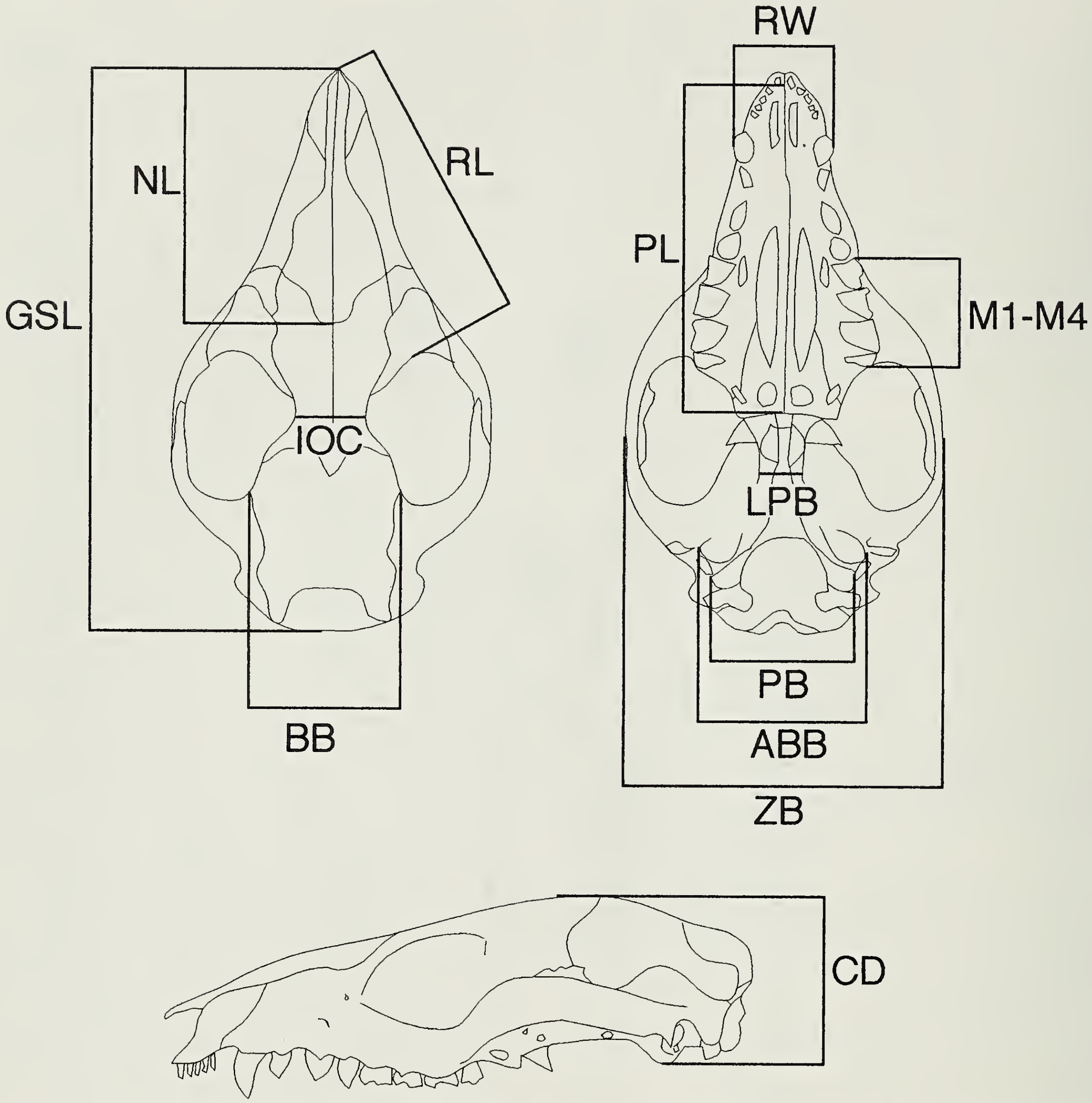

Fig. 2. Thirteen cranial measurements recorded from *G. agilis* and *G. microtarsus*, as follows: GSL—Greatest skull length: from the most anterior margin of the rostrum to the posterior margin of the occiput. ZB—Zygomatic breadth: greatest breadth across the zygomatic arches. BB (measurement 7 of Tate 1933:236)—Braincase breadth: breadth taken above the squamosal root of the zygomatic arch. IOC—Least interorbital constriction: minimal breadth across the roof of the skull above the orbits. RL—Rostral length: from the anterior margin of the orbit to the midline tip of the nasals. NL—Nasal length: midline distance from anterior tip to posterior margins of nasals. RW—Rostral width: width of the rostrum at the level of the canines. M1–M4—Molar toothrow length: taken on the labial margin of the toothrow from M1 to M4. LPB (measurement 1 of Tate 1933:236)—Least pterygoid breadth: least breadth across pterygoid bones. PB (measurement 3 of Tate 1933:236)—Petrosal breadth: breadth across tympanic process of pars petrosa. ABB (measurement 2 of Tate 1933:236)—Alisphenoid bulla breadth: breadth across tympanic processes of alisphenoid. PL—Palatal length: midline distance from the posterior margins of the first upper incisor to the posterior margin of the hard palate. CD—Cranial depth: vertical distance between ventral margins of bullae and top of cranium.

were examined by maximum parsimony using PAUP*, version 4.0b8 (Swofford 1999). Trees were constructed using the heuristic search option via stepwise addition, with 10 replicates and random sequence addition of taxa. The support for internal branches was evaluated by decay indices (Bremer 1988) and bootstrap analyses

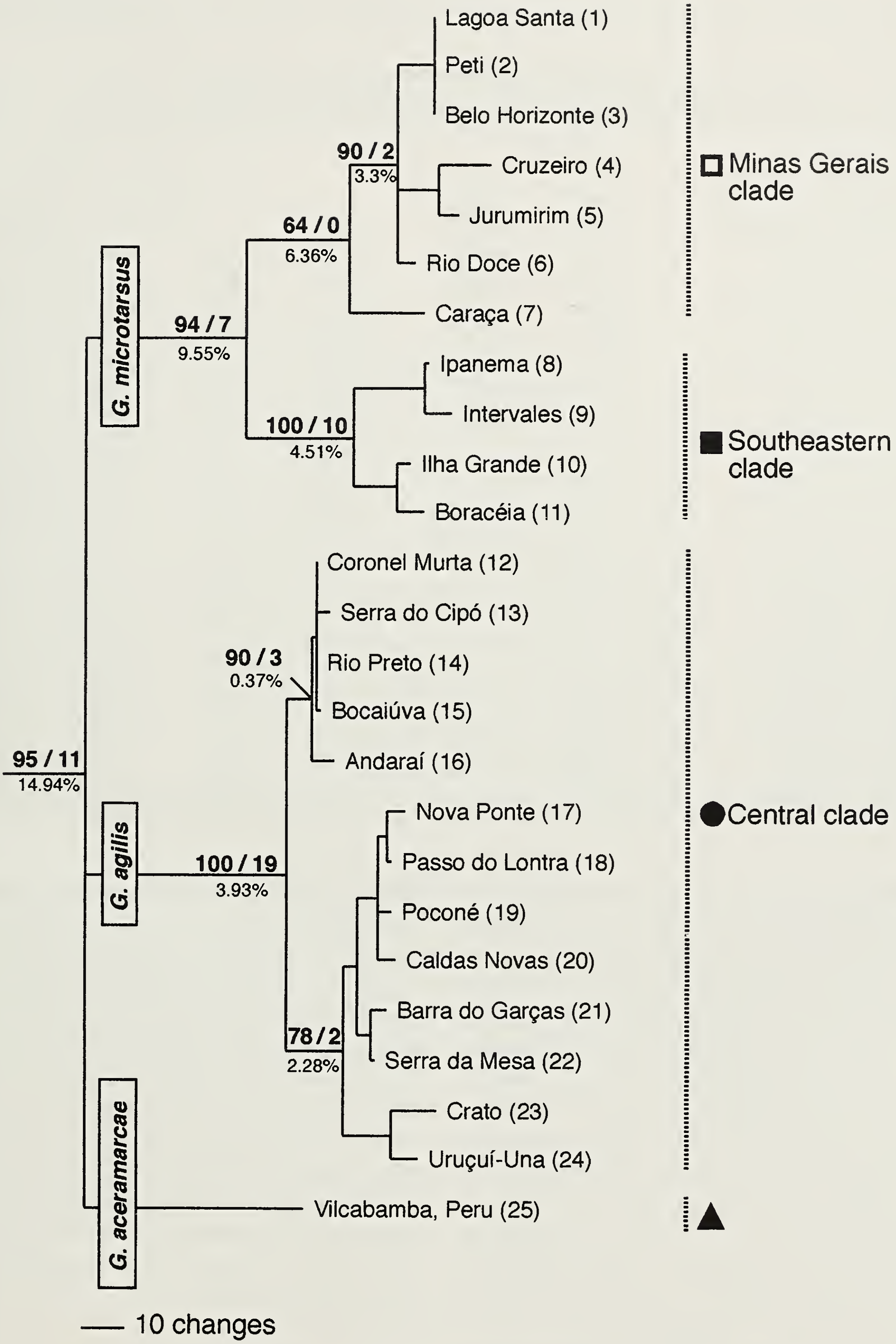

Fig. 3. Bootstrap consensus tree based on maximum parsimony analysis of cyt *b* gene haplotypes (initial 801bp). *Gracilinanus agilis* and *G. microtarsus* are reciprocally monophyletic and highly divergent species. The two clades within *G. microtarsus* are also highly divergent. Sequences of *Marmosops incanus, Thylamys* sp., and *Marmosa murina* were used as outgroups to root the tree. Bold numbers at internal nodes are bootstrap values/decay indices; percentages are average Kimura two-parameter (K2p) distances. Voucher catalog numbers and localities for each haplotype are given in the gazetteer and correspond to the same localities on the map in Fig. 1. Consistency index = 0.593; homoplasy index = 0.407; retention index = 0.761.

Table 1.—Kimura 2-parameter distances among cyt-b haplotypes of *Gracilinanus*, with *Marmosops incanus* also included.

	LC49 *M. incanus*	MNRJ31445 *G. microtarsus*	MNRJ31447 *G. microtarsus*	MCNM299 *G. microtarsus*	LC1 *G. microtarsus*	RM26 *G microtarsus*
LC49 *M. incanus*						
MNRJ31445 *G. microtarsus*	21.00%					
MNRJ31447 *G. microtarsus*	21.00%	0.00%				
MCNM299 *G. microtarsus*	19.01%	0.00%	0.00%			
LC1 *G. microtarsus*	17.91%	4.95%	4.95%	4.94%		
RM26 *G. microtarsus*	17.01%	1.98%	1.98%	2.00%	3.95%	
MCNM394 *G. microtarsus*	18.33%	2.82%	2.82%	2.80%	3.22%	3.00%
RM4 *G. microtarsus*	18.50%	6.32%	6.32%	6.37%	6.71%	5.76%
LPC805 *G. microtarsus*	20.77%	10.01%	10.01%	9.44%	9.60%	8.05%
MVZ182056 *G. microtarsus*	19.77%	10.26%	10.26%	10.21%	10.36%	9.50%
LP40 *G. microtarsus*	19.23%	8.60%	8.60%	8.59%	9.60%	8.03%
MAM427 *G. microtarsus*	20.67%	10.86%	10.86%	9.81%	10.59%	9.27%
LC189 *G. agilis*	19.02%	14.75%	14.75%	14.00%	16.56%	14.15%
MNRJ31396 *G. agilis*	18.56%	14.36%	14.36%	14.31%	15.44%	13.72%
YL64 *G. agilis*	19.03%	14.75%	14.75%	14.00%	16.56%	14.14%
LPC241 *G. agilis*	19.56%	14.76%	14.76%	14.02%	16.34%	13.93%
AP22 *G. agilis*	18.85%	14.59%	14.59%	13.80%	16.33%	13.93%
LPC304 *G. agilis*	20.53%	15.22%	15.22%	14.53%	17.16%	16.29%
LPC599 *G. agilis*	19.87%	15.23%	15.23%	14.54%	16.90%	16.03%
LPC581 *G. agilis*	19.40%	15.05%	15.05%	14.31%	16.72%	15.43%
UHECO4722 *G. agilis*	19.23%	14.73%	14.73%	14.15%	16.53%	15.25%
LPC476 *G. agilis*	18.66%	13.72%	13.72%	13.62%	14.99%	14.28%
UHESM1759 *G. agilis*	18.69%	14.58%	14.58%	13.75%	15.99%	14.79%
LPC250 *G. agilis*	19.72%	14.08%	14.08%	12.94%	14.98%	13.65%
UUP1292 *G. agilis*	19.49%	14.51%	14.51%	13.20%	15.10%	13.65%
LHE1342 *G. aceramarcae*	19.89%	15.71%	15.71%	14.28%	15.66%	13.85%

(Felsenstein 1985), with 100 bootstrap replicates each consisting of a full heuristic search as described above. On the assumption that *Gracilinanus* is monophyletic (Gardner & Creighton 1989; Voss et al. 2001), all trees were rooted by including sequences of *Marmosops incanus, Marmosa murina,* and *Thylamys* sp. as outgroups. Sequence divergence was calculated using the Kimura two-parameter algorithm (Kimura 1980) as implemented in PAUP*.

Morphological analyses.—Statistical analyses were performed using the computer package StatView (Version 5.0, SAS Institute Inc.). For analysis of external morphological data, we used 71 specimens of *G. agilis* from 10 localities, and 25 specimens of *G. microtarsus* from 9 localities in the states of São Paulo, Rio de Janeiro, and Minas Gerais (see Appendix and Fig. 1). External measurements (total length and lengths of tail, ear, and hindfoot including claws) and weight (mass) were taken from specimen labels. We subtracted tail length from total length to obtain the length of the head and body. For analyses of cranial measurement data, we examined 60 specimens of *G. agilis* and 16 of *G. microtarsus.* Each individual was classified as young or adult, adults being defined as those individuals possessing a complete set of teeth (including the permanent third premolar, and four molars). We recorded 13 cranial measurements (Fig. 2) taken with digital calipers from each individual.

Results and Discussion

Phylogenetic analysis.—The maximum parsimony analysis resulted in 80 most-parsimonious trees of 672 steps each, with 215 of the 801 characters parsimony-informa-

Table 1.—Extended.

	MCNM394 *G. microtarsus*	RM4 *G. microtarsus*	LPC805 *G. microtarsus*	MVZ182056 *G. microtarsus*	LP40 *G. microtarsus*	MAM427 *G. microtarsus*
LC49 *M. incanus*						
MNRJ31445 *G. microtarsus*						
MNRJ31447 *G. microtarsus*						
MCNM299 *G. microtarsus*						
LC1 *G. microtarsus*						
RM26 *G. microtarsus*						
MCNM394 *G. microtarsus*						
RM4 *G. microtarsus*	6.71%					
LPC805 *G. microtarsus*	9.16%	9.52%				
MVZ182056 *G. microtarsus*	9.79%	10.46%	1.34%			
LP40 *G. microtarsus*	8.24%	8.56%	3.88%	4.39%		
MAM427 *G. microtarsus*	9.64%	9.52%	4.60%	5.17%	1.43%	
LC189 *G. agilis*	14.75%	14.10%	15.98%	14.98%	14.31%	14.80%
MNRJ31396 *G. agilis*	13.88%	14.38%	14.57%	14.20%	13.50%	14.79%
YL64 *G. agilis*	14.74%	14.09%	15.97%	14.97%	14.31%	14.80%
LPC241 *G. agilis*	14.69%	13.88%	15.98%	14.97%	14.33%	15.14%
AP22 *G. agilis*	14.54%	13.87%	15.80%	14.73%	14.10%	14.64%
LPC304 *G. agilis*	15.98%	16.04%	17.85%	15.78%	14.85%	16.82%
LPC599 *G. agilis*	15.51%	15.80%	17.43%	15.76%	14.41%	16.41%
LPC581 *G. agilis*	15.71%	15.52%	16.60%	16.50%	14.58%	15.91%
UHECO4722 *G. agilis*	15.56%	15.33%	16.10%	15.82%	14.00%	15.10%
LPC476 *G. agilis*	14.04%	14.94%	15.76%	15.83%	14.62%	16.04%
UHESM1759 *G. agilis*	14.65%	14.69%	16.45%	15.84%	14.44%	15.76%
LPC250 *G. agilis*	14.01%	15.21%	16.27%	16.12%	15.11%	15.92%
UUP1292 *G. agilis*	14.43%	14.75%	16.36%	15.04%	15.09%	16.52%
LHE1342 *G. aceramarcae*	14.88%	11.76%	15.24%	16.10%	13.86%	14.68%

tive. We present only the bootstrap consensus tree (Fig. 3) since it identifies the well-supported nodes and its topology does not differ significantly from the strict consensus of the most-parsimonious trees. A matrix of Kimura 2-parameter (K2p) distances among the 25 unique haplotypes of *Gracilinanus,* plus *Marmosops incanus,* is given in Table 1.

The bootstrap tree (Fig. 3) shows a basal, unresolved trichotomy between the *G. aceramarcae* sample, a clade from central Brazil (Figs. 1 and 3; localities 1–11), and a third clade formed by two groups from eastern Brazil (Figs. 1 and 3; localities 12–24). These three clades are highly divergent from each other, differing by an average K2p distance of about 15%. The two clades from eastern Brazil [Minas Gerais (localities 1–7; Fig. 1) and Southeastern clades (localities 8–11)] are also quite divergent (average K2p value of 9.55%), remarkably so considering the small geographic distances separating them. On the other hand, there is a surprisingly amount of homogeneity among the samples of the Central clade since its representatives come from widely separated localities but are only 3.93% divergent on average. Yet, the Central clade is divided into sub-clades: a more divergent one encompassing the northern part of Minas Gerais and central Bahia (localities 12–16; Fig. 1), another in the Northeast (localities 23–24), and a wide-spread third in central Brazil in the states of Mato Grosso, Mato Grosso do Sul, Goiás and western Minas Gerais (localities 17–22).

The bootstrap tree and the strict consensus of the parsimony trees differ only in the placement of two samples. First, *G. aceramarcae* is sister to *G. agilis* and *G. microtarsus* in the strict consensus tree, but with

Table 1.—Extended.

	LC189 *G. agilis*	MNRJ31396 *G. agilis*	YL64 *G. agilis*	LPC241 *G. agilis*	AP22 *G. agilis*	LPC304 *G. agilis*
LC49 *M. incanus*						
MNRJ31445 *G. microtarsus*						
MNRJ31447 *G. microtarsus*						
MCNM299 *G. microtarsus*						
LC1 *G. microtarsus*						
RM26 *G. microtarsus*						
MCNM394 *G. microtarsus*						
RM4 *G. microtarsus*						
LPC805 *G. microtarsus*						
MVZ182056 *G. microtarsus*						
LP40 *G. microtarsus*						
MAM427 *G. microtarsus*						
LC189 *G. agilis*						
MNRJ31396 *G. agilis*	0.60%					
YL64 *G. agilis*	0.00%	0.60%				
LPC241 *G. agilis*	0.76%	1.00%	0.76%			
AP22 *G. agilis*	0.13%	0.84%	0.13%	0.88%		
LPC304 *G. agilis*	4.49%	3.31%	4.49%	4.83%	4.66%	
LPC599 *G. agilis*	4.01%	3.07%	4.01%	4.34%	4.18%	0.77%
LPC581 *G. agilis*	3.47%	3.19%	3.48%	3.74%	3.61%	1.22%
UHECO4722 *G. agilis*	3.34%	3.28%	3.34%	3.88%	3.47%	0.93%
LPC476 *G. agilis*	3.33%	3.13%	3.33%	3.30%	3.57%	2.30%
UHESM1759 *G. agilis*	3.48%	3.06%	3.48%	3.75%	3.61%	2.01%
LPC250 *G. agilis*	4.82%	4.94%	4.82%	5.38%	4.96%	4.95%
UUP1292 *G. agilis*	4.30%	3.99%	4.31%	4.85%	4.44%	3.79%
LHE1342 *G. aceramarcae*	13.26%	14.84%	13.26%	13.59%	13.11%	14.67%

low support (bootstrap < 50%), while the three form an unresolved polytomy in the bootstrap tree (Fig. 3). Second, in the strict consensus tree, the Caraça sample (locality 7; Fig. 1) falls in a trichotomy with the Southeastern and Minas Gerais clades, while in the bootstrap tree it joins the Minas Gerais clade, but again with low support (bootstrap = 64%; decay index = 0) and high sequence divergence (6.4% on average; Fig. 3). The ambiguous position of the Caraça sample and the degree of divergence separating it from the remaining samples highlight its uniqueness and indicates that populations from this mountain range might have been isolated for a considerable period of time.

Taxon allocation of the phylogeographic clades.—We identify three phylogeographic clades of *Gracilinanus* in eastern and central Brazil: Southeastern, Minas Gerais, and Central clades (Fig. 1). The Southeastern clade includes a specimen from Ipanema, the type locality of *G. microtarsus* (locality 8; Fig. 1; Appendix) and for that reason, as well as by comparison to the description of the holotype given by Tate (1933:191), we refer it to this species. The allocation of names to the two other clades, however, is more complicated. The name *G. agilis* has been historically applied to populations in central Brazil, from the state of Ceará in northeastern Brazil southwest to Lagoa Santa, and then continuing southwest, but interior to the coastal regions of São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul, to the Chaco of Paraguay and Argentina (Tate 1933). This range matches the distribution of our samples from the Central clade. However, the Minas Gerais clade includes a specimen from Lagoa Santa (locality 1; Fig. 1), the type locality of *G. agil-*

Table 1.—Extended.

	LPC599 *G. agilis*	LPC581 *G. agilis*	UHECO4722 *G. agilis*	LPC476 *G. agilis*	UHES1759 *G. agilis*	LPC250 *G. agilis*	UUP1292 *G. agilis*
LC49 *M. incanus*							
MNRJ31445 *G. microtarsus*							
MNRJ31447 *G. microtarsus*							
MCNM299 *G. microtarsus*							
LC1 *G. microtarsus*							
RM26 *G. microtarsus*							
MCNM394 *G. microtarsus*							
RM4 *G. microtarsus*							
LPC805 *G. microtarsus*							
MVZ182056 *G. microtarsus*							
LP40 *G. microtarsus*							
MAM427 *G. microtarsus*							
LC189 *G. agilis*							
MNRJ31396 *G. agilis*							
YL64 *G. agilis*							
LPC241 *G. agilis*							
AP22 *G. agilis*							
LPC304 *G. agilis*							
LPC599 *G. agilis*							
LPC581 *G. agilis*	0.45%						
UHECO4722 *G. agilis*	0.79%	0.88%					
LPC476 *G. agilis*	2.07%	2.05%	2.16%				
UHESM1759 *G. agilis*	1.55%	1.26%	1.39%	1.10%			
LPC250 *G. agilis*	4.47%	3.88%	3.75%	5.07%	3.62%		
UUP1292 *G. agilis*	3.31%	3.10%	2.97%	3.24%	2.84%	2.04%	
LHE1342 *G. aceramarcae*	14.68%	14.38%	13.74%	15.83%	14.39%	14.38%	15.11%

is, which is situated on the border with the Central clade. To resolve this problem, we compared our specimens with the descriptions of each holotype. If our specimen from Lagoa Santa is the same as Burmeister's type of that taxon, then *G. agilis* would become the name available for the Minas Gerais clade, recognized either as a separate species, or as a synonym of *G. microtarsus.* In either case, the Central clade, which we identify, would require another name, presumably one of those currently listed as synonyms of *G. agilis.* On the other hand, if the type specimen of *G. agilis* matches the morphology of the specimens from the Central clade, then we are left with a decision to make about the Minas Gerais clade, which could be recognized as a more interior clade of *G. microtarsus* or a separate, undescribed species, by virtue of its high level of divergence from topotypic *G. microtarsus.*

The type of *G. agilis* is a young adult from Lagoa Santa, collected by H. Burmeister and deposited at the Zoologisch Museum in Halle, Germany. The skin is mounted and the skull is in fragments, with only the rostrum and palate intact (Tate 1933: Plate 24, photo 215). Since we have not seen the type material of *G. agilis,* the best we can do at present is to follow Tate's (1933) diagnosis. The following is his description (p. 195) of the type of *G. agilis*: "Skin of type very faded brown. The hair rather close and even in length. Chest and posterior parts gray-based; throat and neck with self-colored hairs, buff-white. Vibrissae short; eye-rings elongate before and behind, narrowed above and below. Feet small. Tail thickly covered with fine hair."

Table 2.—Means (±*SE*) and ranges for selected external and cranial variables of *G. agilis* and *G. microtarsus*[a]. Weight in grams, measurements in millimeters.

	Gracilinanus agilis				*Gracilinanus microtarsus*		
Character	Male		Female		Male		Female
Head and	100.0 ± 7.06	***	89.63 ± 7.28	**	104.0 ± 14.55	ns	95.20 ± 16.86
body length	82–115		81–108	ns	86–129		81–116
	n = 44		n = 27		n = 20		n = 5
Tail length	137.91 ± 9.30	***	123.96 ± 7.54	***	154.20 ± 7.13	**	140.20 ± 9.34
	110–158		110–139	***	139–167		131–155
	n = 43		n = 27		n = 20		n = 5
Hind foot	16.86 ± 0.98	***	15.63 ± 1.21	*	17.95 ± 1.39	*	15.80 ± 0.84
length	15–19		13–18	ns	15–20		15–17
	n = 44		n = 27		n = 20		n = 5
Ear length	22.39 ± 1.32	**	21.52 ± 1.01	**	20.60 ± 1.23	*	19.20 ± 0.84
	20–25		20–24	**	19–23		18–20
	n = 44		n = 27		n = 20		n = 5
Mass (g)	23.56 ± 6.01	***	16.15 ± 2.96	**	27.40 ± 10.62	ns	22.40 ± 10.74
	15–40		13–25	**	17–52		12–37
	n = 44		n = 27		n = 20		n = 5
Greatest	28.47 ± 1.07	***	26.95 ± 1.08	***	30.27 ± 1.54	*	28.29 ± 1.48
skull length	25.87–30.59		25.23–29.69	*	28.16–33.20		26–80
	n = 36		n = 24		n = 12		29.75
							n = 4
Zygomatic	15.49 ± 0.66	***	14.63 ± 0.70	**	16.37 ± 1.13	ns	15.51 ± 1.24
breadth	14.32–17.00		13.68–16.65	*	14.77–18.38		14.28–16
	n = 35		n = 24		12		99
							n = 4
Braincase	11.40 ± 0.32	***	11.04 ± 0.33	***	11.94 ± 0.20	*	11.63 ± 0.20
breadth	10.75–11.91		10.23–11.59	**	11.30–12.25		11.35–11.80
	n = 36		n = 24		n = 12		n = 4
Least	4.67 ± 0.22	**	4.46 ± 0.22	***	5.24 ± 0.34	ns	4.98 ± 0.28
interorbital	4.20–5.06		3.96–4.86	**	4.73–5.93		4.70–5.29
constriction	n = 36		n = 24		n = 12		n = 4
Rostral length	10.75 ± 0.53	***	10.17 ± 0.49	***	11.55 ± 0.79	*	10.59 ± 0.96
	9.29–11.56		9.28–11.03	ns	10.30–12.98		9.68–11.45
	n = 36		n = 24		n = 12		n = 4
Nasal length	12.17 ± 0.61	***	11.39 ± 0.74	**	12.98 ± 1.04	ns	12.13 ± 1.40
	10.32–13.37		10.22–13.18	ns	11.22–14.52		10.61–13.63
	n = 36		n = 24		n = 12		n = 4
Rostral width	4.49 ± 0.23	***	4.21 ± 0.26	*	4.69 ± 0.36	ns	4.43 ± 0.39
	4.03–4.98		3.74–4.75	ns	4.32–5.46		4.03–4.85
	n = 36		n = 24		n = 12		n = 4
Molar toothrow	5.49 ± 0.16	ns	5.41 ± 0.15	***	5.73 ± 0.19	ns	5.66 ± 0.20
length	5.19–5.83		5.12–5.63	**	5.50–6.07		5.42–5.90
	n = 36		n = 24		n = 12		n = 4
Least pterygoid	3.02 ± 0.21	ns	2.93 ± 0.20	***	3.32 ± 0.14	ns	3.36 ± 0.11
breadth	2.36–3.44		2.59–3.34	**	3.11–3.59		3.25–3.48
	n = 36		n = 24		n = 12		n = 4
Petrosal	8.34 ± 0.25	**	8.17 ± 0.20	***	8.78 ± 0.32	ns	8.63 ± 0.38
breadth	7.81–8.84		7.79–8.45	**	8.0–9.16		8.12–9.01
	n = 36		n = 24		n = 12		n = 4
Alisphenoid bulla	9.12 ± 0.28	ns	8.96 ± 0.33	***	9.61 ± 0.25	ns	9.31 ± 0.31
breadth	8.56–9.82		8.15–9.35	ns	9.12–10.04		9.04–9.72
	n = 35		n = 24		n = 11		n = 4
Palatal length	13.89 ± 0.56	***	13.06 ± 0.67	***	14.70 ± 0.83	*	13.75 ± 0.93
	12.68–14.95		12.08–14.39	ns	13.11–16.08		12.75–14.57
	n = 36		n = 23		n = 12		n = 4

Table 2.—Continued.

	Gracilinanus agilis				*Gracilinanus microtarsus*		
Character	Male		Female		Male		Female
Cranial depth	9.61 ± 0.31 8.80–10.10 n = 36	**	9.39 ± 0.34 8.63–9.84 n = 24	** ns	9.97 ± 0.33 9.41–10.52 n = 12	*	9.57 ± 0.18 9.34–9.74 n = 4

[a] Mean and standard deviation, with range below, for adult specimens of both sexes. The significance levels between males and females of each species and between the two species for both males (above) and females (below) are indicated: ns = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

He then (p. 195) gives a more complete description of a specimen from Sapucay, Paraguay deposited at the British Museum (now Natural History Museum of London; BM 3.4.7.22): "Dorsal color a dull, almost dusty shade, nearest to russet (R.) or Brussels brown (R.). Color ventrally between warm buff (R.) and cinnamon-buff (R.). Gray-based hairs throughout, except from upper chest to chin and around the scrotal region. Face not markedly paler than dorsum; ears large, light gray-brown; vibrissae short; feet rather pale; tail very slightly bicolor, brown." Finally, in comparison with *G. microtarsus,* Tate wrote (p. 191): "*Microtarsus* is much more vividly colored than *agilis,* and the spreading of the gray-based hairs completely across the ventral area, except for the chin, affords another probably constant difference."

Tate's description of *G. agilis* fits quite well the individuals from the Central clade, especially the appearance and color of the dorsal pelage, the lack of strong contrast between face and dorsum, and in the extent to which the gray-based hairs cover the ventral region. All seven specimens examined from the Minas Gerais clade—including the individual from near the type locality of *G. agilis* at Lagoa Santa (MNRJ 31445)—are warm-brown on the dorsum with a much paler face, and gray-based hairs cover most of the underparts, except the chin. These are features that characterize individuals of *G. microtarsus.* In contrast, all 62 specimens of the Central clade are grayish-brown and without a sharp distinction between face and dorsum. The gray-based hairs in the underparts are restricted to the lower pectoral and abdominal area leaving upper chest, throat and chin covered with self-colored hairs (same color from base to tip). These and other traits (discussed below) convince us that the specimens forming the Central clade correspond to *G. agilis.* Despite the high genetic divergence found between the Southeastern clade and the Minas Gerais clade (Fig. 3), and the clear geographic break separating them (Serra da Mantiqueira; Fig. 1), at this time we allocate the Minas Gerais clade also to *G. microtarsus,* since we could find no diagnostic morphological characters that justify specific distinction. Nevertheless, we point out that our sample size of *G. microtarsus* is small and it is possible that more individuals will provide the morphological support for distinction at the species level. It is important to note that *G. agilis* and *G. microtarsus* occur in near-sympatry in the state of Minas Gerais, since both species are now known from the general vicinity of Lagoa Santa. This locality is in a contact area between two biomes: the Cerrado, which has savanna-like vegetation characteristic of central Brazil, and the Atlantic Forest, represented at Lagoa Santa by semi-deciduous forests. Based on current distributional information, *Gracilinanus agilis* occurs primarily in the Cerrado domain, while *G. microtarsus* is an Atlantic Forest species.

In the following section we compare the two species and give an extended description of both *G. agilis* and *G. microtarsus.*

Morphological comparisons.—External body measurements: *Gracilinanus agilis* is sexual dimorphic, as males are significantly

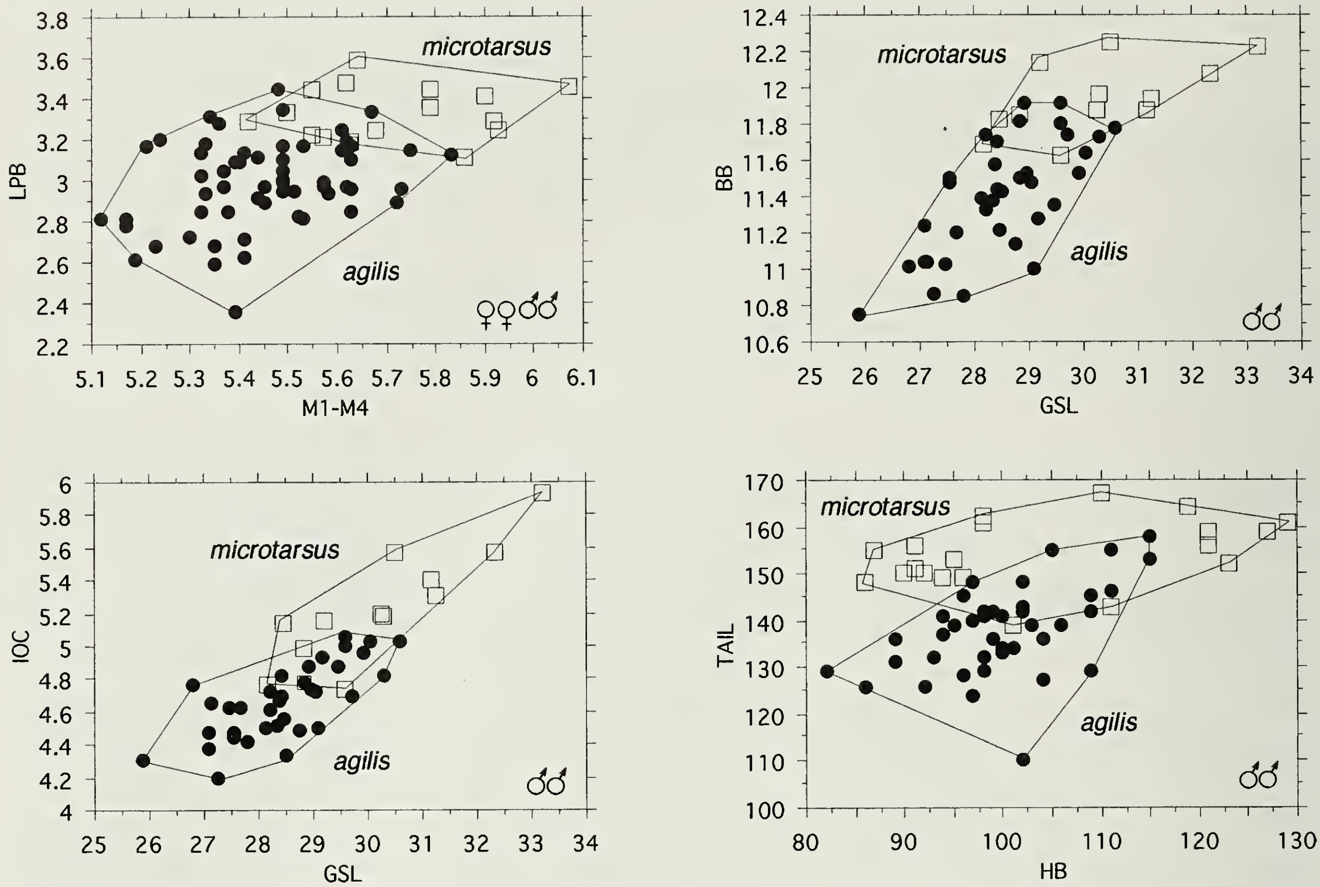

Fig. 4. Bivariate plots comparing selected external body and craniodental measurements of *Gracilinanus agilis* (open squares) and *G. microtarsus* (solid circles). Above left: molar toothrow length (M1–M4) versus least pterygoid breadth (LPB) of males and females. Above right: greatest skull length (GSL) versus braincase breadth (BB) of males. Below left: GSL versus least interorbital constriction (IOC) of males. Below right: head and body length (HB) versus tail length (TAIL) of males.

larger than females in every trait examined (see Table 2). Adult males range in head and body length from 82 to 115 mm and weigh from 15 to 40 g. Females range in head and body length from 81 to 108 mm and weigh from 13 to 25 g. The tail is longer in males, reaching 158 mm, while in females the tail reaches a maximal length of 139 mm. The ears of *G. agilis* are large, averaging more than 21 mm in both sexes. In *G. microtarsus* the tail, foot, and ears are longer in males than in females, while head and body and weight do not differ significantly (Table 2). In comparison, *G. agilis* is generally smaller than *G. microtarsus,* with females of *G. microtarsus* almost as heavy as males of *G. agilis,* and males of *G. microtarsus* approximately 17% heavier on average than males of *G. agilis.* The tail in *G. microtarsus* is also longer, by about 11% more in both sexes (Table 2; Fig. 4). The ears are the only trait that is larger in *G. agilis* than in *G. microtarsus,* which may be related to the warmer and drier habitats this species occupies.

Pelage differences: In both species, the bases of the hairs on the upper parts are dark gray and the tips are orange to buffy. However, in *G. agilis* the terminal (orange or buffy) portion of each hair is shorter than in *G. microtarsus,* giving the dorsal pelage a more grizzled tone, while *G. microtarsus* has a more uniformly colored reddish-brown pelage (Fig. 5; Table 3). The general color of the dorsal pelage is also paler in *G. agilis* than in *G. microtarsus* (Fig. 5). The fur is slightly longer and more lax in *G. microtarsus* than in *G. agilis,* although the series of *G. microtarsus* from Ipanema have the shortest fur of all specimens examined. Although Tate (1933) emphasized the presence of numerous over-hairs in *G.*

Fig. 5. Differences in dorsal and ventral color patterns of *Gracilinanus agilis* and *G. microtarsus*. *Gracilinanus agilis*: first (LPC 599) and third (LPC 581) from left; and *G. microtarsus*: second (LPC 805) and fourth (LC 1) from left. Note the grizzled and paler dorsal pelage of *G. agilis*, and the ventral gray-based hairs extending to the throat in *G. microtarsus*. Note also the sharp contrast between face and body in *G. microtarsus*, and the gradual change in *G. agilis*.

microtarsus, making the pelage "rough or shaggy-looking", our specimens appear smooth-coated.

The general color of the ventral fur is yellowish cream in both species, but as mentioned above, the gray-based hairs of *G. agilis* are restricted to the lower pectoral and abdominal area, leaving the upper chest, throat and chin self-colored (Fig. 5). Also, the gray tone on the venter is slightly paler than that of the dorsum, making the gray color less evident. Individuals from the two more interior clades of *G. agilis* have the underparts of the arms also self-colored. *Gracilinanus microtarsus*, in turn, has gray-based hairs throughout the ventral parts, except on the chin (Fig. 5), and the gray tone of the venter is as dark as it is in the dorsum, making it obvious. Apparently, the population of *G. microtarsus* in the type locality is an exception to this generality. Among the series of six topotypes we collected, one individual has the self-colored area restricted to the chin; three individuals have the self-colored hairs reaching the upper chest; and the last individual has the self-colored hairs reaching as far as the lower abdominal area. Tate's description (1933:191) of the type specimen of *microtarsus* is "Underparts cinnamon-buff, the

Table 3.—Diagnostic characters of *G. agilis* and *G. microtarsus*.

Character	*G. agilis*	*G. microtarsus*
External		
appearance of dorsum pelage	grizzly grayish-brown	uniform reddish-brown
spreading of gray-based hairs across the ventral area	throughout, except from upper chest to chin (underparts of arms also often self-colored)	variable, but usually throughout except for the chin
ocular-mark	thin, small and not extending to nose and ears	broad, large, and extending to nose and ears
face	not markedly paler than dorsum; transition is gradual, not sharp contrast with the rest of body	markedly paler than dorsum, producing a sharp contrast with the rest of body
ears	larger; >21 mm in average	smaller; <21 in average
tail	shorter; <140 mm in average	longer; >140 mm in average
Cranial		
posterolateral vacuities on palate	size larger or comparable to that of the posteromedial vacuities	always smaller than posteromedial vacuities

hairs gray-based, and only those of the chin self-colored", although he also recognized some variation since on page 189 he wrote: "underparts, posterior to the throat, with the hairs entirely gray-based". Intraspecific variation is also found in *G. agilis*: the series of 13 individuals from Crato (locality 23) are even paler than the remaining specimens of this species, the color of the dorsal region approximating a grayish tone and the self-colored parts in the underparts being whitish cream.

The ocular ring in *G. microtarsus* is broad and very dark (Fig. 6); the face is distinctly paler than the body—approximately the same color as the cheeks—resulting in a sharp contrast between the face and body (Fig. 5). Although the mask is also prominent in *G. agilis,* it is thinner and antero-posteriorly restricted (Fig. 6); the face is not as pale—the color on top of the head is darker than the cheeks—and the transition between the face and body is gradual (Fig. 5).

Cranial differences: When comparing *G. microtarsus* and *G. agilis* Tate (1933:191) observed that "The skulls are extremely alike, differing solely in finer detail". The only differences he pointed out were the

Fig. 6. Side view of the heads of *Gracilinanus agilis,* above (LPC 599), and *G. microtarsus,* below (LPC 805), showing the differences in size and shape of the ocular mask.

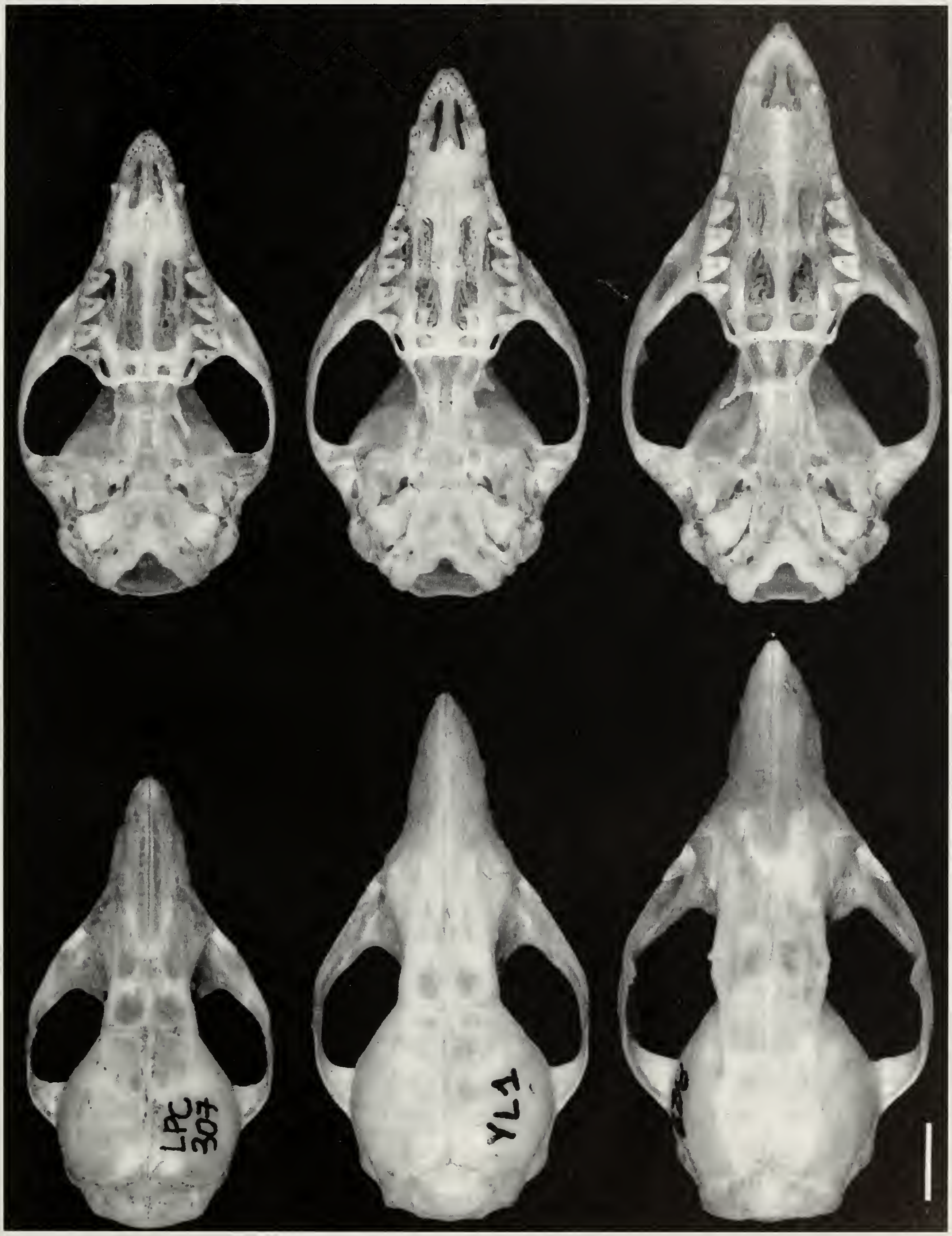

Fig. 7. Ventral and dorsal views of skulls of *Gracilinanus agilis* to the left (LPC 307, from Nova Ponte, Minas Gerais), *G. microtarsus* from the Minas Gerais clade (YL 1, from Santa Rita de Jacutinga, Minas Gerais) in the middle, and a topotype of *G. microtarsus* from the Southeastern clade to the right (MVZ 197436, from Ipanema, São Paulo). Scale bar = 5 mm. Note the larger posterolateral palatal foramina in *G. agilis,* when compared to the size of the posteromedial vacuities.

longer tooth rows of *G. microtarsus*, its somewhat broader and shorter pterygoids and proportionately greater breadth across the pars petrosa. While we confirmed Tate's findings with confidence for both males and females (Table 2; Fig. 4), we also detected additional differences. Skulls of *G. microtarsus* are longer (Figs. 4 and 7), and they also have a wider braincase, wider zygomatic arches, and broader interorbital region (Table 2; Fig. 4). Although the small number of females of *G. microtarsus* compromises our statistical analyses, there is a significant difference between males of both species in all remaining traits examined (Table 2), despite a comparable range of age classes.

In terms of qualitative characters, the size of the posterolateral foramina of the palate is comparable to that of the posteromedial vacuities in *G. agilis*, being proportionally larger than in *G. microtarsus* in which they are always smaller than the posteromedial vacuities (Fig. 7). Incipient postorbital processes can be present in both species, contrary to Hershkovitz's (1992) observation that both species lack them.

Conclusion

Gracilinanus agilis and *G. microtarsus* appear to represent valid species, distinguishable by morphological and molecular characters, with levels of sequence divergence equivalent to those separating each of them from a third species, *G. aceramarcae*. In short, these two do not even form a well-supported sister-pair within the genus, even with the very limited number of taxa sampled. However, it is also possible that the samples we allocate to *G. microtarsus* in fact represent two separate species, as indicated by the cyt *b* data. Verification of this hypothesis will have to wait until more samples are available.

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Literature Cited

Bremer, K. 1988. The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction.—Evolution 42:795–803.

Costa, L. P. 2002. Relações filogenéticas intergenéricas de marsupiais didelfídeos. *In* N. C. Cáceres and E. L. A. Monteiro-Filho, eds., Marsupiais Brasileiros Editora da Universidade Federal do Paraná, Paraná (in press).

Creighton, G. K. 1984. Systematic studies on opossums (Didelphidae) and rodents (Cricetidae). University of Michigan, Ann Arbor, 220 pp.

Eisenberg, J. F., & K. H. Redford. 1999. Mammals of the Neotropics: the central Neotropics, vol. 3: Ecuador, Peru, Bolivia, Brazil. The University of Chicago Press, Chicago, 609 pp.

Emmons, L. H., & F. Feer. 1997. Neotropical rainforest mammals: a field guide, 2nd edition. University of Chicago Press, Chicago, 307 pp.

Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap.—Evolution 39:783–791.

Gardner, A. L. 1993. Order Didelphimorphia. Pp. 15–23 *in* D. E. Wilson and D. M. Reeder, eds., Mammal species of the world. Smithsonian Institution Press, Washington, D.C., 1206 pp.

Gardner, A. L., & G. K. Creighton. 1989. A new generic name for Tate's (1933) *microtarsus* group of South American mouse opossums (Marsupialia: Didelphidae).—Proceedings of the Biological Society of Washington 120:3–7.

Hershkovitz, P. 1992. The South American gracile mouse opossum genus *Gracilinanus* Gardner and Creighton, 1989 (Marmosidae, Marsupialia): a taxonomic review with notees on general morphology and relationships.—Fieldiana: Zoology, New Series 70:1–56.

Kimura, M. 1980. A simple method for estimating evolutionary rate of base substitutions through comparative studies of nucleotide sequences.—Journal of Molecular Evolution 16:111–120.

Papavero, N. 1971. Essays on the history of neotropical dipterology, with special reference to collectors (1750–1905), vol. 1. Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Patton, J. L., & L. P. Costa. 2003. Diversidade, limites geográficos e sistemáticos de marsupiais brasilerios. *In* N. C. Cáceres and E. L. A. Monteiro-Filho, eds., Marsupiais Brasileiros. Editora da Universidade Federal do Paraná, Curitiba (in press).

Patton, J. L., M. N. F. da Silva, & J. R. Malcolm. 2000. Mammals of the Rio Juruá and the evolutionary and ecological diversification of Amazonia.—Bulletin of the American Museum of Natural History 244:1–306.

Saiki, R. K., et al. 1988. Primer-directed enzymatic amplification of DNA with a thermostable DNA polymerase.—Science 239:487–491.

Swofford, D. L. 1999. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods), version 4. Sinauer Associates, Sunderland, Massachusetts.

Tate, G. H. H. 1933. A systematic revision of the marsupial genus *Marmosa*, with a discussion of the adaptive radiation of the murine opossums (*Marmosa*).—Bulletin of the American Museum of Natural History 66:1–250.

Vanzolini, P. E. 1993. As viagems de Johann Natterer no Brasil, 1817–1835.—Papèis Avulsos de Zoologia 38(3):17–60.

Voss, R. S., D. B. Lunde, and N. B. Simmons. 2001. The mammals of Paracou, French Guiana, a Neotropical lowland rainforest fauna, part 2. Nonvolant species.—Bulletin of the American Museum of Natural History 263:3–236.

Walsh, P. S., D. A. Metzger, & R. Higuchi. 1991. Chelex 100 as a medium for simple extraction of DNA for PCR-based typing from forensic material.—Biotechniques 10:506–513.

Appendix

Gazetteer.—Localities from which we examined material of *Gracilinanus* for this study are listed by species and numbered to correspond with the mapped points in Fig. 1 and the labeled terminals in Fig. 3. Voucher numbers for specimens examined are given parenthetically for each locality; those marked with an asterisk correspond to haplotypes used in the molecular analysis, and boldface place names are used to label the tree. Specimens examined are deposited in the collections of the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); Museu de Zoologia da Universidade de São Paulo (MZUSP); Museu Nacional, Rio de Janeiro (MNRJ); and Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCN); and Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Peru (MUSM). Specimens identified by other prefixes correpond to collector's field number: AP (Adriano Paglia), CEMIG (Luiz Fernando B. M. Silva), RM (Raquel Moura) to be deposited at the Departamento de Zoologia, Universidade Federal de Minas Gerais, Belo Horizonte; LC and LPC (Leonora Pires Costa), LP (Luciana Pereira), UUPI (Maria José de J. Silva) and YL (Yuri Leite) to be deposited at one of the above Brazilian institutions; and UHECO and UHESM (Nelson da Silva) to be deposited at the Universidade Católica de Goiás, Brazil.

Gracilinanus microtarsus

1 Fazenda das Bicas, 7.8 km (by rd.) SSE Lagoa Santa, Minas Gerais, Brazil, 19°38′S, 43°53′W (MNRJ 31445*).

2 Estação de Pesquisas de Peti (CEMIG), 10 km (by rd.) São Gonçalo do Rio Abaixo, Minas Gerais, Brazil, 19°49′S, 43°21′W (MNRJ 31447*, CEMIG 51).

3 Parque das Mangabeiras, Belo Horizonte, Minas Gerais, Brazil, 19°55′S, 43°56′W (MCN 299*).

4 Cruzeiro, 8 km NE Santa Rita de Jacutinga, Minas Gerais, Brazil, 22°5′S, 44°2′W 560 m (LC 1*, LC 2, YL 1).

5 Jurumirim, Minas Gerais, Brazil, 20°8′S, 42°41′W (MCN 394*).

6 Parque Estadual do Rio Doce, 13 km E Marliéria, Minas Gerais, Brazil, 19°43′S, 42°39′W 300 m (MVZ 197587*).

7 Parque do Caraça, 25 km SW Santa Bárbara, Minas Gerais, Brazil, 20°5′S, 43°30′W 1300 m (RM 4*).

8 Floresta Nacional de Ipanema, 20 km NW Sorocaba, São Paulo, Brazil, 23°26′7″S, 47°37′41″W 701 m (LPC 801*, LPC 820–822, MVZ 197463). This is the historical site of "Ypanema", the type

locality of *G. microtarsus,* where the collector, Johann Natterer, lived and worked (see Papavero 1971, Vanzolini 1993), and renamed as a formal conservation unit by IBAMA on May 20, 1992.

9 Fazenda Intervales, Base do Carmo, 5.5 km S Capão Bonito, São Paulo, Brazil, 24°20′S, 48°25′W 700 m (MZUSP 29158–29161, MZUSP 29165, MVZ 182054, MVZ 182055, MVZ 182056*, MVZ 182057).

10 Vila Dois Rios, Ilha Grande, Angra dos Reis, Rio de Janeiro, Brazil, 23°9′S, 44°14′W (LP 40*).

11 Estação Biológica de Boracéia, São Paulo, Brazil, 23°39′S, 45°54′W 850 m (MZUSP 29162, MZUSP 29163*, MZUSP 29164).

Gracilinanus agilis

12 Ponte do Colatino, margem esquerda do Rio Jequitinhonha, Coronel Murta, Minas Gerais, Brazil, 16°36′S, 42°12′W (LC 189*).

13 Vargem do Retiro, Ribeirão Mascates, Parque Nacional da Serra do Cipó, Minas Gerais, Brazil, 19°14′S, 43°33′W 800 m (MNRJ 31396*).

14 Parque Estadual do Rio Preto, 15 km S São Gonçalo do Rio Preto, Minas Gerais, Brazil, 18°9′S, 43°23′W 950 m (YL 64*, LC 71).

15 Fazenda Corredor, Bocaiúva, Minas Gerais, Brazil, 17°22′14″S, 43°52′16″W (AP 22*).

16 Fazenda Santa Rita, 8 km E Andaraí, Bahia, Brazil, 12°48′6″S, 41°15′41″W 399 m (LPC 241*).

17 Mata do Vasco, 12 km W Nova Ponte, Minas Gerais, Brazil, 19°10′15″S, 47°42′29W 878 m (LPC 296–299, LPC 304*, LPC 305–307, LPC 309–311, LPC 314–316, LPC 318, LPC 324, LPC 325, LPC 327–328, LPC 330–331, LPC 339–340, MVZ 197438–197446, 197451–197453, 197473, 197649–197652, 197654–197657).

18 Rio Miranda, above Passo do Lontra, Mato Grosso do Sul, Brazil, 19°34′35″S, 56°55′44″W 100 m (LPC 599*, LPC 602, MVZ 197455).

19 Base de Pesquisa do Pantanal—CENAP/IBAMA, 110 km SSW Poconé, Mato Grosso, Brazil, 17°7′12″S, 56°56′47″W 98 m (LPC 581*, MVZ 197454).

20 Usina Hidrelétrica de Corumbá, 30 km SE Caldas Novas, Goiás, Brazil, 18°0′S, 48°30′W (UHECO 4722*).

21 Fazenda Lagoa Bonita, 36 km N Barra do Garças, Mato Grosso, Brazil, 15°34′50″S, 52°22′29″W 331 m (LPC 476*).

22 Usina Hidrelétrica de Serra da Mesa, Serra da Mesa, Goiás, Brazil, 13°50′S, 48°18′W (UHESM 1759*).

23 Chapada do Araripe, 7 km SW Crato, Ceará, Brazil, 7°16′39″S, 39°27′3″W 960 m (LPC 243, LPC 244, LPC 249, LPC 250*, LPC 251, LPC 269–271, LPC 276–277, LPC 294, MVZ 197447–197450, MVZ 197647–197648).

24 Estação Ecológica de Uruçuí-Una, Piauí, Brazil, 8°50′S, 44°10′W (UUPI 292*).

Gracilinanus aceramarcae

25 Cordillera de Vilcabamba, La Convencíon (Camp 1), Junín, Peru, 11°39′56″S, 73°38′31″W (MUSM 13002*).

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 10. *Cyanomyia salvini* Brewster, 1893, is an intergeneric hybrid of *Amazilia violiceps* and *Cynanthus latirostris*

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Abstract.—*Cyanomyia salvini* Brewster, 1893, collected in Sonora, Mexico, is shown to be a hybrid between *Amazilia violiceps ellioti* and *Cynanthus latirostris magicus,* whose breeding ranges overlap extensively in northwestern Mexico. This specimen represents the only known intergeneric hybrid between species currently placed in *Amazilia* and *Cynanthus* (Sibley and Monroe 1990).

The unique type of *Cyanomyia salvini* Brewster, 1893, was collected by John C. Cahoon at Nichosari, Sonora, Mexico, on 31 March 1887. Early references treat *C. salvini* as a valid species (Boucard 1895, Ridgway 1911, Cory 1918, Simon 1921), although only Ridgway's entry indicated a personal examination of the specimen. Griscom (1934:378) proposed a hybrid origin for *C. salvini* in his revision of *Amazilia violiceps*:

> "By inference I had always doubted the existence of another species of this genus [*Amazilia*] in Sonora. Geographically and faunally there is no basis for one, and the failure to duplicate the type in over 40 years has further significance, and in part at least strengthens this view. My late esteemed colleague Outram Bangs always supposed that *salvini* was of hybrid origin. A careful study of the color and structural characters of the type convinces me that *Cyanomyia salvini* Brewster is a hybrid between *Amazilia violiceps conjuncta* [= *Amazilia violiceps ellioti*] and *Cynanthus latirostris* Swainson."

Griscom's brief description was insufficient to make a convincing case for hybridization, but Peters (1945) and Phillips (1964) cited Griscom's treatment without substantive comment. A second hypothesis was introduced in a succinct footnote by Friedmann et al. (1950), who suggested that *Cyanomyia salvini* is an aberrant example of *Amazilia violiceps*. This idea was later endorsed by Weller & Schuchmann (1997) and Weller (1999), but neither of these references provided corroborating evidence. As a consequence, the taxonomic status of *Cyanomyia salvini* is still in doubt. Here I provide a taxonomic assessment of *Cyanomyia salvini* employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990), as modified by the findings of Graves (1998, 1999b).

Methods

The type of *Cyanomyia salvini,* (J. C. Cahoon field number 505), originally part of the William Brewster Collection (No. 24,124), was eventually cataloged in the Museum of Comparative Zoology, Harvard University (received in 1918, No. 224,124). The type was sexed as ♂ on the Brewster Collection label and appears to be in definitive plumage as judged by the absence of striations on the maxillary ramphotheca, the absence of distinctive buffy feather tips on the dorsal plumage, and the presence of a strongly iridescent coronal patch. Descriptions in this paper refer to definitive male plumage. I compared the type of *Cyanomyia salvini* with specimen series of *Calypte annae, C. costa, Selasphorus platycercus, S. rufus, S. sasin, Stellula calliope, Archilochus alexandri, Calothorax luciferi, He-*

Table 1.—Ranges (mean ± standard deviation) of measurements (mm) of wing chord, bill length, and rectrix length (R1–R5) of adult males of *Amazilia violiceps ellioti, Cynanthus latirostris magicus* and a probable hybrid, *Amazilia violiceps ellioti* × *Cynanthus latirostris magicus* (= type of *Cyanomyia salvini* Brewster, 1893; MCZ 224, 124).

Character	*Amazilia violiceps* N = 15–17	*Cynanthus latirostris* N = 14–15	*Cyanomyia salvini*
Wing	53.5–56.1 (54.6 ± 0.7)	48.4–51.9 (50.4 ± 0.8)	52.9
Bill	20.1–22.5 (21.4 ± 0.6)	18.7–21.6 (20.3 ± 0.8)	21.4
R1	26.3–29.3 (28.2 ± 0.8)	22.4–25.3 (23.8 ± 0.7)	27.7
R2	28.0–30.5 (29.4 ± 0.9)	23.9–27.0 (25.8 ± 0.7)	28.0
R3	28.3–31.4 (30.1 ± 1.0)	26.3–29.4 (28.6 ± 0.8)	29.1
R4	28.3–32.5 (30.7 ± 1.1)	28.7–32.4 (30.8 ± 1.0)	30.6
R5	28.8–32.6 (30.7 ± 1.2)	31.0–33.8 (32.5 ± 0.7)	31.2

liomaster constantii, Eugenes fulgens, Lampornis clemenciae, Amazilia beryllina, A. violiceps (including the type of *Amazilia violiceps conjuncta* Griscom, 1934; MCZ No. 224,112), *Hylocharis leucotis,* and *Cynanthus latirostris magicus,* all of which occur in Sonora, Mexico (Friedmann et al. 1950, Howell & Webb 1995), in the collections of the Museum of Comparative Zoology. Because the generic allocation of species traditionally placed in *Amazilia* by Peters (1945) is in flux, I use the species taxonomy of Sibley & Monroe (1990). Detailed descriptions and photographs of the type of *Cyanomyia salvini* were compared with series of the aforementioned species in the National Museum of Natural History, Smithsonian Institution, and with a supposed immature specimen of *Cyanomyia salvini* collected at Palmerlee, Cochise County, Arizona, on 5 July 1905 (Bishop 1906). The latter specimen (Field Museum of Natural History 160,998; wing chord = 53.4 mm; bill length = 21.2; R4 = 29.7; R5 = 29.9) appears to be a female *Amazilia violiceps* and will not be further discussed.

Measurements were taken with digital calipers and rounded to the nearest 0.1 mm: wing chord; bill length (from anterior extension of feathers); and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix) (Table 1). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5). Scatter plots of measurements and least squares regression lines were used to illustrate size differences among specimens.

General color descriptions presented in Appendix 1 were made under natural light. I evaluated the color of the medial vane of the dorsal surface of R1 (7 mm from tip) with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent feathers are acutely dependent on the angle of measurement, the curvature of plumage surfaces in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. In

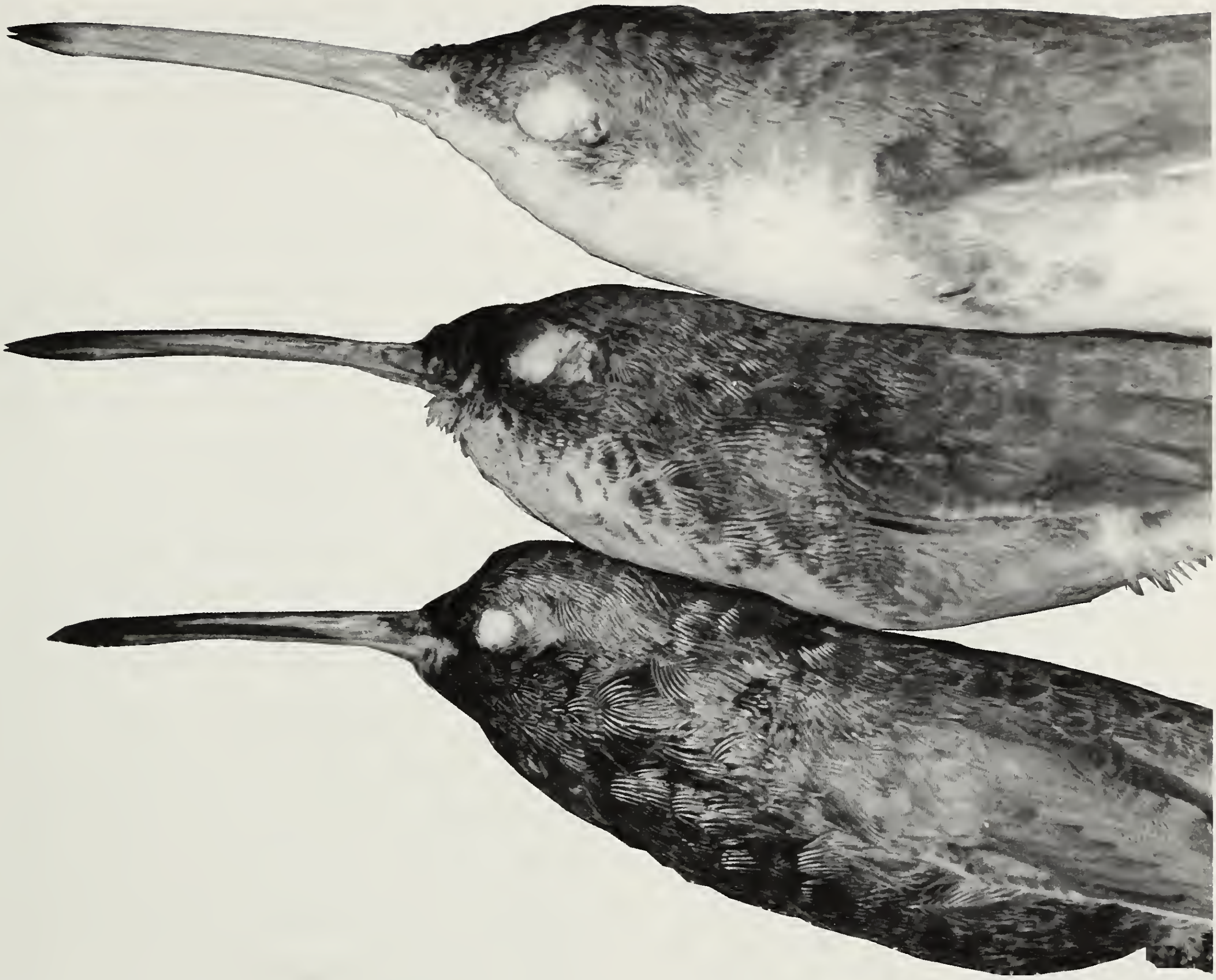

Fig. 1. Lateral views of males in definitive plumage: *Amazilia violiceps ellioti* (top), *Cynanthus latirostris magicus* (bottom), and a probable hybrid, *Amazilia violiceps ellioti* × *Cynanthus latirostris magicus* (= type of *Cyanomyia salvini* Brewster, 1893; MCZ 224,124).

order to reduce measurement variation, I held the aperture flush with the rectrix surface without depressing it. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure twice (five times for the type of *Cyanomyia salvini*), removing the aperture between trials. Thus, each datum summarized in Table 2 represents the mean of 6 (parental species) or 15 (type of *C. salvini*) independent colorimetric measurements.

Colorimetric characters were described in terms of opponent-color coordinates (*L, a, b*) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as dark-light (*L*), green-red (*a*), and blue-yellow (*b*). The rationale is that a color cannot be perceived as red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value, *a*, which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by *b* for yellows and −*b* for blues. The third coordinate, *L*, ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage, the higher the *L* value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans and the relevance of opponent color coordinates to colors perceived by

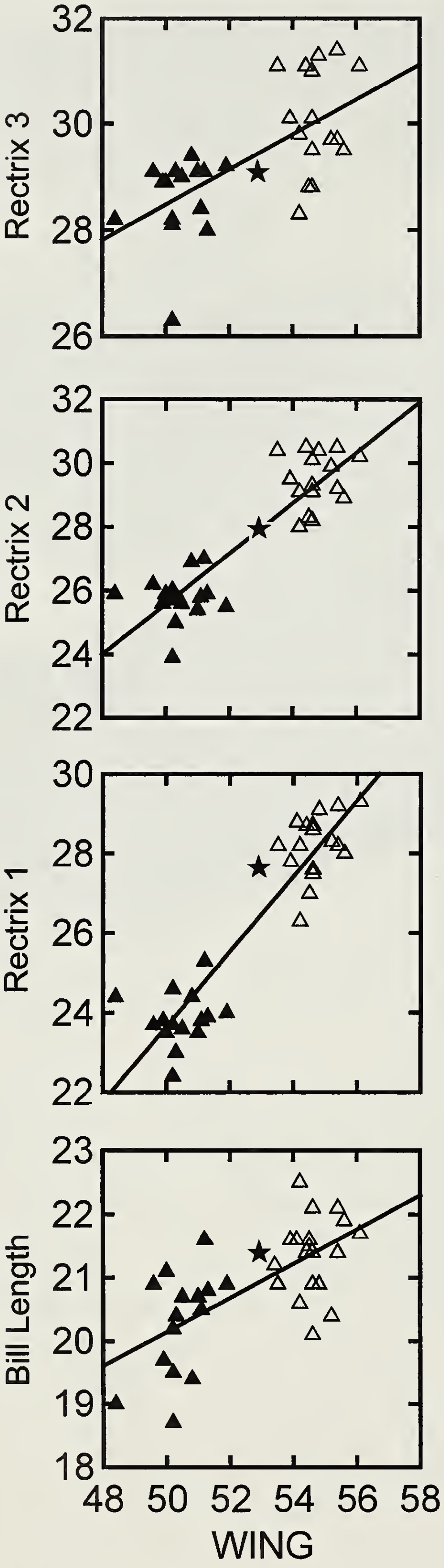

Fig. 2. Bivariate plots of measurements (see Table 1): *Amazilia violiceps ellioti* (hollow triangle), *Cynanthus latirostris magicus* (▲), and a probable hybrid, (☆) *Amazilia violiceps ellioti* × *Cynanthus latirostris magicus* (= type of *Cyanomyia salvini* Brewster, 1893; MCZ 224,124).

hummingbirds is unknown. In any case, the *L, a, b* color system permits plumage color to be unambiguously characterized for taxonomic purposes.

Results and Discussion

I considered three hypotheses proposed by previous authors—*Cyanomyia salvini* represents (1) a hybrid, *Amazilia violiceps* × *Cynanthus latirostris,* (2) an aberrant example of *Amazilia violiceps,* or (3) a valid species. For brevity I use the epithet, *salvini,* in the remainder of the paper.

I found no evidence that *salvini* represents a subdefinitive plumage or geographic variant of any known taxon. The possibility that *salvini* represents an aberrant plumage of *Amazilia violiceps* can be rejected because *salvini* has substantially shorter wings. All evidence is consistent with the hypothesis that *salvini* represents an intergeneric hybrid, *Amazilia violiceps* × *Cynanthus latirostris.* Several characters of *salvini* facilitate the identification of its parental species (Appendix 1): (a) brilliant bluish-purple crown; (b) white chin, throat, midline of breast and abdomen white; (c) greenish-blue subterminal spots or bars on white feathers at the lateral margins of the throat and upper breast; and (d) absence of rufous or buff pigmentation on the secondaries or rectrices (Fig. 1).

Here I present a synopsis of the critical steps of the hybrid diagnosis. The pool of potential parental species may be quickly narrowed by focusing on the white ventral plumage of *salvini.* Among the potential parental species that occur in Sonora, Mexico, only *Amazilia violiceps* possesses white ventral plumage from chin to undertail coverts. Bluish-green spotting on the lateral margins of the chin, throat, and breast feathers of *salvini* were inherited from the other parental species. Both *Amazilia beryllina* and *Cynanthus latirostris* have green or bluish-green plumage from chin to upper breast. Because brown or reddish-brown pigments appear to exhibit consistent penetrance in hummingbird hybrids (Banks & Johnson 1961, Graves & Newfield 1996), *A. beryllina* can be eliminated from further consideration because the secondaries and rectrices of *salvini* lack buff or rufous pigment. Only one pair of species (*A. violiceps* × *C. latirostris*) could have contributed the unique combination of characters exhibited by *salvini* (Appendix 1).

Hybridization of *Amazilia violiceps* with any of the small gorgeted species (i.e., *Calypte annae, C. costa, Selasphorus platycercus, S. rufus, S. sasin, Stellula calliope, Archilochus alexandri, Calothorax lucifer*) would likely produce offspring with one to many iridescent gorget feathers (Graves & Zusi 1990; Graves 1996, 1999a). In a similar fashion, *Lampornis clemenciae* (brilliant gorget and large white tail spots), *Eugenes fulgens* (brilliant gorget and black breast and abdomen), *Hylocharis leucotis* (white postocular stripe and black chin and auriculars), and *Heliomaster constantii* (brilliant gorget and semi-concealed white rump patch) are unlikely to be a parental species because they each possess a suite of plumage characters not observed, even as traces, in *salvini.*

As a second step, I tested the restrictive hypothesis with an examination of size and external proportions (Fig. 2). Measurements of trochiline hybrids fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic mode of inheritance (Banks & Johnson 1961). Measurements of *Amazilia violiceps elliotí* and *Cynanthus latirostris* overlap in four of the seven characters and the percent difference in character means is modest (larger species divided by smaller): wing chord (8.3%), bill length (5.4%), R1 (18.5%), R2 (14.0%), R3 (5.2%), R4 (0.3%), and R5 (5.9%). Measurements of *salvini* fall at or between the character means (or 1.0 mm less than the mean value for R4 of *A. violiceps*) of the postulated parental species, and, in several cases, approximate the values predicted by least squares regression. Rectrix color values in *salvini* fall between

Table 2.—Minima, maxima, and means (± standard deviation) of opponent color coordinates (*L, a, b*) of rectrix 1 (RI) of adult males of *Amazilia violiceps ellioti, Cynanthus latirostris magicus* and a probable hybrid, *Amazilia violiceps ellioti* × *Cynanthus latirostris magicus* (= type of *Cyanomyia salvini* Brewster, 1893; MCZ 224, 124).

		L			−*a*/*a*			−*b*/*b*		
		Lightness			Green/red			Blue/yellow		
		Min.	Max	Mean ± SD	Min	Max	Mean ± SD	Min.	Max	Mean ± SD
Amazilia violiceps	*N* = 19	25.2	32.2	29.8 ± 1.9	−1.7	3.2	0.7 ± 1.4	5.5	13.5	10.6 ± 1.8
Cynanthus latirostris	*N* = 14	13.6	20.2	16.9 ± 1.7	−0.3	4.4	1.9 ± 1.4	−4.3	1.6	−1.6 ± 1.8
Cyanomyia salvini				22.2			−1.6			7.7

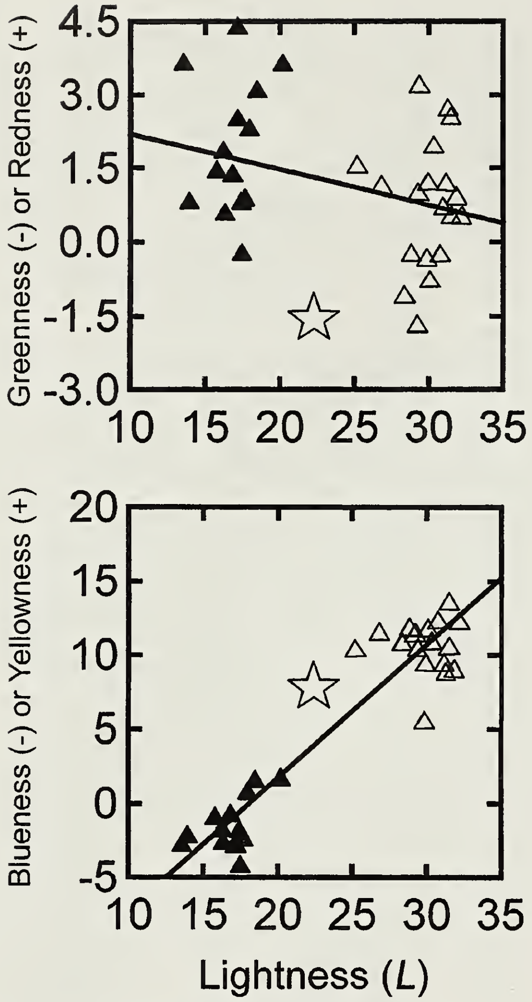

Fig. 3. Bivariate relationships of *L, a, b* color coordinates: *Amazilia violiceps ellioti* (hollow triangle), *Cynanthus latirostris magicus* (▲), and a probable hybrid (☆), *Amazilia violiceps ellioti* × *Cynanthus latirostris magicus* (= type of *Cyanomyia salvini* Brewster, 1893; MCZ 224,124).

the character means of the postulated parental species (Table 2, Fig. 3).

In summary, evidence obtained from plumage color and pattern, as well as from external size and shape, is consistent with the hypothesis that *Cyanomyia salvini* is an intrageneric hybrid between *Amazilia violiceps ellioti* and *Cynanthus latirostris magicus,* whose breeding ranges overlap extensively in northwestern Mexico. *Cyanomyia salvini* Brewster, 1893, is thus available in taxonomy only for the purposes of homonymy.

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Literature Cited

Banks, R. C., & N. K. Johnson. 1961. A review of North American hybrid hummingbirds.—Condor 63:3–28.

Bishop, L. B. 1906. *Uranomitra salvini* in Arizona.—Auk 23:337–338.

Boucard, A. 1893. Genera of humming birds, part 2. Published by the author, London.

Brewster, W. 1893. Description of a new hummingbird from northern Mexico.—Auk 10:214–215.

Cory, C. B. 1918. Catalogue of birds of the Americas, part 2, No.1.—Field Museum of Natural History Zoological Series 13:1–315.

Friedmann, H., L. Griscom, & R. T. Moore. 1950. Distributional check-list of the birds of Mexico, part 1. Pacific Coast Avifauna No. 29, 202 pp.

Goldsmith, T. H., & K. M. Goldsmith. 1979. Discrimination of colors by the black-chinned hummingbird, *Archilochus alexandri.*—Journal of Comparative Physiology A 130:209–220.

Graves, G. R. 1990. Systematics of the "green-throated sunangels" (Aves: Trochilidae): valid taxa or hybrids?—Proceedings of the Biological Society of Washington 103:6–25.

———. 1996. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 2. Hybrid origin of *Eriocnemis soderstromi* Butler.—Proceedings of the Biological Society of Washington 109:764–769.

———. 1998. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 6. An intergeneric hybrid, *Aglaiocercus kingi* × *Metallura tyrianthina,* from Venezuela.—Proceedings of the Biological Society of Washington 111:511–520.

———. 1999a. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 7. Probable parentage of *Calliphlox iridescens* Gould 1860.—Proceedings of the Biological Society of Washington 112:443–450.

———. 1999b. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 8. A provisional hypothesis for the hybrid origin of *Zodalia glyceria* (Gould, 1858).—Proceedings of the Biological Society of Washington 112:491–502.

———, & N. L. Newfield. 1996. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 1. Characterization of *Calypte anna* × *Stellula calliope* and the possible effects of egg volume on hybridization potential.—Proceedings of the Biological Society of Washington 109:755–763.

———, & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* × *Heliangelus amethysticollis*) from northern Colombia.—Condor 92:754–760.

Griscom, L. 1934. The ornithology of Guerrero, Mexico.—Bulletin of the Museum of Comparative Zoology 75:368–422.

Howell, S. N. G. & S. Webb. 1995. The birds of Mexico and northern Central America. Oxford University Press, Oxford, UK, 851 pp.

Hunter, R. S., & R. W. Harold. 1987. The measurement of appearance, 2nd edition. Wiley, New York, 411 pp.

Peters, J. 1945. Check-list of birds of the world, vol. 5. Museum of Comparative Zoology, Cambridge, Massachusetts, 306 pp.

Phillips, A. R. 1964. Notas sistematicas sobre aves Mexicanas, III.—Revista de la Sociedad Mexicana de Historia Natural 25:217–242.

Ridgway, R. 1911. Birds of North and Middle America. Bulletin of the United States National Museum 50, part 5.

Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.

Simon, E. 1921. Histoire naturelle des Trochilidae (synopsis et catalogue). Encyclopedia Roret, L. Mulo, Paris.

Weller, A.-A. 1999. Violet-crowned Hummingbird, *Agyrtria violiceps*. P. 599 *in* J. del Hoyo, A. Elliott, & J. Sargatal, eds., Handbook of the Birds of the World, vol. 5. Barn-owls to Hummingbirds. Lynx Edicions, Barcelona, 759 pp.

———, & K.-L. Schuchmann. 1997. The hybrid origin of a Venezuelan trochilid, *Amazilia distans* Wetmore & Phelps 1956.—Ornithologia Neotropical 8:107–112.

Appendix 1

Comparative description of selected characters of adult male *Amazilia violiceps ellioti, Cynanthus latirostris magicus,* and a probable hybrid, *A. violiceps ellioti* × *C. latirostris magicus* (= *Cyanomyia salvini* Brewster; MCZ 224,125). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

The forecrown and crown of *violiceps* exhibit brilliant bluish-purple iridescence when viewed head-on in direct light. The remainder of the dorsum from hindneck to the rectrices is grayish-olive; the transition between the purple crown and olive hindneck is abrupt. The back, shoulders, upper tail coverts, and central rectrices are faintly glossed with silvery-green when viewed head-on. The rectrices are unmarked.

Feathers of the forecrown and crown of *latirostris* (to a point immediately posterior of the eyes) are dark green, margined with bronze giving the forehead and frontal part of the crown a dull appearance. The remainder of the dorsum from hindcrown to rump is glossy green (showing scattered bluish-green, brilliantly iridescent feather barbs when viewed head-on). Uppertail coverts are darker, contrasting slightly with the green rump and the bluish-black rectrices. The outer two or three pairs of rectrices (R3, R4, R5) are narrowly tipped with gray.

The crown of *salvini* is intermediate in appearance between that of *violiceps* and *latirostris,* showing a mixture of deep blue, purplish-blue iridescence, becoming greener toward the posterior of the coronal area. The intensity of iridescence increases posteriorly from the forecrown to center of the crown (viewed head-on). This bluish-green iridescence at the posterior edge of the coronal area blends into deep bluish-green on the hindneck and back, changing to dull green on the lower back and rump. The back and scapulars of *salvini* appear bluer than those of either parental species. This seems to be another example of the "bluing" phenomenon observed in some hummingbird hybrids (Graves 1998, 1999b). The intensity of iridescence on the lower back of *salvini* is intermediate between that observed in the postulated parental species. There is no appreciable contrast between uppertail coverts and rectrices in *salvini.* The rectrices are intermediate in color between those of *latirostris* and *violiceps* (Table 2). The outer rectrices (R4, R5) of *salvini* are worn and appear to be retained from a subdefinitive plumage. R1 and R2 are fresh and unworn, whereas the tip of R3 is slightly worn. Wing coverts and flight feathers of *salvini* are intermediate in color and degree of melanism to those of *violiceps* and *latirostris.*

The ventral plumage of *violiceps* is snowy white from chin to undertail coverts. Feathers on the chin, throat, and upper breast are pure white to the base, with only a few pale gray barbs at the base of the rachises.

The chin and upper throat of *latirostris* are deep purple (extending laterally to the auriculars and eyering), blending into dark bluish-green on the lower throat; this latter color continuing posteriorly to the vent. A few feathers in the chin are fringed with white. Feather disks from chin to vent exhibit iridescent highlights when viewed head-on. Vent feathers are white. Undertail coverts of *latirostris* are gray, paling to white at the distal margins (most coverts are gray along the rachis to the tip). Some shorter coverts have an oval gray subterminal spot.

The chin and throat of *salvini* are white but basal feather barbs are much grayer than in *violiceps.* The auriculars are iridescent purple and greenish-purple (posteriorly). Feathers at the sides of the throat have purple (anterior) or purplish-green (posteriorly) subterminal bars, imparting a spotted appearance to the sides of the throat. This spotting coalesces on the sides of the breast to form an incomplete pectoral band formed of white feathers with large subterminal greenish-blue or greenish-purple disks. The sides of *salvini* are dark bluish-green (about the same color as in *latirostris*). The tendency toward an incomplete pectoral band is present in *violiceps* in the form of grayish-olive sides, with scattered weakly iridescent, pale bluish-green feather disks. However, the medial extension of darker feather tips observed in *violiceps* never reaches the extent observed in *salvini.* The few undertail coverts remaining on the specimen of *salvini* are pure white.

The bill of *violiceps* is dull grayish-yellow (red in life) tipped with dark brown or blackish-brown (<15% of the bill length). Bill color in *latirostris* is similar but the dark tip is more extensive. The pattern of pigmentation in *salvini* is intermediate of that observed in adult male specimens of *violiceps* and *latirostris.*

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A new species of caracara (*Milvago*) from Quaternary asphalt deposits in Cuba, with notes on new material of *Caracara creightoni* Brodkorb (Aves: Falconidae)

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Abstract.—An extinct caracara, *Milvago carbo,* new species, is described from Quaternary asphalt deposits of Las Breas de San Felipe, northern Matanzas Province, Cuba, from tarsometatarsi, tibiotarsi, and a notarium. This species was much larger than other species of the genus, living or extinct. New material of the extinct species *Caracara creightoni* provides additional information on its characters and distribution.

Resumen.—Se describe una nueva especie de caraira, *Milvago carbo,* sobre la base de tarsometatarsos, tibiotarsos, y un notarium, procedentes de Las Breas de San Felipe (depósitos cuaternarios de asfalto), al norte de la provincia de Matanzas, Cuba. Esta especie era mayor que las demás conocidas del género, vivientes o extinguidas. Nuevo material de la especie extinta *Caracara creightoni* suministra información adicional sobre sus caracteres y distribución.

The caracaras (Caracarinae = Polyborinae auct.) comprise 10 species of mainly terrestrial Falconidae found throughout the Neotropics and in southern Florida and in temperate southern South America. The larger species are at least partly scavengers with somewhat vulture-like habits. The only living representative of the group in the West Indies is the widespread Crested Caracara, *Caracara cheriway* Jacquin, found in Cuba and the Isle of Pines (now Isla de la Juventud) (American Ornithologists' Union 1998, Raffaele et al. 1998). The Cuban populations cannot be distinguished from those of the mainland and are thought to result from a relatively recent colonization of the island (Suárez and Olson 2001).

Despite their modern paucity, the fossil record indicates that caracaras were much more diverse in the West Indies in the Quaternary. *Caracara creightoni* Brodkorb (1959b) is known from the Quaternary of New Providence Island, Bahamas (Olson and Hilgartner 1982), and of Cuba (Suárez and Olson 2001). *Caracara latebrosus* Wetmore (1920) from Puerto Rico is enigmatic as it is known so far only from two bones that are not particularly diagnostic (Olson 1976). A caracara from Grand Cayman reported as *C. creightoni* (Morgan 1994), is too large for that species but smaller than a very large, nearly flightless caracara discovered on Jamaica (Olson, unpublished data).

Smaller caracaras of the genus *Milvago* have hitherto been known in the West Indies only from Hispaniola, home to *Milvago alexandri* Olson (1976), a species about the size of the living *M. chimachima.* The latter species, essentially South American in distribution, expanded into southern Costa Rica from Panama about 1973 (Stiles and Skutch 1989), but probably once occurred throughout Middle America and southern North America because it is known from the Pleistocene of Florida. The Florida fossils were originally described as *Falco readei* Brodkorb (1959a), which was transferred to *Milvago* by Campbell (1980), and then synonymized with *M. chimachima* by Emslie (1998). Fossils of *Milvago* of about this size have also been recovered from Cuba (Suárez and Arredondo 1997), but those known so far are too incomplete to be diagnostic at the specific level (Suárez and Olson, pers. obs.).

During the processing of bird fossils from asphalt deposits of Las Breas de San Felipe, northern Matanzas Province, Cuba (see Iturralde-Vinent et al. 2000), new evidence of yet another species of caracara came to light. Although of relatively large size, this species is nevertheless referable to the genus *Milvago.* We also report previously unknown skeletal elements of *Caracara creightoni* from additional localities in Cuba.

Methods and comparative material examined.—Measurements were taken with digital calipers to the nearest 0.1 mm. Osteological terminology follows Howard (1929) and Baumel and Witmer (1993). Skeletons of Caracarinae examined at the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), include the following species: *Milvago chimango* (7), *M. chimachima* (8), *Daptrius ater* (5), *D. americanus* (2), *Phalcoboenus australis* (5), *P. carunculatus* (1), *P. megalopterus* (1), *Caracara plancus* (7), *C. cheriway* (12), and *C. lutosa* (1). Fossil specimens examined included: *Milvago alexandri,* holotypical right tarsometatarsus USNM 214573, Haiti, Hispaniola; *Milvago* sp., proximal end of left tarsometatarsus, collection of William Suárez, La Habana, Cuba (WS 977); *Caracara creightoni,* distal end of right tibiotarsus lacking posterior rim of internal condyle, Museo Polivalente de Sagüa La Grande, Villa Clara, Cuba (MPSG 83), complete left tarsometatarsus MPSG 103, and distal half of left tarsometatarsus MPSG 106, Cuba. The description and illustrations of the extinct caracara *Milvago brodkorbi* Campbell (1979), of Peru, were also used for comparison.

Systematics

Class Aves
Family Falconidae

Fossils were referred to the Falconidae instead of Accipitridae by the characteristic three openings on the distal portion of the tibiotarsus; tarsometatarsus with medial calcaneal ridge of the hypotarsus longer and centrally placed rather than short and medial. Referral to the subfamily Caracarinae instead of Falconinae is indicated by the short hypotarsus, with an abruptly truncate distal margin, rather than being long and tapering gradually down the shaft as in the Falconinae.

Genus *Milvago* Spix, 1826

The new species is referred to *Milvago* rather than to *Caracara, Daptrius,* or *Phalcoboenus* by having the tarsometatarsus very slender, trochlea for digit 2 broad at base, rotated slightly posteriad and with posterior wing straight, projecting posteriorly perpendicular to the main axis of the shaft (see Campbell 1980).

Milvago carbo, new species
(Fig. 1)

Holotype.—Nearly complete right tarsometatarsus, Museo Nacional de Historia Natural, La Habana, Cuba (MNHNCu P4569), lacking most of the posterior edge of the medial calcaneal ridge and part of the outer cotyla. Collected by members of the Geology and Paleontology Group of the MNHNCu, during field expeditions in 1998.

Type locality and age.—Cuba, Matanzas Province, Municipality of Martí, 5.5 km west of the town of Martí, asphalt deposit known as Las Breas de San Felipe, San Felipe II site (Instituto Cubano de Geodesia y Cartografia 1986, 1:50,000 map, sheet Martí 4084-IV, X502, Y347). Quaternary, prob-

Fig. 1. Tarsometatarsi in anterior, posterior, and medial views: A, *Milvago chimango* (USNM 18473); B, *Milvago carbo,* new species, holotype, MNHNCu P4569 (specimen coated to enhance photography); C, *Caracara creightoni* MPSG 103 (image reversed to facilitate comparison). Scale = 2 cm.

ably late Pleistocene or early Holocene; not directly dated (for description, associated fauna, and discussion of the age of the deposit, see Iturralde-Vinent et al. 2000).

Measurements (mm) of holotype.—Total length, 85.7; least width and depth of shaft, 4.5 × 3.6; distal breadth, 3.0; width and depth of trochlea for digit 3, 4.6 × 6.1.

Topotypical paratypes.—Fragmentary notarium MNHNCu P4567; distal ends of left tibiotarsi MNHNCu P4568, MNHNCu P4570, MNHNCu P4571; proximal half of left tarsometatarsus lacking part of the medial and lateral calcaneal ridges MNHNCu P4572; shaft of left tarsometatarsus MNHNCu P4573; proximal right tarsometatarsus MNHNCu P4574; distal halves of right tarsometatarsi MNHNCu P4575, MNHNCu P4576 (abraded); distal ends of left tarsometatarsi MNHNCu P4577, MNHNCu P4578.

Etymology.—L. *carbo,* charcoal, coal, from the black color of the tar-impregnated fossils.

Diagnosis.—Much larger than any other species of the genus *Milvago* living or extinct (Table 1).

Description.—Notarium large, slender and laterally compressed (smaller, relatively shorter but also compressed in *Milvago chimachima* and *M. chimango*). Although the tibiotarsus is large, no qualitative characters could be discerned, as this element shows great intraspecific variation in *Milvago* (Emslie 1998). Tarsometatarsus large with the flattened medial (inner) surface angled towards the midline of the posterior face so that the posterior crest that it forms is near the midline and nearly continuous with the medial calcaneal ridge, and the posterior metatarsal groove is narrow, as in *M. chimango,* and as opposed to *M. chimachima,*

Table 1.—Skeletal measurements (mm) of fossil and living species of *Milvago*. Sequence is: range (mean) n.

Measurement	*M. carbo*	*M. alexandri**	*M. brodkorbi***	*M. chimachima****	*M. chimango****
Notarium					
Total length	33.7	—	—	24.4–25.9 (24.9) 3	22.1–27.2 (24.7) 7
Tibiotarsus					
Distal width	10.6–11.2 (10.8) 3	—	8.2–9.9 (9.1) 23	7.5–8.9 (8.3) 8	7.1–9.5 (7.8) 9
Tarsometatarsus					
Length	85.7	56.2	57.9–61.8 (59.8) 5	50.0–54.2 (51.8) 8	56.8–63.8 (59.7) 9
Proximal width	11.3–11.6 (11.4) 2	8.2	9.4–10.9 (10.0) 9	8.5–9.5 (8.8) 8	7.9–10.1 (8.5) 9
Least width of shaft	4.5 (4.5) 3	3.4	3.6–4.4 (4.0) 15	3.2–3.7 (3.5) 8	2.9–3.8 (3.2) 9
Least depth of shaft	3.4–3.6 (3.4) 4	2.6	—	2.3–2.7 (2.5) 8	2.2–2.7 (2.4) 9
Distal width	12.2–13.0 (12.5) 3	9.1	9.1–10.4 (9.7) 14	8.2–10.0 (8.7) 8	8.2–10.2 (8.8) 9
Width of trochlea for digit 3	3.9–4.6 (4.2) 3	3.4	3.4–4.1 (3.7) 19	3.2–3.8 (3.3) 8	3.0–3.7 (3.2) 9
Depth of trochlea for digit 3	5.2–6.1 (5.6) 3	—	—	3.7–4.5 (4.1) 8	3.4–4.2 (3.7) 9

Measurements from Olson (1976)*, Campbell (1979)** and Emslie (1998)***.

M. alexandri, and *M. brodkorbi,* in which the posterior crest is offset medially and the groove is wider. The roughly triangular excavation lying medial and distal to the hypotarsus is short in *M. carbo* and *M. chimango,* and longer, extending farther down the shaft in *M. chimachima, M. alexandri,* and *M. brodkorbi.* Trochlea for digit 2 very wide and very excavated medially in posterior view, in this respect resembling the species of *Phalcoboenus.* Distal foramen high, more proximal on the shaft (similar to *M. chimachima* and *M. alexandri,* as opposed to the more distal placement in *M. chimango,* and *M. brodkorbi*).

Remarks.—The much greater diversity of the family Falconidae in the Quaternary of the West Indies than at present is again increased with the addition of *Milvago carbo.* This is the second fossil species of *Milvago* known in the Greater Antilles, and the third overall. *Milvago brodkorbi* Campbell (1979), from the Talara Tar Seeps, Peru, is larger than *M. alexandri* Olson (1976) of Hispaniola, but both would have been dwarfed by *M. carbo.*

The Cuban species *Milvago carbo* and *Falco kurochkini* Suárez and Olson (2001), the latter of the subfamily Falconinae, agree in the marked elongation of the tarsometatarsus. Of the two living species of *Milvago, M. chimango,* which ranges from southern Brazil and Chile south to Tierra del Fuego, has a long and slender tarsometatarsus and occurs in open country, whereas *M. chimachima,* which ranges from Panama and Costa Rica southward east of the Andes to northern Argentina, has a shorter tarsometatarsus and is more arboreal in habits (Vuilleumier 1970). From its size and the proportions of its tarsometatarsus, *M. brodkorbi* appears to be a trans-Andean representative of *M. chimango.*

Milvago carbo would probably have been at least as terrestrial in habits as *M. chimango* or *M. brodkorbi* but was much larger. The total length of its tarsometatarsus is between that of *Caracara creightoni* (smaller) and *C. cheriway* (larger), but because it is much more gracile, *M. carbo* probably took smaller prey than either.

Genus *Caracara* Merrem, 1826
Caracara creightoni Brodkorb, 1959
(Fig. 2; Table 2)

Referred material.—Las Breas de San Felipe II, municipality of Martí, Matanzas: fragmentary anterior half of notarium MNHNCu P4579, 4 distal ends of left MNHNCu P4580–83 and two distal ends of right tibiotarsi MNHNCu P4584–85, 6 distal ends of right MNHNCu P4586–91 and two distal ends of left tarsometatarsi MNHNCu P4592–93. Cueva de Paredones, about 3 km SE of Ceiba del Agua, municipality of Caimito, La Habana: complete left femur WS 1933. Cueva de Sandoval, about 4 km south of Vereda Nueva, municipality of Caimito, La Habana: proximal end of right humerus WS 1035 and proximal end of right femur WS 587.

Comparisons with other species of Caracara.—The fragment of notarium agrees with *Caracara* in the less laterally compressed anterior vertebrae, unlike *Milvago,* in which these vertebrae are greatly compressed and thin anteriorly. It differs from *C. plancus, C. cheriway,* and *C. lutosa* in its relatively small size and by the lower position of the foveae costales. The proximal end of the humerus is smaller with a capital groove that is thin, rather than wide as in *Milvago.* The femur is similar to that in the species of *Caracara,* but differs specifically from *C. plancus, C. cheriway,* or *C. lutosa* in being smaller, with a very thin shaft at the midpoint and relatively wide proximal and distal ends (Table 2). The head of the femur is not reflected proximally; the pneumatic foramen is large; the external condyle is thin and more vertical; and the intercondylar sulcus is wider. Thus this specimen agrees with two portions of femora recorded by Suárez and Arredondo (1997) as *C. creightoni,* but not further described by Suárez and Olson (2001) because of their fragmentary condition.

The additional tarsometatarsi of *C.*

Fig. 2. Left femora (A, B) and right humeri (C, D) of *Caracara*: A, *C. creightoni* WS 1933; B, *C. cheriway* USNM 19670; C, *C. creightoni* WS 1035; D, *C. cheriway* USNM 19670. Scale = 2 cm.

creightoni from Las Breas de San Felipe indicate points of distinction not previously mentioned by Suárez and Olson (2001): the trochlea for digit 2 is reduced and not rotated posteriad, as opposed to being larger and more posteriorly rotated in *Caracara plancus, C. cheriway,* and *C. lutosa.* This character is present in all specimens available and does not represent intraspecific variation as we first supposed.

Table 2.—Measurements (mm) of the humerus and femur in fossil and living species of *Caracara.* Sequence is: range (mean) n.

Measurement	*C. creightoni*	*C. cheriway*	*C. plancus*	*C. lutosa*
Humerus				
Depth of the head	5.7	5.9–7.2 (6.7) 13	6.0–8.8 (7.1) 7	7.0
Least width of shaft	7.1	7.3–8.3 (7.7) 12	7.4–9.8 (8.3) 7	8.4
Femur				
Length	65.6	68.4–76.8 (72.0) 12	66.1–80.8 (73.6) 7	71.1
Proximal breadth	13.7, 14.4	13.2–15.2 (14.3) 12	13.2–18.5 (15.4) 7	14.8
Least width of shaft	6.2	6.8–8.2 (7.5) 12	6.9–8.8 (7.6) 7	7.5
Least depth of shaft	5.8	6.2–7.4 (6.9) 12	5.9–8.4 (7.0) 7	7.0
Distal breadth	13.7	13.4-16.4 (15.0) 12	13.7–18.4 (15.7) 7	16.0

Remarks.—Remains of *Caracara creightoni* occurred together with *Milvago carbo* at Las Breas de San Felipe in a small area of less than 2 m^2 (Suárez, pers. obs.). Although fossils of all known extinct Cuban scavenging birds occur at Las Breas, no remains of *Caracara cheriway* have been found there (Suárez, in prep.). The distal end of a left tarsometatarsus from a cave deposit in La Habana Province that Jiménez (1997) recorded as *Caracara plancus* (=*cheriway*), was re-examined (WS) and found to agree with *C. creightoni* instead. Possibly *C. cheriway* reached Cuba after Europeans introduced domestic animals that provided similar ecological conditions to those that may have been lost following the extinction of most of the large endemic mammals of the West Indies at the end of the Pleistocene and early in the Holocene.

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Literature Cited

American Ornithologists' Union. 1998. Check-list of North American birds, 7th edition. American Ornithologists' Union, Washington, D.C., 829 pp.

Baumel, J. J., & L. Witmer. 1993. Osteologia. Pp. 45–132 *in* J. J. Baumel, ed., Handbook of avian anatomy. Nomina Anatomica Avium, 2nd edition—Publications of the Nuttall Ornithological Club 23. Cambridge, Massachusetts.

Brodkorb, P. 1959a. The Pleistocene avifauna of Arredondo, Florida.—Bulletin of the Florida State Museum, Biological Sciences 4:269–291.

———. 1959b. Pleistocene birds from New Providence Island, Bahamas.—Bulletin of the Florida State Museum, Biological Sciences 4:349–371.

Campbell, K. E., Jr. 1979. The non-passerine Pleistocene avifauna of the Talara Tar Seeps, northwestern Peru.—Royal Ontario Museum, Life Sciences Contributions 118:1–203.

———. 1980. A review of the Rancholabrean avifauna of the Itchetucknee River, Florida.—Natural History Museum of Los Angeles County, Contributions in Sciences 330:119–129.

Emslie, S. D. 1998. Avian community, climate, and sea-level changes in the Pilo-Pleistocene of the Florida Peninsula.—Ornithological Monographs 50:1–113.

Howard, H. 1929. The avifauna of the Emeryville Shellmound.—University of California Publications in Zoology 32:301–394.

Iturralde-Vinent, M., R. D. E. MacPhee, S. Díaz-Franco, R. Rojas-Consuegra, W. Suárez, & A. Lomba. 2000. Las Breas de San Felipe, a Quaternary asphalt seep near Martí (Matanzas Province, Cuba).—Caribbean Journal of Science 36:300–313.

Jiménez, V. O. 1997. Seis nuevos registros de aves fósiles en Cuba.—El Pitirre 10(2):49.

Morgan, G. S. 1994. Late Quaternary fossil vertebrates from the Cayman Islands. Pp. 465–508 *in* M. A. Brunt and J. E. Davies, eds., The Cayman Islands: natural history and biogeography. Kluwer Academic Publishers, Dordrecht, Netherlands, 604 pp.

Olson, S. L. 1976. A new species of *Milvago* from Hispaniola, with notes on other fossil caracaras from the West Indies (Aves: Falconidae).—Proceedings of the Biological Society of Washington 88:355–366.

———, & W. B. Hilgartner. 1982. Fossil and subfossil birds from the Bahamas. Pp. 22–56 *in* S. L. Olson, ed., Fossil vertebrates from the Bahamas.—Smithsonian Contributions to Paleobiology 48.

Raffaele, H. A., J. Wiley, O. Garrido, A. Keith, & J. Raffaele. 1998. A guide to the birds of the West Indies. Princeton University Press, Princeton, New Jersey, 511 pp.

Stiles, F. G., & A. F. Skutch. 1989. A guide to the birds of Costa Rica. Cornell Univ. Press, Ithaca, New York, 511 pp.

Suárez, W., & O. Arredondo. 1997. Nuevas adiciones a la paleornitología cubana.—El Pitirre 10: 100–102.

———, & S. L. Olson. 2001. Further characterization of *Caracara creightoni* Brodkorb based on fossils from the Quaternary of Cuba (Aves: Falconidae).—Proceedings of the Biological Society of Washington 114:501–508.

Vuilleumier, F. 1970. Generic relations and speciation patterns in the caracaras (Aves:Falconidae).—Breviora 355:1–29.

Wetmore, A. 1920. Five new species of birds from cave deposits in Porto Rico.—Proceedings of the Biological Society of Washington 33:77–82.

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116(2):308–316. 2003.

A new species of penguin (Spheniscidae: *Spheniscus*) and other birds from the late Pliocene of Chile

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Abstract.—We describe a new species of penguin, *Spheniscus chilensis,* from Cuenca del Tiburón, late Pliocene, northern Chile. This species was found in association with a small species of cormorant, *Phalacrocorax* sp., and a caracara, *Milvago* sp., and is the first Pliocene penguin to be described from South America. Other vertebrates at this site include fish, sharks, and cetaceans. An extensive invertebrate fauna, including the late Pliocene muricid gastropod *Herminespina mirabilis,* also is present. The avifauna suggests a low diversity of seabirds existed in northern Chile from the late Pliocene to the present, unlike the much higher diversity found in Patagonia in the late Oligocene/early Miocene.

The coastal region of southern Peru and northern Chile is well known for its massive layers of marine shell beds exposed in cliffs. Geologic studies of these beds have provided considerable information on marine faunas in the Miocene through late Pleistocene of this region. Previous investigations in Chile have concentrated on the age and structure of the invertebrate faunas, and eustatic changes in sea level in correlation with tectonic uplift (Herm 1969, 1970; Tsuchi et al. 1988; Padilla & Elgueta 1992). Deposition of these beds occurred over a period of millions of years in coastal forearc basins, the eastern sections of which were later uplifted during crustal deformations of the continental margin (Dunbar et al. 1990). Extensive and diverse deposits of late Pleistocene marine mollusks also occur throughout this region (Ortleib et al. 1994).

In 1994, we visited an exposure of marine shell beds on the Península de Mejillones and approximately 14 km northwest of the Antofagasta airport and 6 km from the coast (Fig. 1). Here, over 10 m of marine sediments are exposed on eroded slopes of valleys and hills that contain abundant marine mollusks. The upper layers of these exposed sediments also contain numerous sharks' teeth, fish bones, and fragmentary and complete bones of marine mammals and birds. This fossil exposure lies within the upper beds of the Caleta Herradura de Mejillones Formation (23°21.453″S; 70°32.061″W), dating to the late Pliocene (Tsuchi et al. 1988). In addition, the fossils were found in association with the muricid gastropod *Herminespina mirabilis,* which is only known from the late Pliocene of Peru and Chile (DeVries & Vermeij 1997).

The area of concentration of the vertebrate fossils, known locally as Cuenca del Tiburón, is particularly rich in birds. Dozens of disarticulated bones of a single species of penguin (Spheniscidae) and a small cormorant (Phalacrocoracidae) are scattered on the surface, having eroded from exposed layers of shell beds nearby. Fossils of this penguin originally were found by one of us (CGC) at the locality in 1980. We visited the site twice in 1994 and once in 1997 to

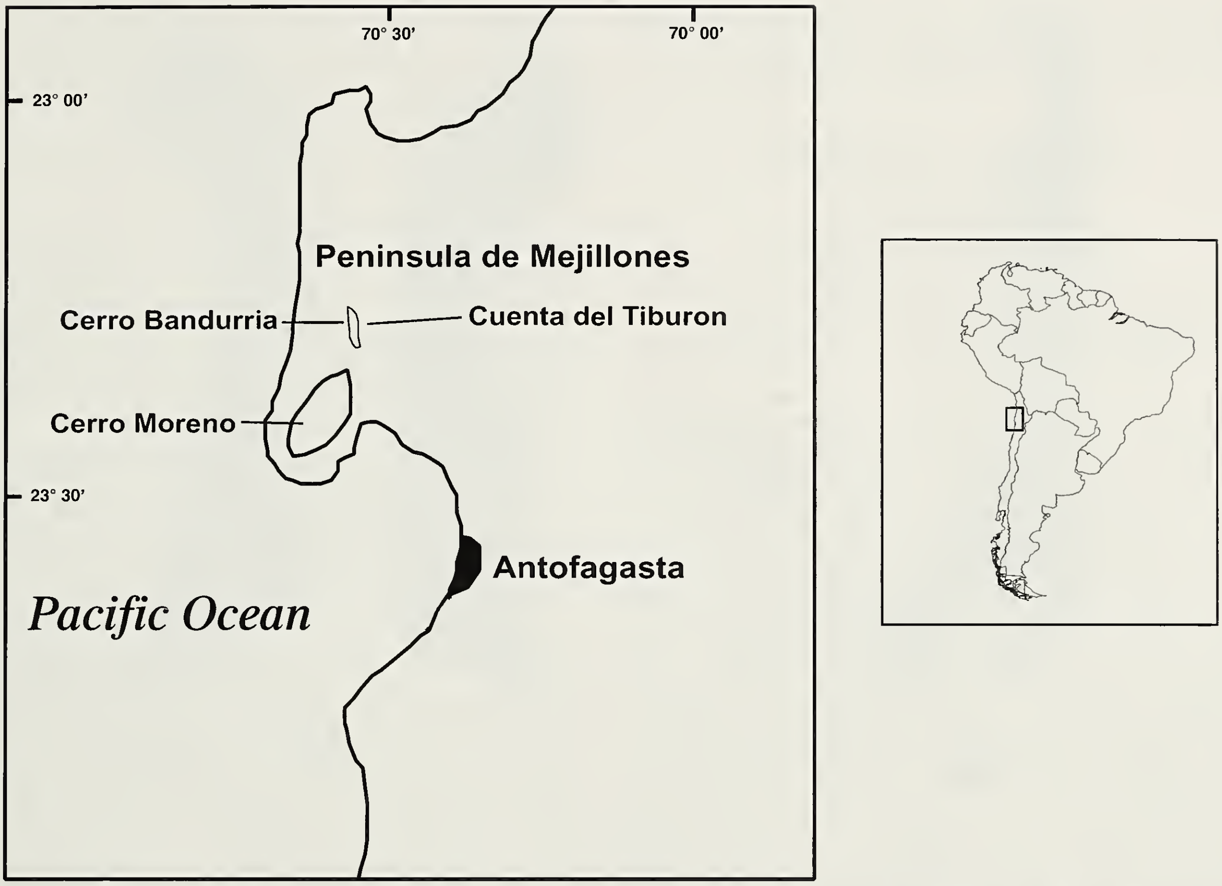

Fig. 1. Map showing the location of Cuenca del Tiburón on the Península de Mejillones, northern Chile.

collect additional material of this and other birds that are presented here.

All the disarticulated penguin material appears to represent a new species of penguin that is referable to *Spheniscus* by the relatively long and slender mandibular shaft, humerus with relatively deep proximal end and large pneumatic fossa that is weakly bipartite, proximal shaft slightly angled internally and not straight, and tarsometatarus relatively short and broad with external proximal foramen equal or larger and placed slightly higher on shaft than internal foramen. The fossil material most closely approaches the living *S. humboldti* and *S. magellanicus* in size and proportions, but differs from all species in this genus by distinct characters of the humerus and other postcranial elements. These comparisons indicate that the fossils represent a new species of penguin that is described herein; fossils of two other taxa of birds associated with the penguin material also are identified.

Materials and Methods

Measurements and comparisons of Recent skeletons of penguins were completed in the collections of the Florida Museum of Natural History (FLMNH), Gainesville, and the American Museum of Natural History (AMNH), New York. Fossil material was examined at the Museo de La Plata (MLP), Argentina, the Universite Claude Bernard Lyon 1, France, and at AMNH. Measurements were taken with Vernier calipers to the nearest 0.1 mm and are self-descriptive. Measurements of the humerus include greatest length (GL), proximal breadth and depth (PB, PD), least breadth and depth of shaft (LBS, LDS), and distal breadth and depth (DB, DD). Terminology follows that of Howard (1929) and Simpson (1946).

Fossil specimens reported here are housed at the Museo Geológico Prof. Humerto Fuenzalida V., Universidad Católica del Norte (UCN), Antofagasta, Chile, or at

FLMNH where they are catalogued with University of Florida (UF) numbers.

Systematic Paleontology

Class Aves
Order Sphenisciformes
Family Spheniscidae
Spheniscus chilensis, new species
Fig. 2

Holotype.—complete left humerus, UCN-1-130697 (Fig. 2A). Collected by Carlos Guerra Correa, 1980. Cast of specimen housed at FLMNH, UF 143300.

Paratypes.—2 left mandibles missing ends, UF 144101, 144153; cervical vertebra, UF 144102; 2 right scapulae, UF 143296–143297; right coracoid, 144154 (Fig. 2B); four right coracoids missing sternal ends, UF 144124–144125, 144155–144156; shaft of right coracoid, UF 144103; two left humeri, UF 144104–144105; 6 left humeri missing proximal ends, UF 144106, 144126, 144157–144159, 144171; 4 right humeri, UF 143295, 144107–144109; 3 right humeri missing proximal ends, UF 144127–144128, 144160; left radius, UF 144129; 6 right radii, UF 143299 (Fig. 2C), 144110, 144130–144133; 3 left ulnae, UF 144134, 144161–144162; right ulna, UF 144163; 3 left carpometacarpi, UF 143298 (Fig. 2C), 144111, 144135; 5 right carpometacarpi, UF 144112, 144136–144138, 144164; wing phalanx, UF 144139; synsacrum, UF 144113; proximal end of synsacrum, UF 144147; left femur with ends damaged, UF 144165; proximal left femur, UF 144114; left femur missing proximal end, UF 144140; 3 distal halves left femora, UF 144115, 144141, 144148; distal end left femur, UF 144166; right femur, UF 144116 (Fig. 2D); two right femora missing proximal ends, UF 144117, 144149; 2 right femora missing distal ends, UF 144118–144119; distal end right femur, UF 144167; shaft of right femur, UF 144142; two distal left tibiotarsi, UF 144150, 144168 (Fig. 2D); proximal end right tibiotarsus, UF 144169; distal shaft of right tibiotarsus, UF 144143; shaft of right tibiotarsus, UF 144170; right fibula, UF 144144; 3 left tarsometatarsi with damaged proximal ends, UF 143293–143294, 144120.

Type locality and horizon.—Cuenca del Tiburón Fossil Locality, Península de Mejillones, Chile, late Pliocene (upper beds, Caleta Herradura de Mejillones Formation, Tsuchi et al. 1988). This is the only locality in which the fossil species occurs.

Diagnosis.—Humerus with deep fossa at proximal anconal surface below head (fossa is shallow in *Spheniscus humboldti, S. demersus,* and *S. mendiculus,* shallow to moderately deep in *S. magellanicus*), relatively smaller and narrower entepicondylar process (broad and rounded in all living *Spheniscus*), relatively slender shaft similar to *S. magellanicus* and *S. demerus* (more robust in *S. humboldti*; Table 1), and distal end with or without pneumatic fossa in distal view (no fossa present in all living *Spheniscus*). Tibiotarsus with relatively larger distal foramina and broader distal external shaft than in all living *Spheniscus.* Tarsometatarsus with shallow anterior grooves below proximal foramina (grooves deep in all Recent *Spheniscus*). The ulna, radius, carpometacarpus and femur of the fossil species show minor differences with the living species.

Etymology.—Named after Chile, the country in which the fossil site is located.

Description.—The fossil material most closely approaches the living *S. humboldti* and *S. magellanicus* in size and proportions, but differs from all species in this genus by distinct characters of the humerus and tarsometatarsus. The fossil species is slightly smaller than *Spheniscus humboldti* and similar in size to *S. magellanicus* (Table 1). Only one other fossil species is known, *S. predemersus* from the early Pliocene of South Africa (Simpson 1971). The humerus of that species, however, is much longer (length, 84.7 mm) and more slender in the shaft (medial breadth, 8.6 mm) than *S. chilensis* (Table 1, plus see measurements in

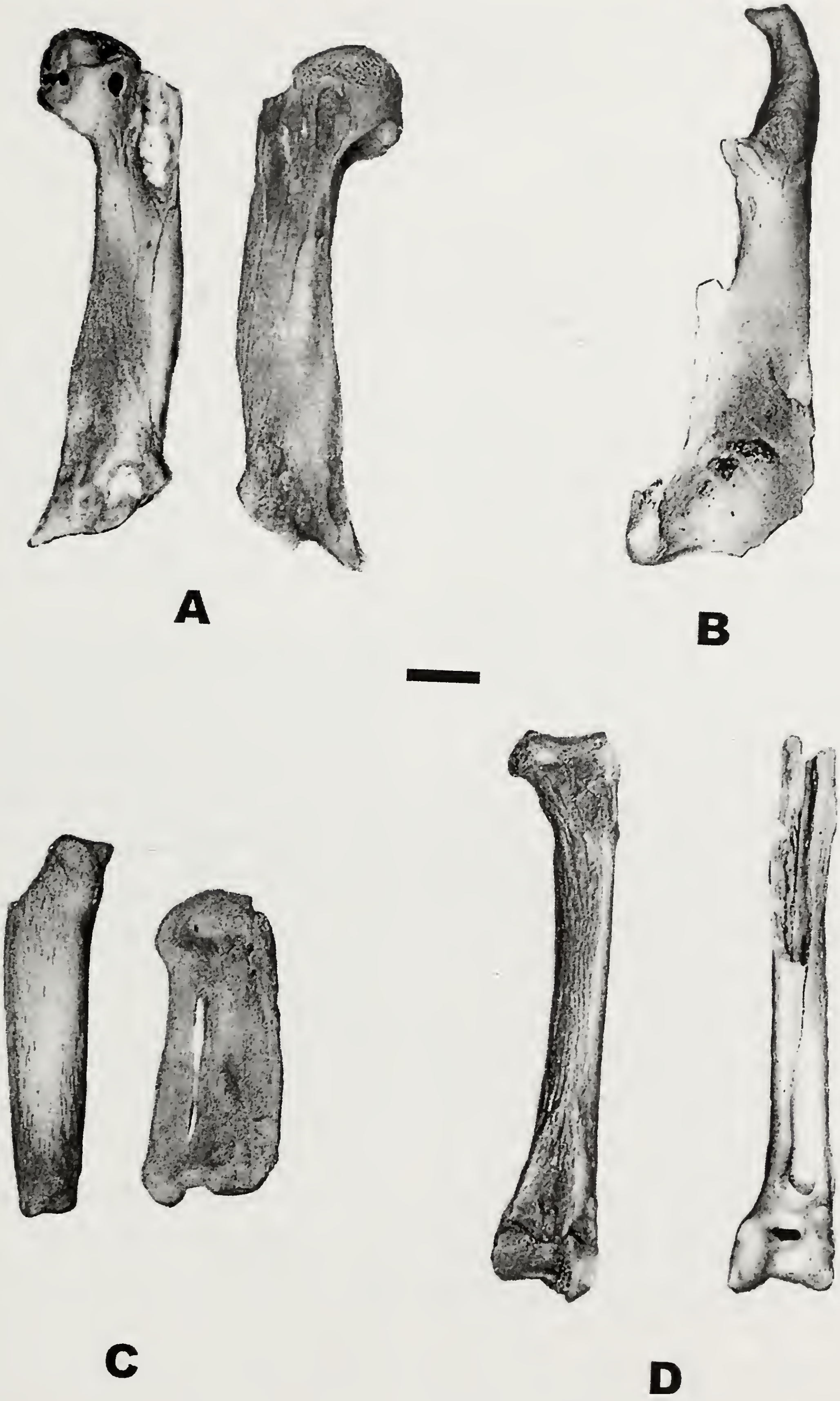

Fig. 2. Fossil specimens of *Spheniscus chilensis* from Cuenca del Tiburón: (A) holotype left humerus, UCN-1-130697, in palmar (left) and anconal (right) view; (B) dorsal view of right coracoid, UF 144154; (C) anconal view of right radius (left), UF 144110, and internal view of left carpometacarpus (right), UF 144111; (D) posterior view of right femur, UF 144116 (left), and anterior view of distal left tibiotarsus; UF 144168. Scale bar = 1 cm.

Table 1.—Measurements (mm) of humeri of Recent *Spheniscus* in comparison to *S. chilensis.* For each entry, the top row is mean ± standard deviation and bottom row is range. See text for key to measurement acronyms.

Species	GL	PB	PD	LBS	LDS	DB	DD
S. humboldti	75.3 ± 1.5	22.8 ± 0.9	15.9 ± 0.8	13.1 ± 0.5	5.8 ± 0.3	21.3 ± 1.1	8.0 ± 0.4
(N = 8)	73.3–78.1	21.8–24.2	14.5–16.8	12.6–14.1	5.5–6.4	20.2–23.3	7.5–8.7
S. magellanicus	69.1 ± 5.7	20.1 ± 1.2	14.5 ± 0.8	11.6 ± 0.6	5.0 ± 0.4	19.9 ± 0.7	7.2 ± 0.4
(N = 4)	62.8–75.0	18.9–21.1	13.8–15.6	11.0–12.5	4.5–5.5	19.2–20.8	6.8–7.8
S. demerus	70.7 ± 4.7	21.4 ± 2.6	14.7 ± 2.6	12.3 ± 2.1	5.2 ± 1.3	20.0 ± 1.9	7.2 ± 0.6
(N = 2)	67.3–74.0	19.5–23.2	12.9–16.5	10.8–13.7	4.2–6.1	18.6–21.3	6.8–7.6
S. mendiculus	57.0 ± 1.6	16.7 ± 0.1	11.2 ± 0.2	9.6 ± 0.5	4.1 ± 0.2	16.0 ± 1.3	6.2 ± 0.1
(N = 3)	56.0–58.8	16.6–16.8	11.1–11.4	9.2–10.1	3.9–4.3	14.8–17.3	6.1–6.3
S. chilensis							
UCN-1-130697	72.2	20.3	15.5	12.5	5.6	19.0	7.4
UF 144109	68.2	20.7	14.2	11.9	5.2	20.3	7.4
UF 144107	69.2	18.1	13.1	10.1	4.8	16.7	6.3
UF 144105	71.6	20.3	—	12.5	6.4	19.4	7.5
UF 144104	—	22.3	14.6	12.5	6.4	—	—
UF 144157	—	—	—	11.5	5.1	17.7	6.7
UF 144158	—	—	—	12.3	5.7	20.0	8.1

Simpson 1971, table 1). A large undescribed species of penguin close to *Spheniscus* is known from the late Miocene/Pliocene Pisco Formation, Peru (Cheneval 1993). Bones of this species were examined at the Universite Claude Bernard Lyon 1, France, and differ by their greater size, humerus with more strongly bipartite pneumatic fossa (see Simpson 1946 for description of this character) and deeper medial fossa, and broad and rounded entepicondylar processes. Another fossil penguin from the late Miocene to middle Pliocene Bahía Inglesa Formation in north-central Chile was referred to cf. *Spheniscus* sp. and described as very similar to *S. humboldti,* but at least 25% larger (Walsh & Hume 2001) and could not be referable to *S. chilensis.*

Other fossil penguins that have been described from South America are restricted to the late Oligocene/early Miocene of Patagonia where nine species and four genera are known from this region (Simpson 1946, 1972; Tonni 1980). Species in the genera *Arthrodytes* and *Paraptenodytes* are relatively large penguins with the largest (*A. grandis*) near the size of the modern Emperor Penguin (*Aptenodytes forsteri*). In these genera, the humerus has a relatively straight shaft and, in *Paraptenodytes,* the tarsometatarsus is relatively long and slender. A partial associated skeleton of *P. antarcticus* (AMNH 3338) and several isolated bones of *P. robustus* were examined at AMNH and found to differ from *Spheniscus chilensis* in the characters above and by their greater size and robustness.

Two proximal humeri (AMNH 3341 and 3346) of *Chubutodyptes biloculata* differ from *Spheniscus chilensis* by their larger, more robust size, presence of a strongly bipartite pneumatic fossa, and relatively longer and deeper bicipital furrow. Numerous specimens of *Palaeospheniscus patagonicus* and *P. wimani* at AMNH and MLP approach the size of *S. chilensis,* but are more robust and have a distinctly bipartite pneumatic fossa on the humerus. The tarsometatarsus of this genus also is relatively long and slender with the medial proximal foramen greatly reduced or absent.

Order Pelecaniformes
Family Phalacrocoracidae
Genus *Phalacrocorax* Brisson, 1760

Referred material.—right coracoid missing ends, UF 144122; distal left humerus, UF 144151; proximal half left ulna, UF 144123; proximal end right ulna, UF 144152; left carpometacarpus with ends damaged, UF 144146; right carpometacarpus, UF 144145.

Measurements.—Ulnae, UF 144123 and 144152: PB, 9.3 and 9.4 mm; PD, 8.1 and 8.5 mm, respectively. Carpometacarpus, UF 144145: GL, 50.1 mm; PB and PD, 5.3 and 10.6 mm; LBS and LDS, 3.7 and 2.8 mm. UF 144146: GL, 48.3 mm; LBS and LDS, 3.5 and 2.8 mm.

Discussion.—This material is from a small species of cormorant, near the size of the living *Phalacrocorax brasilianus.* It is possible that it represents an undescribed species, but the material is too fragmentary for systematic analysis with other fossil and living species. Another small cormorant is known from the late Miocene/Pliocene Pisco Formation, Peru (Cheneval 1993). An ulna and carpometacarpus (both catalogued as AGL PPI 139) of this species were examined at the Universite Claude Bernard Lyon 1, France, and found to be slightly larger and more robust than the Cuenca del Tiburón material. In addition, the proximal ulna (PB and PD, 10.0 and 9.3 mm) has a relatively broader impression of brachialis anticus and the carpometacarpus (GL, 51.8; PB, 5.7 mm; LBS and LDS, 5.5 and 5.3 mm) has a proximal end with a relatively deeper intercondylar fossa in anterior view compared to the Cuenca del Tiburón material. A distal humerus from a larger cormorant, near the size of *P. bougainvilli,* also is known from the Bahía Inglesa Formation in north-central Chile (Walsh & Hume 2001). It was not examined here, but

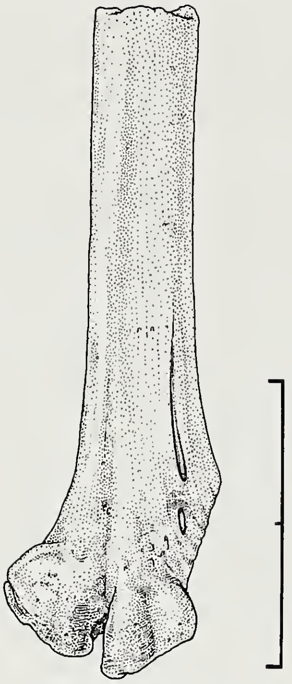

Fig. 3. Distal left tarsometatarsus, UF 144121, of *Milvago* sp. Scale bar = 1 cm.

is considered too large to represent the fossil species at Cuenca del Tiburón.

Order Accipitriformes
Family Falconidae
Genus *Milvago* Spix, 1824
Fig. 3

Referred material.—Distal left tarsometatarsus missing external trochlea, UF 144121.

Description.—The specimen is referable to Falconidae by the presence of two openings of the distal anterior foramen and by the morphology of the distal trochlea. It differs from *Falco* in lacking a long posterior ridge extending distally from the hypotarsus to nearly ¾ the length of the shaft and is most similar to *Milvago* and *Polyborus* in this feature. *Polyborus* and *M. chimachima* have only a single opening for the distal anterior foramen. The specimen is most similar to *M. chimango* in this feature and in size, but the fossil differs in having more robust trochleae similar to *M. chimachima.* UF 144121 also is similar to *M. chimachima* is having only a single opening of the anterior distal foramen. It may represent an undescribed species of *Milvago,* but additional specimens are needed.

Discussion.—Three fossil species have been described in this genus: *Milvago readei,* from the late Pleistocene of Florida (Brodkorb 1959; Campbell 1980) which has been synonymized with the living *M. chimachima* by Emslie (1998), and *M. alexandri* and *M. brodkorbi* from the late Pleistocene of Haiti (Olson 1976) and Peru (Campbell 1980), respectively. These last two species were not examined here, but *M. brodkorbi* is much larger than *M. chimachima* (Campbell 1980) and probably does not represent the fossil species from Cuenca del Tiburón.

Discussion

Only one other marine Pliocene fossil locality is known in Chile, also on the northern Coast. Walsh & Hume (2001) reported a marine avifauna within the Bahía Inglesa Formation, near Copiapó dating to the late Miocene to middle Pliocene based on associated shark teeth, diatoms, and foraminiferans. This deposit contained the earliest records of a cormorant (*Phalacrocorax* sp.) and penguin (cf. *Spheniscus* sp.) in Chile, as well as several other species of seabirds, sharks, fish, reptiles, and marine mammals. Cuenca del Tiburón is now the second marine deposit that also contains fossil sharks, fish, marine mammals, and birds. The vertebrate fauna other than birds remains largely unstudied. The sharks represented at this site include *Carcharodon carcharias, Carcharias* sp., and *Carcharhinus* sp., plus mouth plates from unidentified Myliobatidae. In addition, there are at least two large species of bony fish (Osteichthyes), two small species of dolphin (Odontoceti), one small baleen whale (Balaenopteridae), and one sea lion (Otariidae) (G. Morgan, pers. comm.).

Based on this fauna, as well as invertebrate taxa, the Cuenca del Tiburón deposit represents a nearshore marine community, including both sandy subtidal (from the presence of *Perna, Glycymeris,* and *Chorus*) and rocky intertidal zones (from the presence of *Trochita* and several barnacle genera). Most of the shells appear to have been transported a short distance before deposition occurred, based on leaching and abrasion plus the lack of paired valves (R. Portell, pers. comm.). The penguin remains also exhibit moderate wear and abrasion indicating that they are in a secondary site of deposition.

The fossil record of penguins has been reviewed by Simpson (1946) and Fordyce and Jones (1990). *Spheniscus chilensis* is the first fossil penguin to be described from Chile and from the Pliocene of South America. One other fossil species within this genus was described by Simpson (1971) from the early Pliocene of South Africa. Olson (1983), however, reviewed this and three other taxa named by Simpson from this locality and concluded that they all belong to either one extinct genus or represent a primitive form of *Spheniscus.* In South America, at least nine fossil species have been described from the rich late Oligocene/early Miocene Patagonia Formation of Argentina (see reviews by Simpson 1946 and Tonni 1980), and one from the early Miocene of the Pisco Formation in southern Peru (Cheneval 1993).

The material from Cuenca del Tiburón suggests that a low diversity of penguins occurred on the west coast of South America, similar to today and unlike the earlier fossil record in Argentina and South Africa. This relative low diversity of penguins and other seabirds appears to have persisted along the Chile and Peruvian coasts for millions of years. In Patagonia, penguin diversity has declined considerably since the early Miocene as only one species (*S. magellanicus*) breeds in that region today, while only two species are found along the Chilean and Peruvian coasts (*S. magellanicus* and *S. humboldti*). Future investigations of fossil deposits in northern Chile are needed to further understand the paleoceanographic conditions that prevailed during the Pliocene.

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Literature Cited

Brodkorb, P. 1959. The Pleistocene avifauna of Arredondo, Florida.—Bulletin of the Florida State Museum Biological Sciences 4:269–291.

Campbell, K. E., Jr. 1980. A review of the Rancholabrean avifauna of the Itchtucknee River, Florida.—Natural History Museum of Los Angeles County Contributions in Science 330:119–129.

Cheneval, J. 1993. L'avifaune Mio-Pliocène de la Formation Pisco (Pérou) étude préliminaire.—Documents des Laboratoires de Géologie Lyon 125: 85–95.

DeVries, T. J., & G. J. Vermeij. 1997. Herminespina: new genus of Neogene muricid gastropod from Peru and Chile.—Journal of Paleontology 71: 610–615.

Diaz, H. F., & V. Markgraf. 1992. El Niño–historical and paleoclimatic aspects of the Southern Oscillation. Cambridge University Press, England, 475 pp.

Dunbar, R. B., R. C. Marty, & P. A. Baker. 1990. Cenozoic marine sedimentation in the Sechura and Pisco basins, Peru.—Palaeogeography, Palaeoclimatology, Palaeoecology 77:235–261.

Emslie, S. D. 1998. Avian community, climate, and sea-level changes in the Plio-Pleistocene of the Florida Peninsula.—Ornithological Monographs 50:1–113.

Fordyce, R. Ewan, & C. M. Jones. 1990. Penguin history and new fossil material from New Zealand. Pp. 417–446 *in* L. S. Davis and J. T. Darby, eds., Penguin Biology. Academic Press, New York.

Herm, D. 1969. Marines Pliozän in Nord- und Mittel-Chile unter besonderer Berücksichtigung der Entwicklung der Mollusken-Faunen.—Zitteliana 2:1–158.

Herm, D. 1970. *Bostryx variabilis* n. sp., eine Landschnecke aus dem Altpleistozän von Mejillones, Nordchile.—Mitteilungen Bayerische Staatssammlung für Paläontologie und Historische Geologie 10:189–198.

Howard, H. 1929. The avifauna of Emeryville shellmound.—University of California Publications in Zoology 32:301–394.

Olson, S. 1976. A new species of *Milvago* from Hispanola, with notes on other fossil caracaras from the West Indies (Aves: Falconidae).—Proceedings of the Biological Society of Washington 88:355–366.

———. 1983. Fossil seabirds and changing marine environments in the late Tertiary of South Africa.—South African Journal of Science 79:399–402.

Ortlieb, L., N. Guzmán, & M. Candia. 1994. Moluscos litorales del Pleistoceno superior en el área de Antofagasta, Chile: primeras determinaciones e indicaciones paleooceanograficas.—Estudios Oceanológicos 13:57–63.

Padilla, H., & S. Elgueta. 1992. Neogene marine deposits of Caleta Patillos, northern Chile: their relationship with Neogene sediments of the Península de Mejillones.—Revista Geológica de Chile 19:83–89.

Simpson, G. G. 1946. Fossil Penguins.—Bulletin of the American Museum of Natural History 87: 1–99.

———. 1971. Fossil penguin from the late Cenozoic of South Africa.—Science 171:1144–1145.

———. 1972. Conspectus of Patagonian fossil penguins.—American Museum Novitates 2488:1–37.

Tonni, E. P. 1980. The present state of knowledge of the Cenozoic birds of Argentina. Natural History Museum of Los Angeles County Contributions in Science 330:105–114.

Tsuchi, R., T. Shuto, T. Takayama. A. Koizumi, M. Ibaraki, & R. Martinez-Pardo. 1988. Fundamental data on Cenozoic biostratigraphy of Chile. Pp. 71–91 *in* R. Tsuchi, ed., Reports of Andean Studies, Spec, vol. 2. Shizuoka University, Japan.

Walsh, S. A., & J. P. Hume. 2001. A new Neogene marine avian assemblage from north-central Chile.—Journal of Vertebrate Paleontology 21: 484–491.

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Leptodactylus caatingae, a new species of frog from eastern Brazil (Amphibia: Anura: Leptodactylidae)

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Abstract.—A new species of frog of the genus *Leptodactylus* is described from eastern Brazil. The new species differs little morphologically from *L. latinasus,* but the advertisement calls are very different. The geographic distribution of *L. latinasus* and the new species, together with the respective levels of differentiation of morphology and call, is mirrored in the species pair *L. bufonius* and *L. troglodytes.* Presumably the same historical event or events lead to differentiation of these species pairs.

In a revision of the *Leptodactylus fuscus* species group (Heyer 1978), *Leptodactylus latinasus* was characterized as having a major distribution pattern in Argentina, Uruguay, and the State of Rio Grande do Sul, Brazil and a few disjunct localities in eastern Brazil. The late Dr. Adão J. Cardoso recorded the advertisement call of a male *L. latinasus* from the State of Bahia in Brazil and brought the recording to the attention of WRH, pointing out that its call was very different from the other known recordings of *L. latinasus* from Argentina and Rio Grande do Sul, Brazil. More recently, FAJ collected a series of specimens of this eastern Brazil form from the fossil sand dune region of Bahia. The purpose of this paper is to describe the eastern Brazilian population currently identified as *L. latinasus* as a new species and provide new field observations for the taxon.

Materials and Methods

All specimens of the new species in the MZUSP, UEFS, and ZUEC collections (museum abbreviations follow Leviton et al. 1985 with UEFS being the Universidade Estadual de Feira de Santana) were borrowed and data were taken from them. Data for *Leptodactylus latinasus* are those used in Heyer (1978) with some additional data for eye-nostril distance, tympanum diameter, and belly patterns (data for these characters were not evaluated in the study published as Heyer 1978).

Measurement data include snout–vent length (SVL), head length, head width, eye-nostril distance, thigh length, shank length, and foot length, following Heyer et al. (1990) except for the eye-nostril distance being measured by calipers as the distance from the anterior corner of the eye to mid-nostril and the tympanum diameter being measured by calipers as the maximum diameter of the tympanum including the annulus.

Measurement data were analyzed using the software program SYSTAT 10 for principal component analysis (Stenson and Wilkinson 2000) and discriminant function analysis (Engelman 2000).

The advertisement call analyzed of the new species is USNM recording 234, cut 1, from Joazeiro, Fazenda Mary, Bahia, Brazil, 7 March 1990, air temperature 26°C, 1910 h, voucher ZUEC 8833, by Adão J. Cardoso. All calls were recorded from the single voucher specimen. Call rate was based on eight samplings of the recording for a total of 396 calls. Other call parameters are evaluated from analysis of 10 calls. For comparative purposes, a recording of *Leptodactylus latinasus,* USNM recording 19, cut 1, from Embarcación, Salta, Argentina, 22 December 1971, air temperature 22°C, time not noted, unvouchered, by W. Ronald Heyer, was analyzed. Call rate was based on three samplings of the recording for a total of 57 calls. Other call parameters are evaluated from analysis of seven calls (non-overlapping calls in a chorus) with filter bandpass settings of 600 and 11,205 Hz.

Advertisement calls were analyzed using Canary 1.2 software (Charif et al. 1995). The calls were digitized at a sample rate of 22,050 Hz, sample size of 16 bits. Call component terminology follows Duellman and Trueb (1986) and Heyer et al. (1990). Call duration was measured from the waveform. Dominant frequency was determined using the spectrum analysis in Canary with settings of analysis resolution filter bandwidth 349.70 Hz, frame length 256 points, grid resolution time 128 points, overlap 50%, frequency 43.07 Hz, FFT size 512 points, window function hamming, amplitude logarithmic, clipping level −80 dB. Minimum and maximum call frequencies were measured from the audiospectrogram display (spectrogram in Canary terminology) using settings of analysis filter bandwidth 174.85 Hz, frame length 512 points, grid resolution 256 points, overlap 50%, frequency 43.07 Hz, FFT size 512 points, window function hamming, amplitude logarithmic, clipping level −80 dB, display style smooth. Call amplitude modulation was evaluated from visual inspection of expanded waveform displays. Harmonics were determined using both expanded wave form displays and power spectrum analysis displays.

Advertisement Calls

The call of the new species is given at an average rate of 160/min. The call duration ranges from 64 to 77 ms. Each call has 7–8 distinct pulses (Fig. 1), given at a rate between 102 to 109 pulses/sec. The dominant frequency for the entire call has two peaks (Fig. 2), the slightly less loud peak ranges from 1072 to 1121 Hz, the loudest peak ranges from 1543 to 1648 Hz. The call is frequency modulated as rising from the beginning of the call to a maximum frequency at about ⅔ the call duration, then slightly falling to the end of the call; the lowest dominant frequency ranges from 934 to 963 Hz, the highest dominant frequency ranges from 1543 to 1648 Hz. There are no indications of harmonic structure in the call. (Fig. 3).

The call of the new species is dramatically different from the call of *Leptodactylus latinasus* in terms of amplitude structure (Fig. 1, distinct pulses present in the new species, absent in *L. latinasus*) and frequencies (Fig. 3, Table 1). The call of the new species from Ibiraba, Brazil sounds very similar to Cardoso's recording from Joazeiro, Brazil, and very different from the calls of Argentinian recordings of *L. latinasus* and *L. fuscus,* another species in the same species group that occurs in some of the same localities as the new species (FAJ, pers. obs.) The differences between the calls of the new species and *L. latinasus* convincingly demonstrate that they represent two distinct species.

Morphology

The following variation occurs in the new species.

Dorsal patterns include well-defined to weakly defined single or double mid-dorsal dark chevrons (as in Heyer 1978, Fig. 1A, C, p. 3), chaotically placed small to medium sized dark markings, or almost uniform. A very interrupted light or dark mid-dorsal pin stripe is present or absent.

Lip stripes range from a light stripe well-

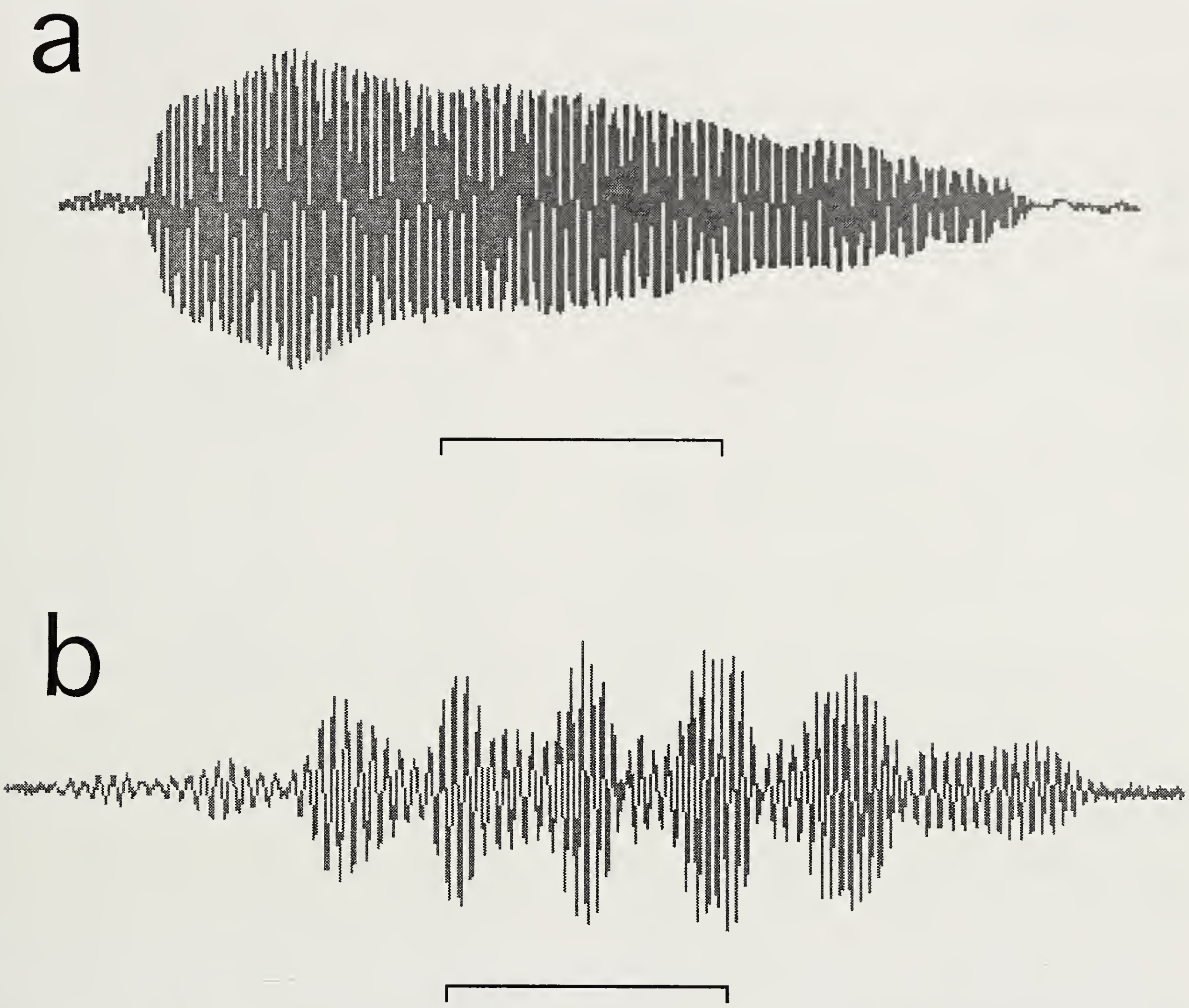

Fig. 1. Wave form of advertisement call of *Leptodactylus latinasus* (a) and the new species from eastern Brazil (b); scale bars = 0.02 sec.

defined both above and below from the tip of the snout passing under the eye and continuing under the tympanum onto the commissural gland to indistinct or indiscernible. All of these conditions occur in specimens from Ibiraba, Bahia; all but one of nine specimens from Itiúba, Bahia have well-defined stripes.

All but one specimen were scored as having a distinct light stripe on the lower face of each posterior thigh surrounded by irregularly shaped broad dark outlines with the rest of posterior thigh having a relatively uniform scattering of melanophores to a mottled pattern. One specimen from Ibiraba, Bahia has a series of light spots, rather than a continuous light stripe.

The upper shanks have irregularly shaped dark transverse bands.

The specimens from Ibiraba, Bahia have a greater development of belly pattern than observed from other localities. The Ibiraba specimens range from having an almost uniform distribution of densely packed melanophores (pale to the eye, but melanophores distinct under magnification), a variegated pattern of melanophores, to groups of melanophores scattered over the belly. Specimens from the other localities either lack a belly pattern, have a weakly variegated pattern of melanophores, or have only a few scattered melanophores lateralmost on the belly.

Many individuals lack any indication of dorsolateral folds. Several individuals have very interrupted folds from the eye to the sacrum. One individual has a very interrupted fold from the eye to the groin. Most

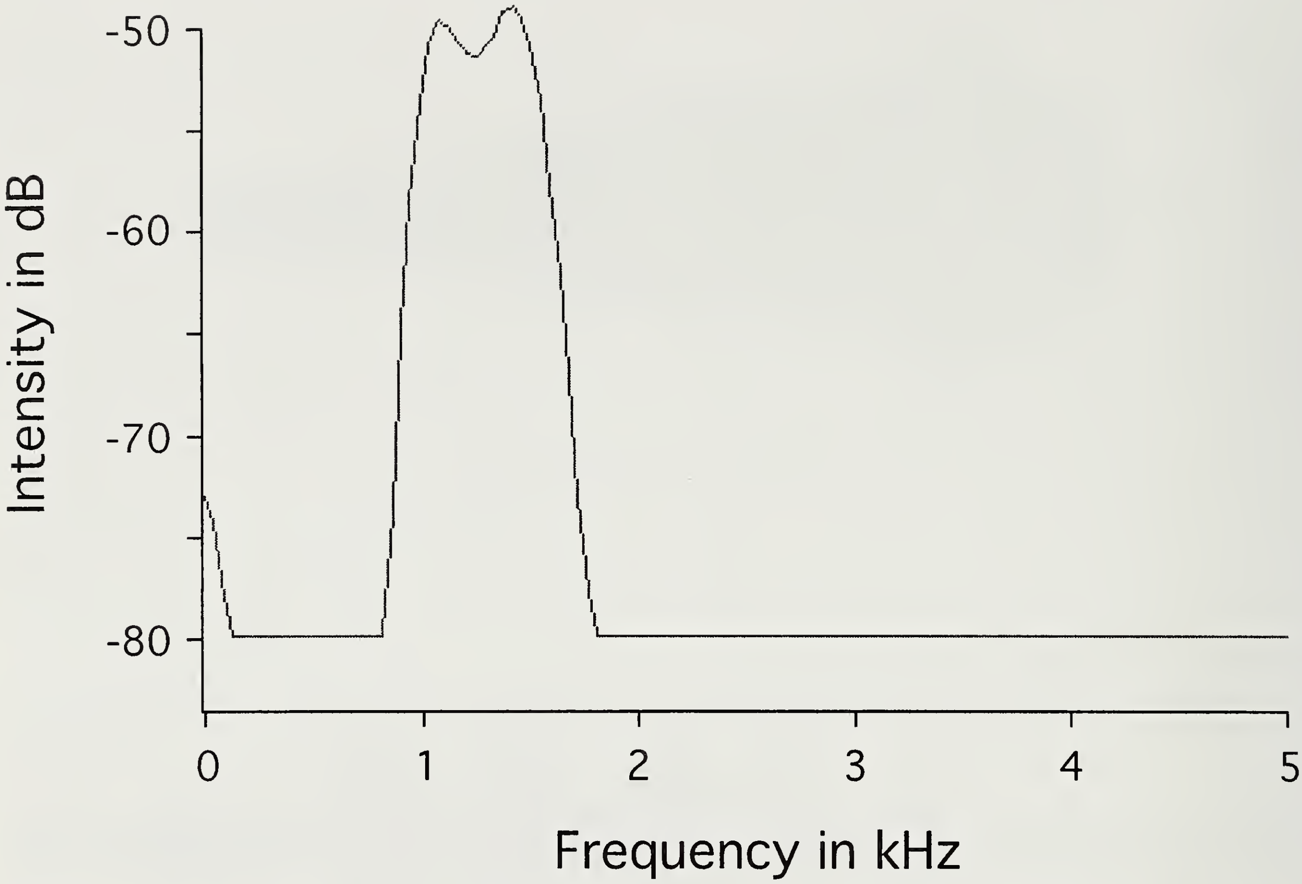

Fig. 2. Power spectrum of advertisement call of new species of *Leptodactylus* from eastern Brazil.

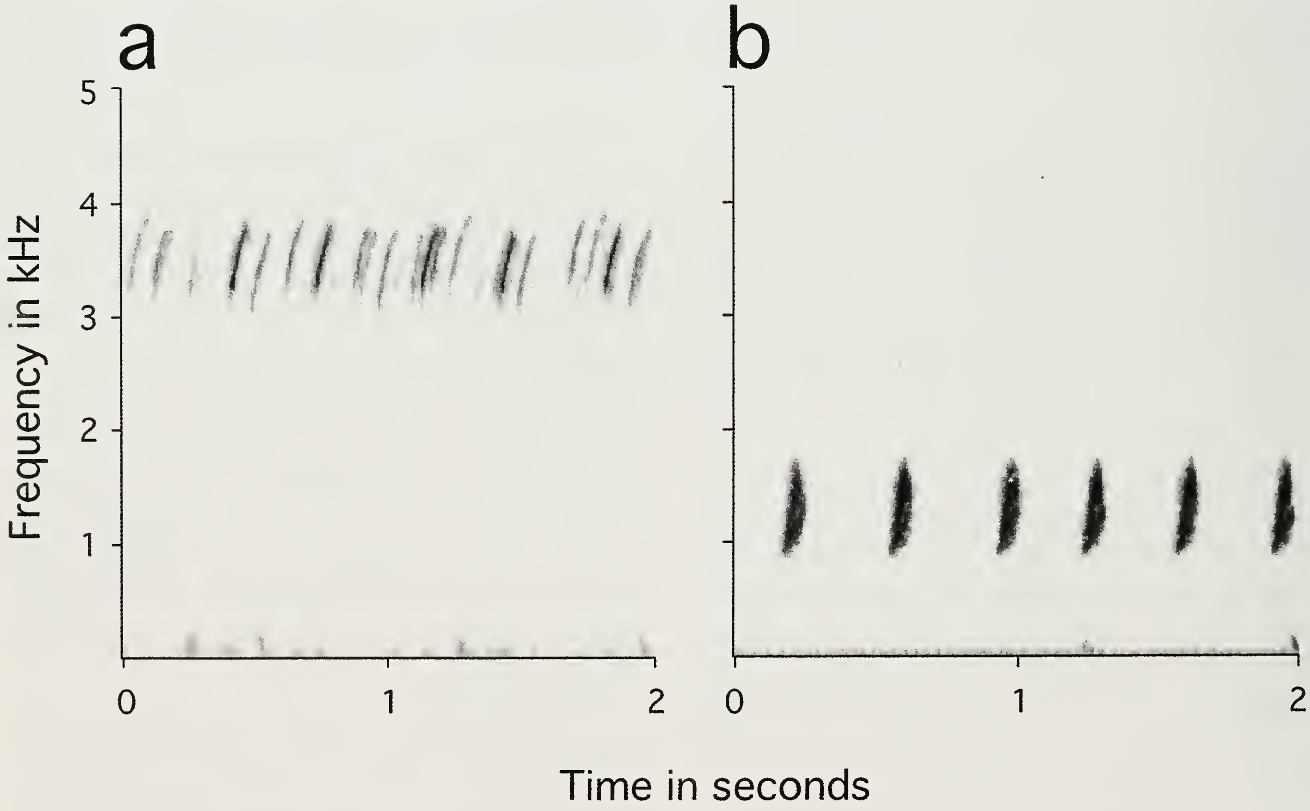

Fig. 3. Audiospectrograms of advertisement calls of *Leptodactylus latinasus* (a) and the new species from eastern Brazil (b).

Table 1.—Advertisement call parameters for *Leptodactylus latinasus* and *L. latinasus*-like specimens from Argentina and Brazil. * indicates data from Barrio (1965). Call data are average values.

Country/state or province	Temperature, celsius	Call rate/min	Call duration/s	Dominant frequency in Hz, entire call	Minimum dominant frequency, Hz	Maximum dominant frequency, Hz
Argentina, Buenos Aires*	26.0	30	0.08[1]		3000	
Argentina, Chaco*	20.0	13	0.09[1]		3500	
Argentina, Salta	22.0	145	0.07	3334	3274	3782
Brazil, Bahia (new species)	26.0	160	0.07	1423	943	1616

[1] Barrio (1965) gave these values as 0.8 and 0.9 s, but his audiospectrograms indicate that the values should be hundredths, not tenths of seconds.

individuals have complete to broken lateral folds.

The upper tibia has scattered to many distinct white tubercles. Twenty of 21 specimens have many distinct white tubercles on the outer tarsal surface and sole of foot. One individual has scattered distinct white tubercles on the outer tarsal surface.

Males range from 32.1 to 36.9 mm SVL (n = 8), females 36.2 and 39.1 mm (n = 2).

The dorsal pattern, lip stripes, posterior thigh pattern, upper shank pattern, mid-dorsal pin stripes, upper shank texture, outer tarsal texture, and sole of foot texture traits are indistinguishable between the new species and *L. latinasus.*

Belly pattern data were not taken for the Heyer (1978) study. WRH examined bellies of all USNM specimens of *L. latinasus* from Argentina, Uruguay, and Rio Grande do Sul, Brazil. Forty-nine individuals lack any belly pattern. One specimen from Argentina (USNM 319587) and two specimens from Uruguay (USNM 535968, 539970) have a few melanophores on the lateralmost venter and/or in the arm insertion portion only of the venter. One individual from Uruguay (USNM 535969) has a pair of small blotches just behind the arm on the sides of the chest. None of the Argentina, Uruguay, or Rio Grande do Sul, Brazil specimens examined have as extensive venter patterns as found in some individuals of the new species.

Body fold development was not scored in the same way for the Heyer (1978) study and this study. A series of 20 well-preserved adult *Leptodactylus latinasus* from Salta Province, Argentina examined for this study shows the same expressions of lateral folds as in the new species, but with different frequencies of occurrences of individual states. Only one of the 20 *L. latinasus* has a very broken dorsolateral fold from the eye to ⅔ distance to the sacrum; the other 19 show no indications of dorsolateral folds. Thus, the new species apparently has a greater frequency of any dorsolateral fold expression than occurs in *L. latinasus.*

There are two sets of measurement data. A more extensive data set (in terms of number of individuals) is available for all adults examined for the Heyer (1978) study for SVL, head length, head width, thigh length, shank length, and foot length. Additional data for eye-nostril distance and tympanum diameter are available for a smaller number of adults for both the new species and *Leptodactylus latinasus.*

Due to the small number of adults available for the new species, principal component analyses are the primary statistical tool used to explore measurement variation in adults of the new species and *Leptodactylus latinasus* (Table 2). The principal component analyses for males show a greater distinction between the two species using the data for all variables versus the data set lacking eye-nostril distance and tympanum diameter data (Fig. 4) than observed in the female data (Fig. 5). The modest differentiation based on measurement data is expected to exceed researcher measurement error, based on previous experience (Hayek et al. 2001). Discriminant function analyses for male data including eye-nostril distance and tympanum diameter data result in 100% correct posterior classification for both the complete data model and backward stepwise model. The discriminant function analyses for the male data lacking eye-nostril distance and tympanum diameter result in 97–98% correct posterior classification of cases for both the complete model and backward stepwise models. Results of multivariate techniques can not be assumed to be generalizable beyond the individual data sets analyzed because any changes in the sample will yield different results to at least some degree (James and McCulloch 1990). Given this caveat, we interpret our results to mean that there is at least some morphological differentiation between the new species and *L. latinasus* that would be confirmed with increased sample sizes.

Overall, the new species and *Leptodac-*

Table 2.—Principal component results, performed with correlation matrices. SVL = Snout-vent length, HL = head length, HW = head width, EN = eye-nostril distance, TD = tympanum diameter, Thigh = thigh length, Shank = shank length, Foot = foot length.

Analyses	Number of specimens	Eigenvalues								% variance explained by components		
		SVL	HL	HW	EN	TD	Thigh	Shank	Foot	1	2	3
Male data, all variables	43	5.45	0.91	0.60	0.41	0.31	0.14	0.11	0.08	68	11	8
Male data, reduced variables	186	4.32	0.73	0.50			0.18	0.14	0.13	72	12	8
Female data, all variables	32	5.13	1.17	0.74	0.40	0.28	0.12	0.09	0.07	64	15	9
Female data, reduced variables	79	4.05	1.19	0.39			0.17	0.13	0.07	67	20	

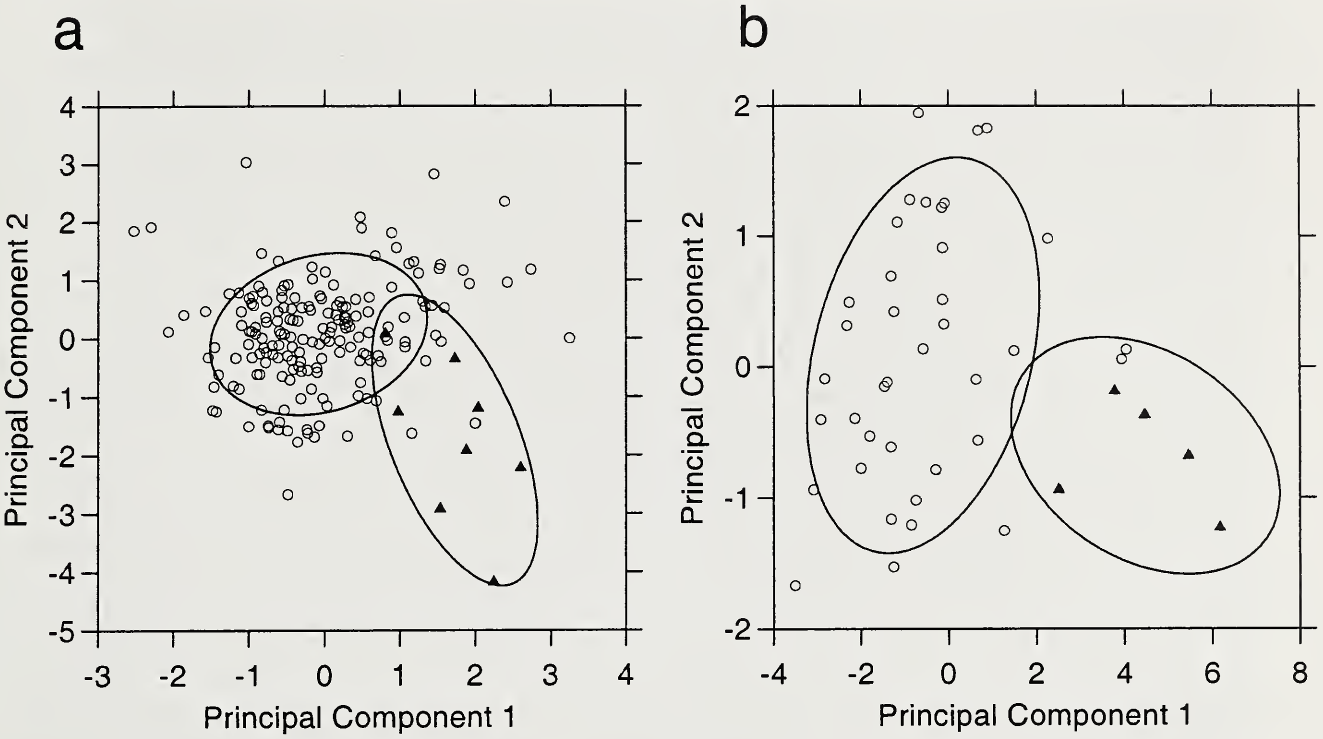

Fig. 4. Male measurement data principal component analyses. A. Reduced variable data set. B. Variable set including eye-nostril distance and tympanum diameter data. Circles = *Leptodactylus latinasus,* filled triangles = new species.

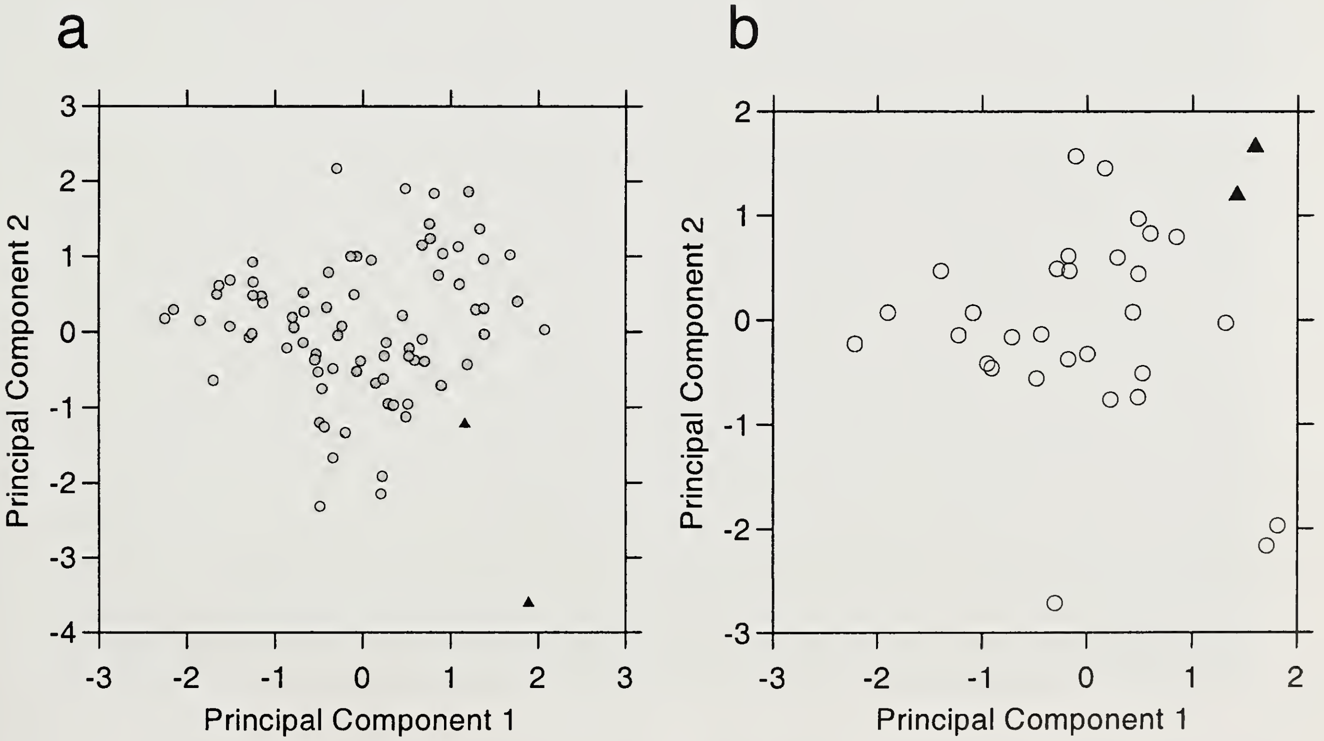

Fig. 5. Female measurement data principal component analyses. A. Reduced variable data set. B. Variable set including eye-nostril distance and tympanum diameter data. Circles = *Leptodactylus latinasus,* triangles = new species.

tylus latinasus are very similar morphologically. There are no characters that completely diagnose the two species. There are a few character states that demonstrate some differentiation between the species. If the only data available were the morphological data, we would interpret the variation to be within-species and would recognize only one species for the two taxa, as was done in the Heyer (1978) study.

Given that the advertisement call data indicate that the specimens from eastern Brazil represent a species distinct from *Leptodactylus latinasus* and there is no name available for it, we hereby describe the taxon lacking a name as:

Leptodactylus caatingae, new species

Figs. 6–7

Holotype.—ZUEC 8833, an adult male from Brazil, Bahia, Joazeiro, 09°25′S, 40°30′W. Collected by Adão J. Cardoso, 7 March 1990.

Referred specimens.—BRAZIL; BAHIA; Bom Jesus da Lapa, 13°15′S, 43°25′W, UMMZ 109991(2); Ibiraba, 10°48′S, 42°50′W, UEFS 686, 688–695; Itiúba, 10°42′S, 39°51′W, MZUSP 38556–38559, 38561–38563, USNM 547844–547845; São José do Rio Grande, 11°49′S, 44°44′W, UMMZ 109992; ESPÍRITO SANTO; São Mateus, 18°44′S, 39°51′W, MCZ A-92142 (recatalogued from the previously lot catalogued specimen MCZ A-1298 cited in Heyer 1978); PERNAMBUCO; Exu, 7°31′S, 39°43′W, MZUSP 51858; Ouricurí, 7°53′S, 40°05′W, MZUSP 77749.

Diagnosis.—The species with a combination of a distinct light stripe on the posterior surface of the thigh and obvious white tubercles on the outer surface of the tarsus and sole of foot in some or all individuals are *Leptodactylus albilabris, caatingae, elenae, fragilis, latinasus,* and *mystaceus. Leptodactylus albilabris* and *mystaceus* have distinct dorsolateral folds (indicated by color pattern in poorly preserved specimens); *L. caatingae* has interrupted, indistinct dorsolateral folds or lacks them. *Leptodactylus caatingae, fragilis,* and *latinasus* have considerable morphological and color pattern overlap and cannot be consistently diagnosed from each other with these characters. The advertisement call of *L. latinasus* is not pulsed and has a high broadcast frequency (3000–3780 Hz); the call of *L. caatingae* is pulsed and has a lower broadcast frequency (940–1620 Hz). The advertisement call of *L. fragilis* is longer (0.19 sec) than the call of *L. caatingae* (0.07 sec). *Leptodactylus caatingae, fragilis,* and *latinasus* have allopatric distributions: *L. fragilis* from southernmost Texas, United States to north coastal Venezuela; *L. caatingae* in eastern Brazil; and *L. latinasus* in southern South America (Argentina, Bolivia, Rio Grande do Sul, Brazil, Uruguay).

Description of holotype.—Snout rounded from above, acutely rounded in profile; canthus rostralis indistinct; lores obtusely convex in cross section; tympanum well defined, moderate size, horizontal diameter about $\frac{5}{6}$ eye diameter; vocal slits elongate, parallel to lower jaw, starting about midtongue level; vocal sac single with distinct lateral expansions indicated by pronounced folds under lower jaws; vomerine teeth in almost straight line patches separated from each other by about ½ length of a single tooth row, well behind and between almost round choanae; finger lengths II $\approx$ IV $\ll$ I just $<$ III; inner sides of fingers II and III with a line of small tubercular-like projections, otherwise sides of fingers entirely smooth; thumb lacking asperities; snout with distinct flaring ridge; arms not hypertrophied; weakest indications of ulnar ridges; dorsum with small scattered pustular-like warts, lower flanks areolate; supratympanic fold well developed and defined, no other folds discernible; well developed commissural glands, a pair of low, ovoid glands behind tympanum and above posterior arm insertion; ventral disk fold well defined; venter smooth except for areolate ventral thigh surfaces; toe tips IV and V rounded, I, II, III slightly swollen; lateral

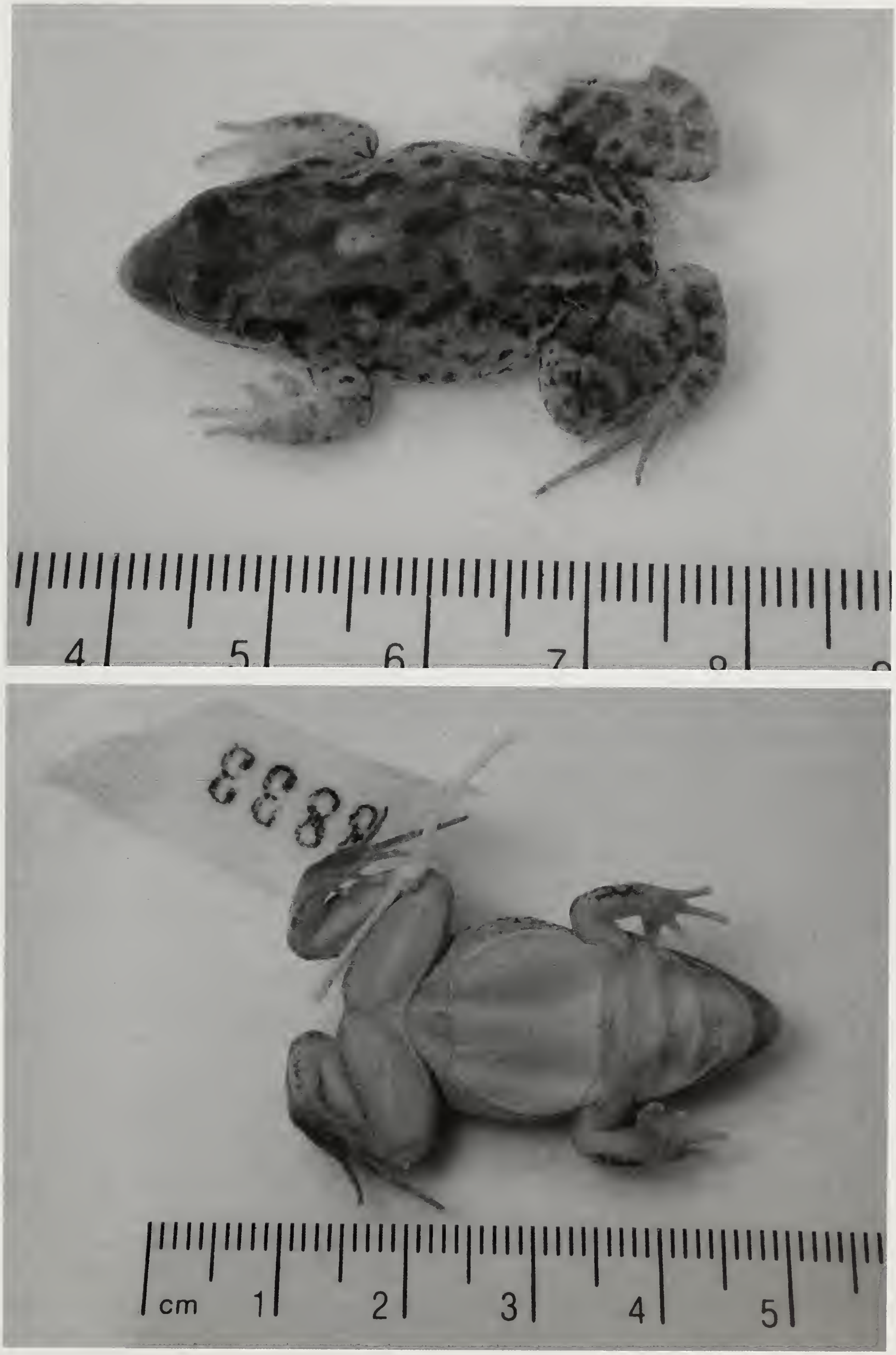

Fig. 6. Holotype of *Leptodactylus caatingae*.

Fig. 7. *Leptodactylus caatingae,* UEFS 695, photo by F. A. Juncá.

toe surfaces lacking ridges or fringes, no indication of basal webbing between toes; subarticular tubercles distinct, pungent; no metatarsal fold; tarsal fold low, broad, glandular, extending ⅞ distance of tarsus, either abutting inner metatarsal tubercle or with a slight gap between fold and tubercle; upper shank surface with scattered white tubercles; outer tarsal surface with many white tubercles; sole of foot with many white tubercles.

SVL 35.3 mm, head length 14.2 mm, head width 12.7 mm, eye-nostril distance 3.3 mm, tympanum diameter 2.9 mm, femur length 13.4 mm, shank length 14.1 mm, foot length 14.9 mm.

Dorsum blotched tans and browns; a very interrupted series of dark dots from between the nostrils to just past the sacrum; upper limbs with weakly and irregularly defined darker transverse bands; face with dark canthal stripe only well defined just in front of eye; moderately well defined light stripe from tip of snout passing under eye and tympanum and extending to end of commissural gland; flanks with indistinctly darker brown blotches on a tan background; posterior face of thigh with a very distinct light ventral stripe, bordered by dark brown, rest of posterior face of thigh mottled tan and brown; lateral chin area mottled with brown, extending onto vocal folds, rest of venter immaculate.

Etymology.—The name, Latinized from the Portuguese word caatinga, refers to the characteristic distribution of this species within the Caatinga Morphoclimatic Domain (Ab'Sáber 1977).

Larval characteristics.—Unknown.

Advertisement call.—See previous description.

Karyotype.—Unknown.

Distribution.—Currently known from a few localities in eastern Brazil (Fig. 8). All but one of the localities occur in the Caatinga Morphoclimatic Domain (Ab'Sáber 1977). The southernmost locality, in Espirito Santo, occurs in the Atlantic Forest Morphoclimatic Domain (Ab'Sáber 1977). The locality of Rio Grande at São José, Minas Gerais, Brazil for UMMZ 109992 given in Heyer (1978) was incorrect and is São José do Rio Grande, Bahia.

Natural history.—FAJ made the follow-

Fig. 8. Distribution map of *Leptodactylus caatingae* and *L. latinasus*. Type locality of *L. caatingae* indicated by dot; other localities by circles. Predicted distribution range of *L. latinasus* indicated by shaded area.

ing observations on specimens from Ibiraba, Bahia. On March 2000, in the rainy season, about 10–20 males were calling within grass bordering a flooded forest area that was totally dry the day before. One of these males was calling in an exposed position and FAJ could observe and collect it. The air temperature was 25°C. Other specimens were collected in pitfall traps, which were put in on one edge of the Icatú River. In that area the vegetation is a typical gallery forest with trees up to 5–7 m tall. In the same area *Leptodactylus fuscus, ocellatus,* and *podicipinus* were calling too. In August 2000 the same area was dry and no individuals of *L. caatingae* were calling, although some *L. podicipinus* males were heard.

Discussion

The call rates of *Leptodactylus latinasus* analyzed for this paper are very different from those analyzed by Barrio (1965, see Table 1) and may impact the call rate described for *L. latinasus* herein. The differences are real and not due to different means of analysis. The major difference between the recordings involved is that Barrio's recordings appear to be of a single calling individual, whereas the recording of *L. latinasus* analyzed herein was a chorus recording, although there seemed to be one primary individual that was louder (i.e., closer to the microphone), but it is possible that two or more individuals were calling equally loudly from the microphone in a manner that their calls did not overlap with each other. Thus, it is possible that the difference in calling rates of *L. latinasus* as presented in Table 1 could be due either to more than one individual actually being analyzed in the Salta recording, or *L. latinasus* increases calling rates when in a chorus of conspecifics. The recorded call of *L. caatingae* has every indication that it is from a single calling male, however.

We are not certain that all of the specimens we have examined of *L. caatingae* represent a single species. There is variation in belly pattern development among specimens of *L. caatingae* from different localities. Advertisement calls are very important in evaluating species limits in the frogs that have been known as *L. latinasus.* Unfortunately, we have only a recording from a single frog of *L. caatingae.* Recordings are needed from the other population samples we have designated as referred specimens of *L. caatingae* in order to determine whether there are additional species contained in the specimens we have examined. Because of the observed belly pattern variation and lack of additional recordings, we think it is inappropriate to designate paratypic specimens for *L. caatingae.*

The currently known distribution of *L. caatingae* is confounding. The Atlantic Forest Morphoclimatic Domain locality of São Mateus, Espírito Santo is peculiar. There are very few species of frogs that occur in both caatinga and Atlantic Forest areas. Copeland Hartt collected MCZ A-92142 in 1865/1866. The available evidence is quite convincing that the specimen was collected from the Atlantic Forest Morphoclimatic Domain and most probably São Mateus itself. Hartt collected amphibians and reptiles from five other localities in addition to São Mateus in the States of Bahia and Espírito Santo. All of these five localities are also from the Atlantic Forest Morphoclimatic Domain. There are no habitat data for MCZ A-92142. There are at least three possibilities to explain a presumably caatinga adapted frog being collected at São Mateus: (1) the São Mateus population inhabits open areas within the Atlantic Forest Morphoclimatic Domain, such as sandy beaches along the ocean coast; (2) the São Mateus population actually represents a new cryptic species of this complex; and (3) this distribution represents another example of how little we really understand about neotropical frog distributions. Collecting new material from São Mateus of *L. caatingae,* including recording its advertisement call, could resolve the current distributional anomaly.

The pattern of differentiation and distribution described herein for *L. caatingae* and *L. latinasus* is very similar to that found between two other members of the same species group (the *L. fuscus* group): *L. bufonius* and *troglodytes.* These two latter species are very similar morphologically and differ markedly in their advertisement calls (Heyer 1978). *Leptodactylus bufonius* has a distribution in the open formations of Argentina, Bolivia, Mato Grosso do Sul, Brazil, and Paraguay. There is an extensive distributional hiatus between *L. bufonius* and *L. troglodytes,* with *L. troglodytes* occurring in open formations of northeast Brazil (compare maps in Figs. 34 and 68 in Heyer [1978]). This similar pattern suggests that the two species pairs shared the same differentiation history, probably the ancestor of each having a general distribution throughout the diagonal of open formations in South America. Whatever event isolated the populations from northeast Brazil from the populations in and adjacent to Argentina was probably the same event that led to speciation of both *L. bufonius–troglodytes* and *L. caatingae–latinasus.* This hypothesis would be corroborated if the levels of molecular differentiation between the pairs of species were identical. If that turns out to be true, the molecular data might provide a suggestion of when the allopatry occurred, which, in turn, might agree with the hypothesis proposed by Vanzolini (1997: 80–84) of separation of dry formation populations by fragmentation due to Pleistocene wet forest expansions during more mesic periods than present.

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Literature Cited

Ab'Sáber, A. N. 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação.—Geomorfologia (52):1–22 + map.

Barrio, A. 1965. Afinidades del canto nupcial de las especies cavícolas del genero *Leptodactylus* (Anura-Leptodactylidae).—Physis 25:401–410.

Charif, R. A., S. Mitchell, & C. W. Clark. 1995. Canary 1.2 user's manual. Cornell Laboratory of Ornithology, Ithaca, New York, 229 pp.

Duellman, W. E., & L. Trueb. 1986. Biology of amphibians. McGraw-Hill Book Company, New York, St. Louis, San Francisco, 670 pp.

Engelmann, L. 2000. Discriminant analysis. Pp. I-275–I-326 *in* SYSTAT® 10. Statistics I, SPSS Inc., Chicago. 663 pp.

Hayek, L-A. C., W. R. Heyer, & C. Gascon. 2001. Frog morphometrics: a cautionary tale.—Alytes 18: 153–177.

Heyer, W. R. 1978. Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae).—Natural History Museum of Los Angeles County, Science Bulletin (29):1–85.

Heyer, W. R., A. S. Rand, C. A. G. Cruz, O. L. Peixoto, & C. E. Nelson. 1990. Frogs of Boracéia.—Arquivos de Zoologia 31:231–410.

James, F. C., & C. E. McCulloch. 1990. Multivariate analysis in ecology and systematics: panacea or Pandora's Box?—Annual Review of Ecology and Systematics 21:129–166.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology: Part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Stenson, H., & L. Wilkinson. 2000. Factor analysis. Pp. I-327–I-363 *in* SYSTAT® 10. Statistics I. SPSS Inc., Chicago, 663 pp.

Vanzolini, P. E. 1997. The silvestrii species group of *Amphisbaena,* with the description of two new Brasilian species (Reptilia: Amphisbaenia).—Papéis Avulsos de Zoologia 40:65–85.

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A review of *Amblyotrypauchen* (Teleostei: Gobiidae), a genus of blind amblyopine gobies

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Abstract.—The Indo-West Pacific gobiid genus *Amblyotrypauchen* Hora is reviewed and defined. *Amblyotrypauchen* is unique within the Amblyopinae in having 10+19 vertebrae, enlarged fang-like teeth in both jaws, partially separate pelvic fins, and scale patches on the opercle, cheeks, and dorsum of head. In contrast to most other members of the subfamily, *Amblyotrypauchen* lacks eyes and has been collected off muddy bottoms from almost 17 m to over 183 m in depth. *Karsten* Murdy is the only other known amblyopine goby that is blind and found at such depths. *Amblyotrypauchen* comprises a single species, *A. arctocephalus,* known from India, Malaysia, Hong Kong, the Philippines, Papua New Guinea, and Australia. A figure of *A. arctocephalus* is provided. *Amblyotrypauchen* is most similar to *Ctenotrypauchen, Karsten, Trypauchen,* and *Trypauchenichthys;* the five genera are compared.

The subfamily Amblyopinae comprises approximately 15 genera and about 25–30 valid goby species. Amblyopine gobies have a continuous dorsal fin and eel-like bodies. The subfamily is typically associated with muddy substrates in shallow waters (a few centimeters to a few meters) in the Indo-Pacific region. The amblyopine goby *Amblyopus arctocephalus* was described by Alcock (1890) from specimens trawled off the east coast of India at depths from 37 m to 92 m over muddy substrate. Alcock did not compare his new species to any other goby but did mention that: (1) the head lacked scales and was compressed into a sharp ridge; (2) the eyes were "hidden"; and (3) the jaws contained large canine teeth. A figure was also provided. Almost 35 years later, Hora (1924) described *Amblyotrypauchen fraseri* as a new genus and species of eel-like goby. Hora based his description on a single specimen trawled off the east coast of India at a depth of 37 m over a mud bottom. Hora (1924) stated that the unique features of his new taxon were "well-marked" canine teeth and relatively large pelvic fins. He also stated that the head of *Amblyotrypauchen* had scales and that the eyes "were not visible but their position is indicated by orbital depressions." A figure of *Amblyotrypauchen fraseri* was provided, which is reproduced here as Fig. 1. Hora (1924) made no reference to *Amblyopus arctocephalus* Alcock.

After examining type material of both *Amblyopus arctocephalus* and *Amblyotrypauchen fraseri* at the Indian Museum (now the Zoological Survey of India), Koumans (1941) synonymized the latter species with the former but retained the genus *Amblyotrypauchen* for *arctocephalus.* In his descriptive account of *Amblyotrypauchen,* Koumans (1941) stated that the eyes were "small." However, in his species account of *A. arctocephalus* that immediately followed the genus account, Koumans stated that the eyes were "hidden." In addition to specimens collected off the east coast of India, Koumans (1941) mentioned that he examined specimens of *A. arctocephalus* at the Indian Museum from the Arabian Sea and the Gulf of Martaban (Myanmar). The only other published record of *A. arctocephalus* that I can locate is that of Herre and

Herald (1951) who reported on *A. arctocephalus* collected by trawl from 35–53 m in Manila Bay, Philippines. Although not having any specimens at hand, Smith (1959) opined that *A. arctocephalus* would eventually be found in the western Indian Ocean.

None of the published accounts definitively state that *A. arctocephalus* lacks eyes. In addition, none remarks on the relative deep-dwelling habits of this species as compared to other amblyopine gobies. As such, the objectives of this study were to: (1) redescribe *Amblyotrypauchen,* (2) define *Amblyotrypauchen* using putative derived characters, (3) to provide characters for differentiating *Amblyotrypauchen* from other amblyopines, and (4) to provide and analyze distributional and ecological data.

Materials and Methods

All measurements are straight-line distances made with dial calipers and recorded to the nearest 0.1 millimeter. All fish lengths given are standard lengths (SL) except where noted as total length (TL). Methods of measurements and counts follow Murdy (1989), and Murdy and Shibukawa (2001).

The vertebral count is separated into precaudal and caudal counts, the latter including the urostylar complex; caudal vertebrae possess a distinct hemal spine that is lacking in precaudal vertebrae. Counts of axial skeletal features (i.e., vertebrae, pleural and epineural ribs, pterygiophores, and epurals) were taken from radiographs and cleared and stained material. The methods of Birdsong et al. (1988) were used in describing the relationship between the spinous dorsal-fin pterygiophores and the underlying vertebrae.

Institutional abbreviations are as listed in Leviton et al. (1985). All specimens examined are listed in the material examined section and grouped by major geographic areas. The total number of specimens examined and size range follow each catalog number. Depth of capture is provided when known.

Systematic Account

Amblyotrypauchen Hora, 1924

Amblyotrypauchen Hora, 1924:160 (type species, *Amblyotrypauchen fraseri* Hora 1924 = *Amblyopus arctocephalus* Alcock, 1890)

Included species.—*Amblyotrypauchen* comprises a single species, *A. arctocephalus* (Alcock, 1890).

Diagnosis.—A genus of Amblyopinae with prominent canine teeth in both jaws; head, cheek and opercle with scale patches; and, typically, 19 caudal vertebrae. Pelvic fins with innermost rays joined for one-third to one-half their length.

Osteology.—Spinous dorsal-fin pterygiophore formula typically 3-1221, one specimen with 3-123. Precaudal vertebrae typically 10, caudal vertebrae typically 19, one specimen with 9+23. Pterygiophore of the second soft dorsal-fin ray (posteriormost pterygiophore inserting in 7th interneural space) lacking a middle radial. Typically three anal-fin pterygiophores anterior to first hemal spine, one specimen with four. Epurals 2. Basihyal spatulate. Symplectic lacking a posteriorly directed arm cartilaginously joining the hyomandibular, consequently, no gap present between dorsal aspect of symplectic and the hyomandibular. Frontal crest prominent, without serrated edge. Atlas with well-developed parapophyses, in contact with first epineural rib. Epineurals present from 1st precaudal vertebra to 14th caudal vertebra. Well-developed pleural ribs on 3rd to 9th precaudal vertebrae.

Amblyotrypauchen arctocephalus
(Alcock, 1890)
(Figs. 1–2, Tables 1–2)

Amblyopus arctocephalus Alcock, 1890: 432 (type locality, off Orissa and Vizagapatam, India)

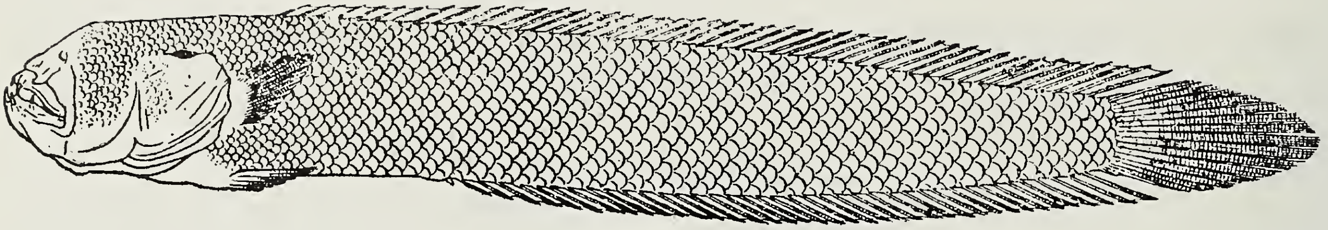

Fig. 1. *Amblyotrypauchen fraseri* (=*arctocephalus*) from Hora (1924). Note that a shallow cavity exists in the area typically occupied by an eye. The figure depicts the dorsal and anal fins not connected with the caudal fin, and a fully scaled cheek. This is in contrast to other published accounts and specimens examined in this study in which the dorsal and anal fins are confluent with the caudal fin, and the cheek is much less densely scaled.

Amblyotrypauchen fraseri Hora, 1924:160, fig. 4a (type locality, off the mouth of the Hugli River, India)

Amblyotrypauchen arctocephalus: Koumans, 1941, new combination

Material examined.—(18 specimens from 10 localities; size range 36.1–137.6 mm). Malaysia, Strait of Malacca: USNM 296958, depth 101 m, 3:47.9–118.2 mm. Hong Kong: AMS I.18552-001, depth 16–18 m, 1:115.1 mm. Philippines, Lingayan Gulf: USNM 151242, depth 82 m, 1:116.1 mm; USNM 113200, 1:125.3 mm. Manila Bay: CAS 53856, 2:120.2–125.7 mm. Western Samar: USNM 113202, depth 37 m, 2:110.1–122.7 mm; USNM 113197, depth 48 m, 3:115.3–129.0 mm. Negros: USNM 151432, depth 176 m, 1:39.1 mm. Cebu: 113238, 1:137.6 mm. Davao: 113198, depth 183 m, 1:36.1 mm. Papua New Guinea, mouth of Rama River: AMS I.16753-024, 1:98.0 mm. Australia, Arafura Sea, AMS I.19289-005, depth 55 m, 1:72.8 mm.

Diagnosis.—As for genus.

Description.—Proportional measurements given in Table 1. The following description of counts (Table 2) is based on radiographs, and one cleared and stained specimen removed from USNM 113197.

Total dorsal-fin elements 48–52; first dorsal fin with six flexible spines; first element of second dorsal fin segmented, branched or unbranched, all others segmented and branched rays; dorsal-fin base long and broadly joined with caudal fin. Total anal-fin elements 39–43, first element segmented and unbranched, all other elements segmented and branched; anal-fin height less than second dorsal-fin height; anal-fin membrane broadly joined with caudal fin. Pectoral fin with 14–18 rays, crescent-

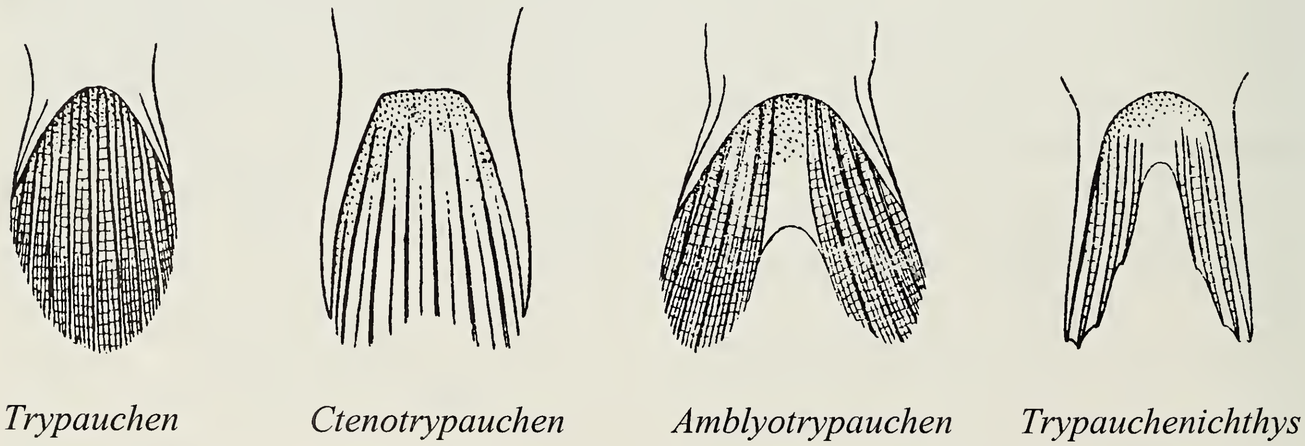

Fig. 2. Pelvic fin shapes of *Trypauchen, Ctenotrypauchen, Amblyotrypauchen,* and *Trypauchenichthys,* from Hora (1924). The pelvic fins of large specimens (>120 mm) of *Amblyotrypauchen* can have the pelvic fins more deeply incised than shown in the figure.

Table 1.—Proportional measurements of *Amblyotrypauchen arctocephalus*.

	n	Mean	Range
Standard length/TL	6	0.845	0.833–0.858
Head length/SL	11	0.201	0.179–0.214
Pelvic-fin length (PEL)/SL	11	0.085	0.062–0.111
Pelvic-fin length/HL	11	0.421	0.320–0.550
Pectoral-fin length/SL	19	0.064	0.042–0.098
Pectoral-fin length/HL	19	0.314	0.206–0.457
Pectoral-fin length/PEL	19	0.764	0.431–1.137
Head width/SL	11	0.094	0.025–0.113
Snout length/SL	11	0.058	0.041–0.115
Jaw length/SL	11	0.068	0.056–0.076
Interorbital width/SL	11	0.031	0.023–0.039
Nape width/SL	11	0.074	0.065–0.083
Body depth/SL	11	0.141	0.124–0.152
Predorsal length/SL	11	0.241	0.183–0.261
Prepelvic length/SL	11	0.192	0.174–0.205
Preanal length/SL	11	0.406	0.370–0.433

shaped with dorsal rays longer than ventral ones; all pectoral-fin rays segmented, some of the longer rays are branched distally. Pelvic-fin rays I, 5; frenum present; basal membrane uniting fins present for approximately one-third to one-half the length of innermost rays; smaller specimens typically have less deeply divided pelvic fins than larger specimens. Caudal fin with 17 segmented rays including 8+7 branched rays and a dorsal and ventral simple ray; unsegmented procurrent rays 4, dorsally and ventrally.

Scales cycloid, present on entire body with scale patches on head, cheek, and opercle, largest scales near caudal-fin base. Scales on head, cheek, and opercle present in patches of as few as two or three to as many as nine or 10 scales, the largest scale patch often posterior to the orbit. Scales on body extending from areas dorsal and ventral to opercle posteriorly to caudal-fin base. Longitudinal scale count 60–77, scales difficult to count with accuracy.

Typically, two lateral rows of teeth in each jaw, more than two rows anteriorly; outer-row teeth much larger and more pointed than those of inner rows; lower-jaw teeth longer than upper-jaw teeth; 2–5 fang-like teeth in outer row of upper jaw, typically interlocking with those of lower jaw; numerous conical teeth in inner row(s) of upper jaw; 4–7 fang-like teeth in outer row of lower jaw; numerous conical teeth in inner row(s) of lower jaw. No palatine or vomerine teeth present. No sexual dimorphism with respect to teeth.

Tongue thick, tip rounded, free from floor of mouth. Gape wide, mouth oblique (about 45°); maxilla extending posteriorly to vertical below anterior half of orbit; posteriorly, near tip of maxilla, upper lip ex-

Table 2.—Selected counts of *Amblyotrypauchen arctocephalus*.

Character	n	Mean	Frequencies
Dorsal-fin rays (total elements)	13	49.7	48(1), 49(6), 50(4), 52(2)
Anal-fin rays (total elements)	13	40.1	39(4), 40(6), 41(2), 43(1)
Pectoral-fin rays	21	16.2	14(2), 15(5), 16(5), 17(5), 18(4)
Longitudinal scale rows	16	69.5	60(3), 67(2), 68(1), 70(3), 71(1), 72(1), 74(2), 76(2), 77(1)
Upper jaw teeth (outer row)	10	3.6	2(2), 3(1), 4(6), 5(1)
Lower jaw teeth (outer row)	10	4.5	4(7), 5(2), 7(1)

panded into large fold that joins similar fold of lower lip at rictus, fold completely covering posterior part of jaws even when agape. No barbels on underside of head.

Eye absent. Posterior naris large and located in cavity where eye normally would be located; anterior naris at tip of small tube-like flap that slightly overhangs upper jaw.

Cephalic sensory canals and pores absent. Head papillae numerous, found on dorsum, cheek, opercle, and along lower jaw line. Papillae grouped in short series (<1 mm) that appear as whitish lines.

Shallow pouch present along the dorsal edge of the operculum. Gill rakers very short, pyramidal-shaped, and not ossified; six or fewer on lower limb of first gill arch. Gill opening narrow, extending only the length of pectoral-fin base or slightly more ventrally.

Genital papilla large and bulbous in females, bilobed in gravid specimens. Male papilla fleshy and triangular with distinct tip.

Coloration.—No fresh specimens were available for this study. Based on Alcock's original description, this species is mottled pink with hyaline fins. In preserved material, dorsum of head and body dark brown to gray, remainder of head and body uniformly pale or pale brown; no spots or stripes on body or fins; fins translucent; fang-like teeth on outer rows of both jaws often reddish brown in larger specimens.

Distribution.—Northeast coast of India eastward to Hong Kong and the Philippines, southward to Papua New Guinea and off the north coast of Australia. Reports of specimens from the Arabian Sea and Gulf of Martaban (Myanmar) by Koumans (1941) are unconfirmed.

Ecology.—This species inhabits muddy bottoms from almost 17 m to over 183 m in depth; for both amblyopines and gobies in general, these are uncharacteristic depths. None of the material examined was collected in typical amblyopine habitats, which are shallow, mud-bottomed areas near river mouths. The type material of *Amblyopus arctocephalus* Alcock (1890) was collected from 37–92 m, whereas the type of *Amblyotrypauchen fraseri* was collected from about 37 m (Hora 1924). The fang-like teeth suggest that this species is carnivorous, and a radiograph of one specimen (AMS I.16753-024) revealed the presence of an elongate fish in the stomach.

Remarks.—The genus *Amblyopus* (Valenciennes in Cuvier & Valenciennes, 1837: 157) is regarded as an unneeded substitute for *Taenioides* Lacepède (1800) and is thus considered an objective synonym of *Taenioides* (Eschmeyer, 1998). *Taenioides* is diagnosed among Gobiidae by its possession of a Y-shaped, second anal-fin pterygiophore (Birdsong et al. 1988); *Amblyotrypauchen* lacks this feature.

After examining the types of both species, Koumans (1941) synonymized *A. fraseri* with *A. arctocephalus.* Similar judgments were rendered by Smith (1959) and Menon and Yazdani (1968). Although wanting to examine the types of *A. arctocephalus* and *A. fraseri,* or at least obtain radiographs of them, I was unable to do so. I also was unable to determine the current status of Alcock's and Hora's types at the Zoological Survey of India. Regardless, there appears to be little reason to dispute the synonymy of *A. fraseri* with *A. arctocephalus* based on comparison of the original descriptions. When Hora (1924) described his new genus and species, he made no mention of Alcock's species, which had been collected in the same general vicinity as Hora's species (NW corner of the Bay of Bengal); I assume Hora was unaware of the existence of Alcock's description.

Two items in Alcock (1890) need mention. First, Alcock described a "short broad barbel" on each side of the upper jaw; this structure is a narial tube rather than a barbel. Secondly, Alcock stated that *A. arctocephalus* possesses 11 abdominal and 17 caudal vertebrae. Whereas it is possible that Alcock was not mistaken, in this study, I radiographed 13 specimens and all but one have 10 precaudal and 19 caudal vertebrae. The atypical specimen has 9 precaudal and 23 caudal vertebrae.

Several items in Hora (1924) also require discussion. First, Hora stated the dorsal-fin ray count of his single specimen as "7/40." Fin rays of amblyopines are very difficult to count without radiography. As none of the radiographed specimens in this study possess seven dorsal-fin spines, I assume Hora's count was in error. Second, Hora mentioned in the text that the dorsal and anal fins were "separated from the caudal by a short distance." However, Alcock (1890) stated that in his specimens, the dorsal and anal fins were confluent with the caudal fin; Koumans (1941) made a similar statement about the specimens he examined. In amblyopines, the membrane uniting the dorsal and anal fins with the caudal fins is thin and easily torn in handling. Some of the specimens examined in this study had torn membranes, and I assume that this also occurred to Hora's specimen. Lastly, Hora's figure of *A. fraseri* (reproduced here as Fig. 1) not only depicts the dorsal and anal fins not connected with the caudal fin, but also shows a cheek more fully scaled than on any specimen examined in this study. Possibly head scales slough off over time or with frequent handling such that older preserved material, like that examined in this study, does not accurately reflect the degree of head scalation found in fresher specimens. Alcock (1890) mentioned that the head was naked in his specimens and Koumans (1941) described the specimens he examined as having "some scales on head behind eye and on cheek and opercle." The degree of scalation of the head of *A. arctocephalus* can probably only be adequately assessed by examining fresh material.

Comparison of Amblyotrypauchen *with other* 'Trypauchen' *group members.*—Based on their shared absence of an interneural gap, Birdsong et al. (1988) created the monophyletic unit called the 'Trypauchen' group that comprised *Amblyotrypauchen, Caragobius, Trypauchen,* and *Trypauchenichthys.* Murdy (2002) added *Ctenotrypauchen* and a new genus (*Karsten*) to the 'Trypauchen' group and provided a key to the 'Trypauchen' group genera. *Caragobius* and *Karsten* lack an opercular pouch whereas the other 'Trypauchen' group genera have one. Hora (1924) distinguished *Amblyotrypauchen* from *Ctenotrypauchen, Trypauchen,* and *Trypauchenichthys* by its possession of canine teeth, as well as by the shape of the pelvic fins (Fig. 2). As a result of this investigation, I can further differentiate *Amblyotrypauchen* from these three genera by its possession of head scales (lacking in the other genera) and 10+19 vertebrae (all other genera typically have 20 or more caudal vertebrae). Murdy (2002) compared *Amblyotrypauchen* to *Karsten,* the only other blind amblyopine. *Karsten* differs from *Amblyotrypauchen* in having a typical spinous dorsal-fin pterygiophore formula of 3-123 or 3-132 (vs. 3-1221 in *Amblyotrypauchen*), possessing nine precaudal vertebrae (vs. 10 in *Amblyotrypauchen*), degree of scalation (scaled only posteriorly in *Karsten* vs. scaled on entire body including scale patches on the head in *Amblyotrypauchen*), in presence/absence of an opercular pouch (absent in *Karsten* vs. present in *Amblyotrypauchen*), and tooth size (slightly enlarged teeth in outer row of jaws vs. very large and fang-like in *Amblyotrypauchen*).

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Literature Cited

Alcock, A. W. 1890. Natural history notes from H. M. Indian marine survey steamer *Investigator,* Commander R. F. Hoskyn, R. N., commanding.—No. 20. On some undescribed shore-fishes from the Bay of Bengal.—Annals and Magazine of Natural History 6: 425–443.

Birdsong, R. S., E. O. Murdy, & F. L. Pezold. 1988. A study of the vertebral column and median fin osteology in gobioid fishes with comments on gobioid relationships.—Bulletin of Marine Science 42:174–214.

Cuvier, G., & A. Valenciennes. 1837. Histoire naturelle des poissons. Tome douzième. Suite du livre quatorzième. Gobioïdes. Livre quinzième. Acanthoptérygiens à pectorales pédiculées. Chez F. G. Lerrault, Paris, 507 pp.

Eschmeyer, W. N. (ed.). 1998. Catalog of fishes. Special publication No. 1 of the Center for Biodiversity Research and Information.—California Academy of Sciences 1–3:1–2905.

Herre, A. W. C. T., & E. S. Herald. 1951. Noteworthy additions to the Philippine fish fauna with descriptions of a new genus and species.—Philippine Journal of Science 79:309–340.

Hora, S. L. 1924. Notes on fishes in the Indian Museum. VI. On a new genus of gobioid fishes (subfamily Trypaucheninae) with notes on related forms.—Records of the Indian Museum 26:155–163.

Koumans, F. P. 1941. Gobioid fishes of India.—Memoirs of the Indian Museum 13:205–329.

Lacepède, B. G. E. 1800. Histoire naturelle des poissons, vol. 2. Chez Plassan, Paris, 632 pp.

Leviton, A. E., R. H. Gibbs, Jr., E. Heal, & C. E. Dawson. 1985. Standards in herpetology and ichthyology, part 1. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

Menon, A. G. K., & G. M. Yazdani. 1968. Catalogue of type-specimens in the Zoological Survey of India, part 2.—Fishes.—Records of the Zoological Survey of India, 61 (pts 1–2) [1963]:91–190. [Not published until 1968.]

Murdy, E. O. 2002. *Karsten,* a new genus of eel goby (Gobiidae: Amblyopinae) with a key to 'Trypauchen' group genera.—Copeia 2002(3):787–791.

———, & K. Shibukawa. 2001. A revision of the gobiid fish genus *Odontamblyopus* (Gobiidae: Amblyopinae).—Ichthyological Research, 48(2001)1:31–43.

Smith, J. L. B. 1959. Gobioid fishes of the families Gobiidae, Periophthalmidae, Trypauchenidae, Taenioididae and Kraemeriidae of the western Indian Ocean,—Rhodes University, Department of Ichthyology, Ichthyological Bulletin, 13: 185–225, pls. 9–13.

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The hyopalatine arch of a 25 mm larva of *Synbranchus* and homology of the single pterygoid in the Synbranchidae (Teleostei: Synbranchiformes)

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Abstract.—Identity of the single pterygoid bone in Synbranchidae is evaluated based on a 25 mm larva of *Synbranchus.* Two hypotheses have been proposed as to its homology: it is 1) the endopterygoid or 2) the ectopterygoid. We show that the bone in question develops in the position of the ectopterygoid and therefore represents the homologue of this bone in other teleosts. Thus synbranchids lack the endopterygoid, an observation that invalidates a previously proposed synapomorphy of this family and the channids (snakeheads).

Synbranchidae, or swamp eels, are a family of highly derived eel-like acanthomorphs, comprising 17 species (Bailey & Gans 1998) from fresh and estuarine waters of Middle and South America, Cuba, West Africa, Asia, and the Indo-Australian Archipelago (Nelson 1994). Several species are well known for their amphibious habits and the presence of accessory air breathing organs (see e.g., Rosen & Greenwood 1976, Liem 1987, Munshi et al. 1989) that enable them to undertake extensive overland excursions.

There are two hypotheses about the relationships of the Synbranchidae to other acanthomorph taxa: 1) synbranchids are the sister group of channids (Lauder & Liem 1983) and 2) synbranchids are the sister group of mastacembeloids (= mastacembelids plus chaudhuriids) (Travers 1984a, Johnson & Patterson 1993, Britz & Kottelat 2003).

One of the characters cited as support for Lauder & Liem's (1983) hypothesis is the presence of an enlarged endopterygoid in both, channids and synbranchids. The single pterygoid of synbranchids was considered an ectopterygoid by Regan (1912), Rastogi (1964), Rosen and Greenwood (1976), Gosline (1983), Travers (1984), and Britz (1996), and an endopterygoid by Lauder & Liem (1983). However, none of these authors specifically addressed the problem of the homology of this bone with respect to the ectopterygoid or endopterygoid of other teleosts. In the present paper we describe the hyopalatine arch of a 25 mm larval specimen of *Synbranchus* sp., to resolve the identity of the synbranchid pterygoid.

Material and Methods

A cleared and double stained larval *Synbranchus* sp. (USNM 372713) of 25 mm total length was studied. A Zeiss Tessovar was used to photograph the specimen. Additional comparative material comprised:

Mastacembelidae; all cleared and stained: *Mastacembelus erythrotaenia*: AMNH 42129 (1, 277 mm); *Mastacembelus* sp. (as

Macrognathus aculeatus) AMNH 097654 (1, 158 mm); *Macrognathus pancalus*: AMNH 217414 (8, 4.5–36 mm).

Synbranchidae; cleared and stained: *Macrotrema caligans*: MCZ 47107 (2, 172–178 mm), *Ophisternon aenigmaticum*: AMNH 31573 (1, 72 mm); *Synbranchus marmoratus*: AMNH 30213 (1, 142 mm), AMNH 74541 (1, 47 mm), MCZ 52376 (3, 65–140 mm; 1, disarticulated); *Monopterus albus*: AMNH 41579 (1, 167 mm); dry skeletons: *Ophisternon aenigmaticum* (as *Synbranchus marmoratus*): USNM 111347 (1, partial skeleton); *Monopterus* sp. (as *Synbranchus bengalensis*): AMNH 220023 (1, ca. 550 mm).

Terminology for the cartilaginous parts of the hyopalatine arch follows Arratia & Schultze (1991).

Results

The 25 mm larva of *Synbranchus* sp. still has a large yolk sac and prominent pectoral fins. The hyopalatine arch is largely cartilaginous (Fig. 1A). The hyosymplectic cartilage articulates with the otic capsule of the chondrocranium. In the area around the foramen for the hyomandibular branch of the facialis, there is a perichondral ossification, the hyomandibular, which bears a conspicuous process of membrane bone that extends ventrally between the body of the cartilage and the pars metapterygoidea of the palatoquadrate. A thin perichondral ossification, the symplectic, surrounds the anteroventral process of the hyosymplectic cartilage. The opercle, which articulates with a posterior process of the hyosymplectic cartilage, and the remaining three opercular bones are present as thin platelets of bone. The palatoquadrate comprises two unconnected parts, the posterior pars quadrata et metapterygoidea and the anterior pars autopalatina (Fig. 1A). The former is a roughly triangular cartilage, the ventral tip of which articulates with the lower jaw. Around this articulation and the lower third of the pars quadrata et metapterygoidea a perichondral ossification is present, the developing quadrate, with the usual posteroventral process of membrane bone. The developing metapterygpoid is present as a thin lamina of perichondral bone surrounding the posterodorsal corner of the pars quadrata et metapterygoidea. The pterygoid extends anteriorly as an elongate thin lamina of bone ventral to the anterodorsal corner of the pars quadrata (Fig. 1A, B). The elongate cartilage of the pars autopalatina sits more anteriorly in the roof of the mouth and bears a long anterolaterally directed process, the distal tip of which articulates with the lacrimal. Ventral to this cartilage is a small splint of bone, the developing dermopalatine (Fig. 1A). The lower jaw consists of the long Meckel's cartilage, its anterior part covered laterally by the dentary, which bears a few teeth, and its posterior part by the angular. The retroarticular is present as a small ossification at the most posterior tip of Meckel's cartilage, but the articular is not yet developed.

Discussion

In most actinopterygians, two dermal bones, the endopterygoid and the ectopterygoid, cover the medial face of the developing palatoquadrate between the pars quadrata and pars autopalatina (Arratia & Schultze 1991). Usually, the pars quadrata and the pars autopalatina are connected by a thin strip of cartilage during at least some period in early development. The endopterygoid ossifies dorsomedial to this cartilage and the ectopterygoid ventromedial to it (see e.g., Arratia & Schultze 1991:figs. 14, 15; Britz 1996:figs. 3–5; Britz & Johnson 2002:figs. 4, 5). Even when the cartilaginous connection between the pars quadrata and the pars autopalatina is resorbed during ontogeny, a small projecting tip on the anterodorsal face of pars quadrata usually remains for some time and can be used as a landmark. Such a stage is shown for a mastacembelid species in Britz (1996: Fig. 5). This landmark is also useful for taxa in

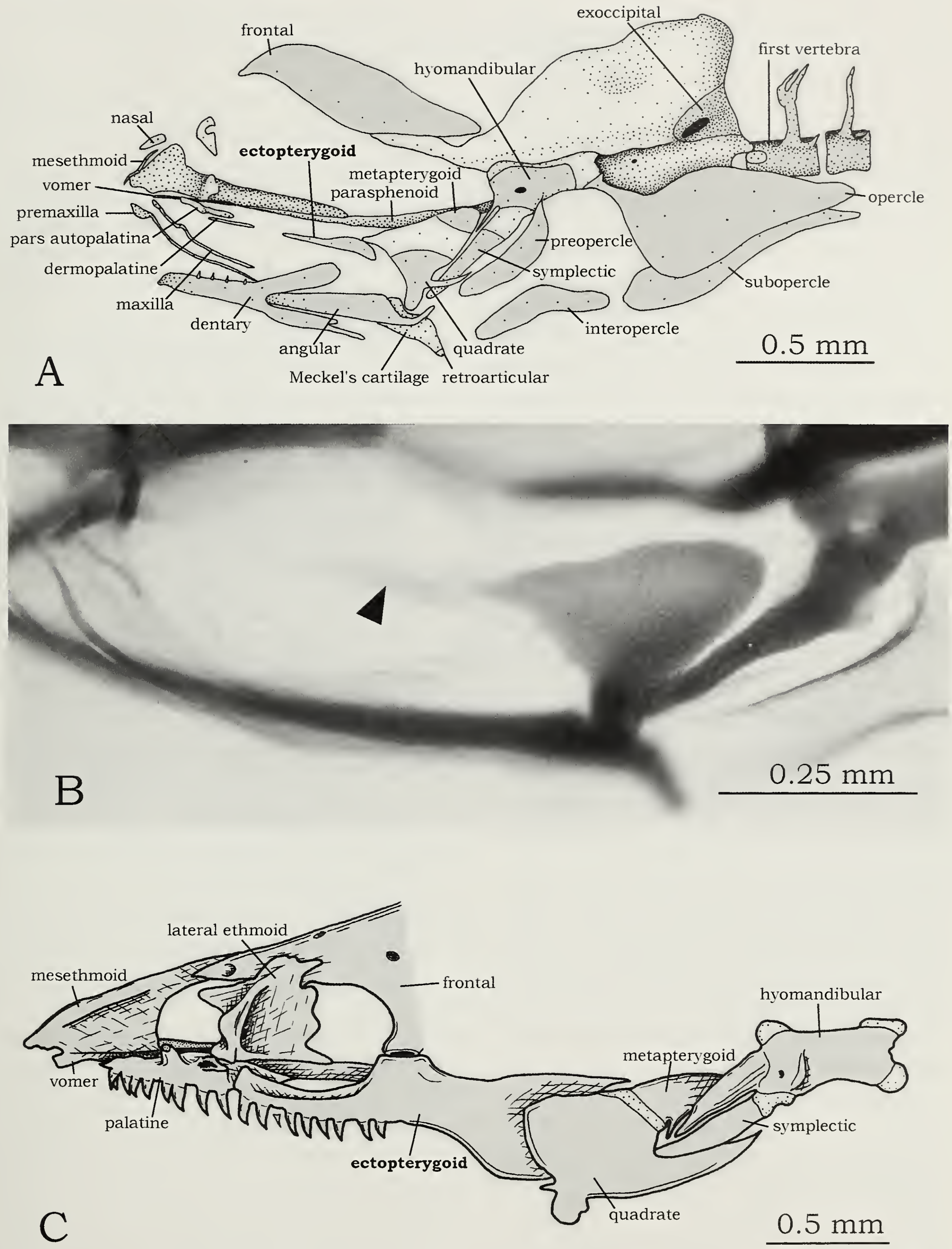

Fig. 1. *Synbranchus* sp., 25 mm: A, Skull and anterior two vertebrae, lateral view, cartilage white, bone light grey; B, Photograph of the hyopalatine area, lateral view, arrow points to ectopterygoid; C, *S. marmoratus*, 47 mm, hyopalatine arch and anterior part of neurocranium, lateral view, modified from Britz (1996), cartilage white, bone light grey.

which the pars quadrata and the pars autopalatina are never connected by cartilage.

The pterygoid bone of the 25 mm *Synbranchus* is located ventromedial to the projecting anterodorsal corner of the pars quadrata.

Thus, the position of the developing pterygoid in *Synbranchus* is identical to that of *Macrognathus* (Britz 1996: fig. 5) or other teleosts (see e.g., Arratia & Schultze 1991: figs. 14, 15; Britz & Johnson: figs. 4, 5) and clearly demonstrates its homology with this bone. During subsequent development the ectopterygoid of *Synbranchus* enlarges greatly and bears numerous strong teeth. It becomes the dominant element of the adult synbranchid palatoquadrate (Fig. 1C, see also Regan 1912:plate IX, fig. 1; Rastogi 1964:figs. 1–3; Rosen & Greenwood 1976: figs. 60, 61; Gosline 1983:fig. 3B; Travers 1984:fig. 10; Britz 1996:fig. 9C). Although we have no developmental information on the pterygoid of other synbranchids, it is reasonable to assume that it also represents the ectopterygoid, given its identical appearance and position to the other bones of the hyopalatine arch. This homology falsifies Lauder & Liem's (1983) interpretation of this bone as the endopterygoid and thus invalidates one of their putative synapomorphies uniting the Synbranchidae and the Channidae. The wider phylogenetic implications of our finding are beyond the scope of this paper and will be discussed in a forthcoming publication reevaluating the additional evidence for both hypotheses of synbranchid relationships.

Acknowledgments

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Literature Cited

Arratia, G., & H.-P. Schultze. 1991. Palatoquadrate and its ossifications: development and homology within osteichthyans.—Journal of Morphology 208:1–81.

Bailey, R. M., & C. Gans. 1998. Two new synbranchid fishes, *Monopterus roseni* from Peninsular India and *M. desilvai* from Sri Lanka.—Occasional Papers of the Museum of Zoology University of Michigan 726:1–18.

Britz, R. 1996. Ontogeny of the ethmoidal region and hyopalatine arch in *Macrognathus pancalus* (Percomorpha, Mastacembeloidei), with critical remarks on mastacembeloid inter- and intrarelationships.—American Museum Novitates 3181:1–18.

———, & G. D. Johnson. 2002. "Paradox Lost": Skeletal ontogeny of *Indostomus paradoxus* and its significance for the phylogenetic relationships of Indostomidae (Teleostei, Gasterosteiformes).—American Museum Novitates 3383: 1–43.

———, & M. Kottelat. 2003. Descriptive osteology of the family Chaudhuriidae (Teleostei, Synbranchiformes, Mastacembeloidei), with a discussion of its relationships.—American Museum Novitates (in press).

Gosline, W. A. 1983. The relationships of the mastacembelid and synbranchid fishes.—Japanese Journal of Ichthyology 29:323–328.

Johnson, G. D., & C. Patterson. 1993. Percomorph phylogeny: a survey of acanthomorphs and a new proposal.—Bulletin of Marine Science 52: 554–626.

Lauder, G. V., & K. F. Liem. 1983. The evolution and interrelationships of the actinopterygian fishes.—Bulletin of the Museum of Comparative Zoology 150:95–197.

Liem, K. F. 1987. Functional design of the air ventilation apparatus and overland excursions by teleosts.—Fieldiana 1379:1–29.

Munshi, J. S. D., G. M. Hughes, P. Gehr, & E. R. Weibel. 1989. Structure of the air-breathing organs of a swamp mud eel, *Monopterus cuchia*.—Japanese Journal of Ichthyology 35: 453–465.

Nelson, J. S. 1994. Fishes of the world. John Wiley & Sons, New York, 600 pp.

Rastogi, M. 1964. The head skeleton of *Amphipnous cuchia* (Ham.).—Acta Zoologica 46:283–292.

Regan, C. T. 1912. The anatomy and classification of the synbranchoid eels.—Annals and Magazine of Natural History, series 8, 9:387–390.

Rosen, D. E., & P. H. Greenwood. 1976. A fourth neotropical species of synbranchid eel and the phylogeny and systematics of synbranchiform fishes.—Bulletin of the American Museum of Natural History 157:1–69.

Travers, R. 1984. A review of the Mastacembeloidei, a suborder of synbranchiform teleost fishes. Part II: Phylogenetic analysis.—Bulletin of the British Museum of Natural History (Zoology) 47: 83–150.

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Skull osteology of the characid fish *Astyanax mexicanus* (Teleostei: Characidae)

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Abstract.—The skull of the characid fish *Astyanax mexicanus* is described based on twenty alizarin-stained adult specimens from Río Salado, Río Conchos, Río Alamo, and Río San Juan populations, all of them Rio Grande tributaries in Northeastern Mexico. The skull has a circular shape in lateral view. The second infraorbital is triangular and never overlaps the inferior margin of the third infraorbital. The third infraorbital never reaches the laterosensory canal of the preopercular bone. The supraoccipital is short. The palatines, ectopterygoids and mesopterygoids lack teeth. We describe two features not reported in *Astyanax* before: teeth on the second suspensory pharyngeal and posterior gill rakers on the four gill arches. Differences in skull osteology between *A. mexicanus* and other described species of *Astyanax* are denoted.

Species of the fish genus *Astyanax* Baird & Girard, 1854, are found from the Nueces River, Texas, to Patagonia, Argentina (Bănărescu 1990). This genus is among the most dominant group of freshwater fishes in this extensive region. The number of valid species of *Astyanax* that inhabits Mexico is uncertain (Contreras-Balderas & Lozano-Vilano 1998, Schmitter-Soto 1998). Because of the overall morphological similarity of the species of this genus, there is considerable confusion concerning species distinctness and distribution. Contributing to this problem is the fact that the original descriptions of many of them are incomplete, and data for collection localities were not clearly provided and are often unknown. These problems are reflected in the present nomenclatorial confusion (Valdez-Moreno 1997, Contreras-Balderas & Lozano-Vilano 1998).

Despite these uncertainties, most researchers, including Contreras-Balderas & Lozano-Vilano (1998), agree that one of the valid species is the northern form, *Astyanax mexicanus* (Filippi, 1853). It is known from central Texas, Rio Bravo (named Rio Grande in the U.S.A.), along Gulf of Mexico drainages such as the lower Pánuco River, and through the Tecolutla–Cucharas systems (Miller 1978, Obregón-Barboza et al. 1994, Valdéz-Moreno 1997). However, some authors, such as Espinosa-Pérez et al. (1993), considered forms from the Rio Balsas and the Papaloapan basins extending to Petén, Guatemala, to be *A. mexicanus* s. l. Others (e.g., Paulo Maya 1994), reported the presence of two distinct forms of *Astyanax* in the Río Balsas samples, without selecting names or referring them to either of the two nominal species described from the basin, *Astyanax nitidus* Bocourt (1868) and *A. fulgens* Bocourt (1868).

The identity of the Río Balsas form is still unresolved. We concur with Miller (in litt.) and Contreras-Balderas & Lozano-Vilano (1998) that Mexican forms of *Astyanax* are not the same as the South American representatives assigned to *A.* "*fasciatus*", and none of the Río Balsas forms are *A.*

mexicanus. Such forms probably represent a species of the *A. aeneus* group. Further research is needed to solve this problem.

Many studies of *A. mexicanus* deal primarily with morphometry (Schuppa 1984, Paulo-Maya 1994). Except for minor references to certain bones by Lozano-Vilano & Contreras-Balderas (1990), none deals with osteology. This approach contrasts with other studies in characid fishes. For example, the osteology of the American characid, *Brycon meeki,* was described in detail by Weitzman (1962). Menezes (1969) considered osteology in his study of the phylogeny of the tribe Acestrorhynchini, and Weitzman & Fink (1983) used osteological characters to elucidate relationships among neon tetras, *Paracheirodon* spp. Vari & Harold (1998) diagnosed the genus *Creagrutus* as a monophyletic group within the family Characidae on the basis of some modifications of skull bones. Malabarba (1998) provided a new diagnosis of the Cheirodontinae using features of the dentary, tooth morphology and other skull bones. Vari (1989a) studied the structure of the skull in members of the family Curimatidae and the genus *Pseudocurimata.* Vari (1983) also used osteological information to hypothesize relationships within Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae, as well as relationships among the Ctenoluciidae (Vari 1995). A cladistic analysis based on osteology by Buckup (1998) proposed relationships of the Characidiinae with the Crenuchinae. Langeani (1998) hypothesized the monophyly of the family Hemiodontidae using characteristics of skull bones along with other data.

The posterior region of skull and pectoral girdle of a female *A. mexicanus* from Guayalejo River, Tamaulipas, Mexico, was described and figured by Weitzman & Fink (1983, 1985), but they did not describe the entire skull of this species. The skull anatomy of *A. "fasciatus"* has been described only for the form from Balsas River, Mexico, by Mejía-Mójica & Díaz-Pardo (1991). Problems with the identity of this form were discussed above.

The purposes of this work are to describe in detail the skull of *A. mexicanus* and to provide a baseline to compare with other species and genera. The use of the cranial characters described herein may provide a means to better study the taxa assigned to the genus *Astyanax* and could be useful to make inferences about the phylogeny of members of the genus or the family.

Methods

Material examined.—Twenty adult specimens of *Astyanax mexicanus* (>40 mm standard length, SL), from the Fish Collection of the Autonomous University of Nuevo León (UANL), were selected from Rio Grande/Río Bravo localities: Río Salado at Socavón, 5.2 km SW from Múzquiz, State of Coahuila (UANL-7271: 3 ♀ and 2 ♂ SL = 57.47 to 74.67 mm); Rio Conchos: Río Chuvíscar at Aldama, State of Chihuahua (UANL-6944; 4 ♀ and 1 ♂ SL = 46.69 to 54.74 mm); Río Alamo in Paso de las Anacuas, 26 km W from Ciudad Mier, State of Tamaulipas (UANL-3932; 3 ♀ and 2 ♂ SL = 53.71 to 60.11 mm), and Río San Juan: Cañón de la Boca, 1 km after the dam Presa de la Boca, State of Nuevo León (UANL-4924; 5 ♀ SL = 67.65–75.54 mm).

The specimens were cleared and stained following the technique of Hollister (1934). Terminology follows Weitzman (1962),

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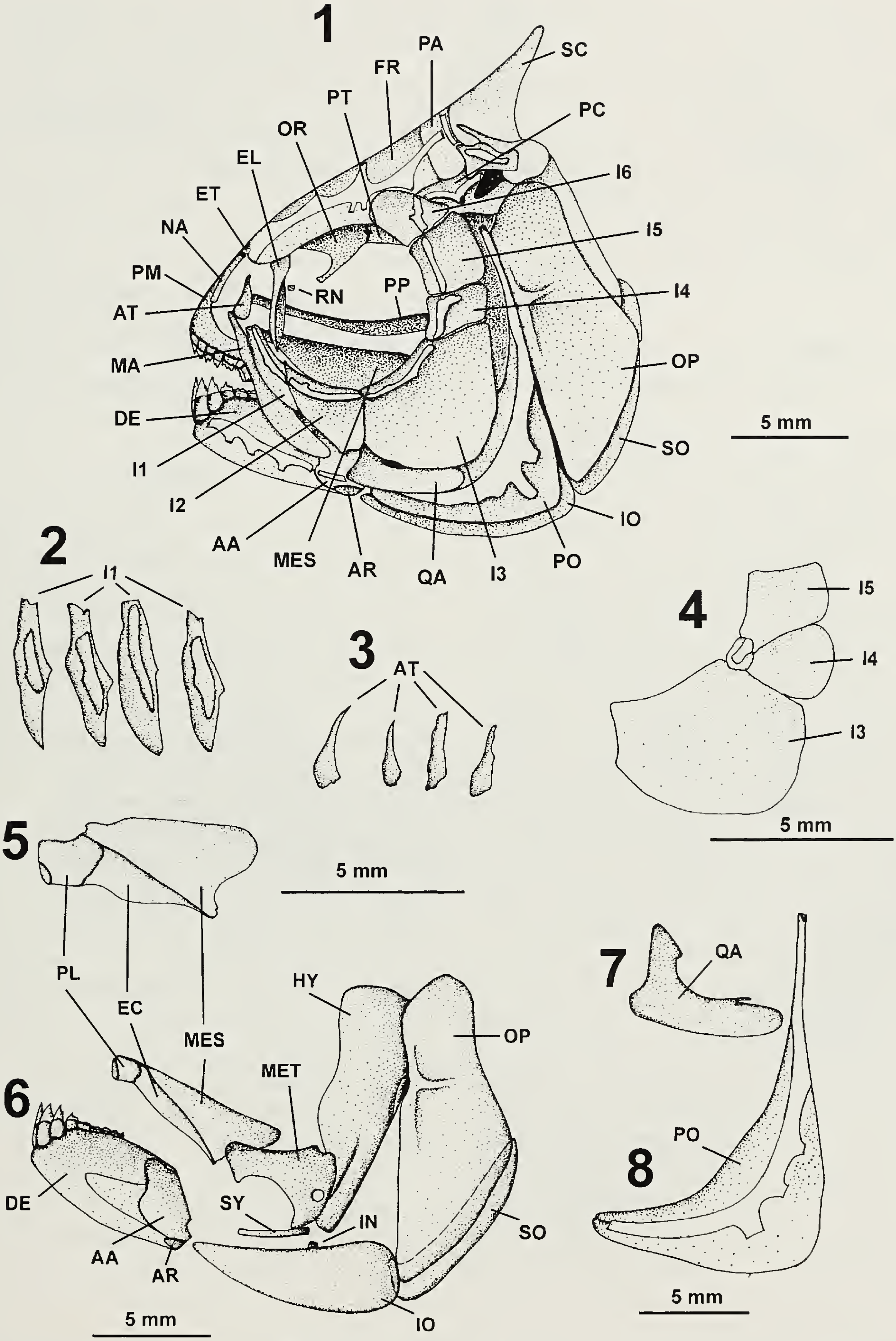
Figs. 1–8. Skull of *Astyanax mexicanus,* lateral view, left side, female, SL 74.29 mm. 1, Full view; 2, Infraorbital I, different shapes; 3, Antorbital, different shapes; 4 Infraorbital 4, malformation; 5, Palatine, ectopterygoid and mesopterygoid; 6, Lower jaw, opercular series, mandibular arch and palatine arch; 7, Quadrate; 8, Preopercular. Abbreviations.—AA—anguloarticular; AT—antorbital; AR—retroarticular; DE—dentary; EC—



ctopterygoid; EL—lateral ethmoid; ET—ethmoid; FR—frontal; HY—hyomandibular; I1—infraorbital 1; I2—infraorbital 2; I3—infraorbital 3; I4—infraorbital 4; I5—infraorbital 5; I6—infraorbital 6; IN—interhyal; IO—interopercle; MA—maxilla; MES—mesopterygoid; MET—metapterygoid; NA—nasal; OP—opercle; OR—orbitosphenoid; PA—parietal; PC—pterotic; PL—palatine; PM—premaxilla; PO—preopercle; PP—parasphenoid; PT—pterosphenoid; QA—quadrate; RN—rhinosphenoid; SC—supraoccipital; SO—subopercle; SY—symplectic.

Fink & Fink (1981) and Weitzman & Fink (1983). Each bone was drawn with the aid of a camera lucida attached to a stereomicroscope (Nikon SMZ10). All base drawings of the bones for *A. mexicanus* were made from specimens collected in the Rio Salado, Coahuila. Morphological differences and similarities between populations were analyzed by direct comparison of shape.

Description of the skull of *Astyanax mexicanus* (Filippi, 1853)

Diagnosis.—Skull circular in lateral profile. Anterior margin of dentary never projecting anteriorly further than that of premaxilla. Opercle almost rectangular. Infraorbital 2 triangular, never overlapping inferior margin of infraorbital 3. Infraorbital 3 semicircular, never reaching laterosensory canal of preopercular bone. Supraoccipital short with wider base; in dorsal view, posterior end of supraoccipital spine slighthly overlapping posterolateral border of epioccipital. Palatines, ectopterygoids and mesopterygoids without teeth. First suspensory pharyngeal triangular, without teeth; second one almost rectangular, with few unicuspid teeth; third one triangular, larger than first and second, with numerous unicuspid teeth. Premaxilla with two rows of teeth. Outer row consisting of four tricuspid teeth, inner row with four to five teeth, each tooth with three to six cusps. Maxilla with single row of one or two teeth, number of cusps per tooth five to eight. Dentary with single row of four teeth followed by several posterior ones; first and third teeth similar in size and appearance. All dentary teeth with five to seven, usually six, cusps. Fifth dentary tooth smaller than first four, with five to six cusps, usually five. Remaining five to ten teeth smaller, each bearing one or two cusps. Symphyseal and lateral diastemmas absent. Total number of anterior gill rakers on first arch 18 to 21, second and third arches 18 to 20, and fourth arch 13 to 18. Five posterior gill rakers on first arch, five to six on second, 14 to 16 on third, and five to six on fourth. Dorsal border of lower pharyngeal with six to ten structures similar to gill rakers. All gill rakers conical in shape and with several short conical spicules arranged irregularly.

Cranium

Ethmoid (Figs. 1, 17, 20, 21).—Most anterior medial bone of the cranium; ethmoid relatively flat but complex in shape. Anteriorly bearing a forward-projecting conical bony process rounded towards the anterior end and two wing-like lateral processes. Ethmoid articulating anteriorly with the nonmovable premaxillae, ventrally with the vomer and lateral ethmoids and posteriorly with the frontals.

Lateral ethmoids (Figs. 1, 17, 20, 21).—Paired bones, each articulating dorsally with a frontal and medially with the vomer. Each lateral ethmoid a thin, triangular plate with a foramen. Angle of internal ventral part of each plate projecting posteriorly and bearing a variable number of small processes with smooth surfaces. Lateral ethmoids separating nasal cavity from ocular cavity and thus, in part, forming anterior wall of eye socket.

Vomer (Figs. 17, 21).—Median bone forming part of roof of mouth cavity. Vomer "T" shaped, the lateral processes artic-

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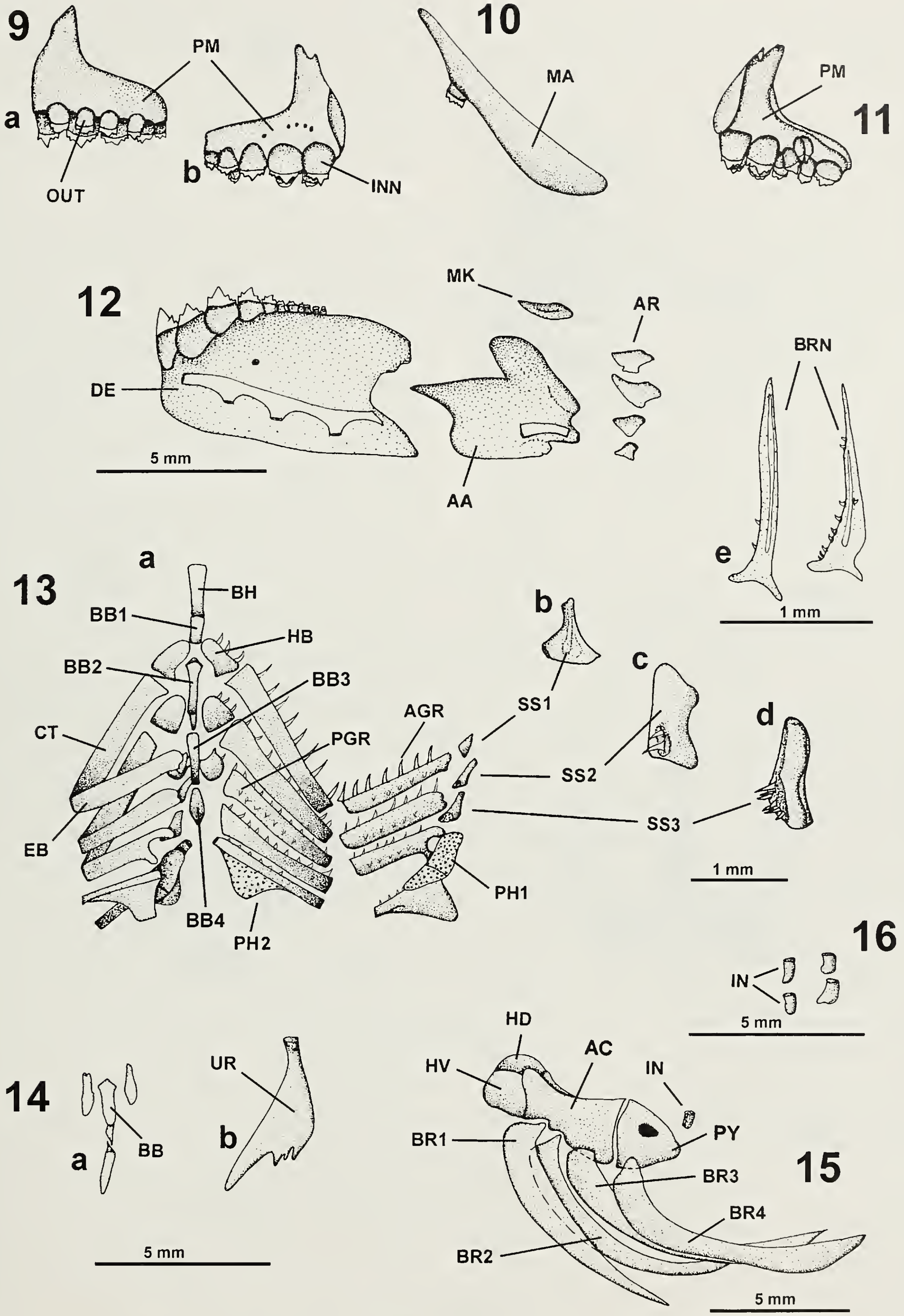
Figs. 9–12. Upper and lower jaws of *A. mexicanus,* female, SL 74.29 mm. 9a, Premaxilla dorsal view; 9b, Premaxilla, ventral view; 10, Maxilla, lateral view; 11, Premaxilla, ventral view, malformation; 12, Dentary, lateral view. Figs. 13, 14a. Branchyal arches of *A. mexicanus,* female, SL 74.29 mm. 13a, Branchyal arches; 13b, suspensory pharyngeal 1; 13c, suspensory pharyngeal 2; 13c, suspensory pharyngeal 3; 13e, gill rakers; 14a, basibranchials malformation. Figs. 14b–16. Hyoid arch of *A. mexicanus,* female, SL 74.29 mm. 14b, Urohyal; 15, Hyoid arch; 16, Interhyal with different shapes. Abbreviations.—AA—anguloarticular; AC—anterior



ceratohyal; AGR—anterior gill rakers; AR—retroarticular; BB1—basibranchials 1; BB2—basibranchials 2; BB3—basibranchials 3; BB4—basibranchials 4; BH—basihyal; BR1—branchiostegal ray 1; BR2—branchiostegal ray 2; BR3—branchiostegal ray 3; BR4—branchiostegal ray 4; CT—ceratobranchials; DE—dentary; EB—epibranchials; HB—Hypobranchials; HD—hypohyal dorsal; HV—hypohyal ventral; IN—interhyal; INN—inner row of teeth; MA—maxillary; MK—meckelian cartilage; OUT—outer row of teeth; PGR—posterior gill rakers; PH1—upper pharyngeal teeth; PH2—lower pharyngeal teeth; PM—premaxilla; PY—posterior ceratohyal; SS1—suspensory pharyngeals 1; SS2—suspensory pharyngeals 2; SS3—suspensory pharyngeals 3; UR—urohyal.

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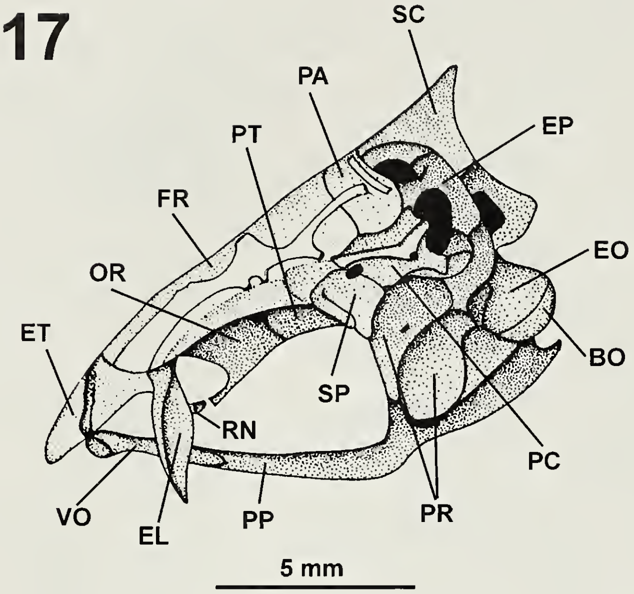

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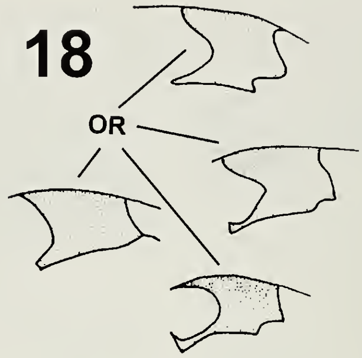

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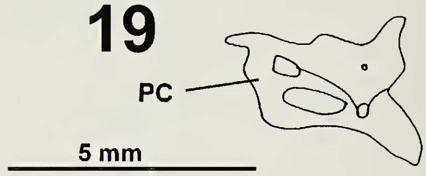

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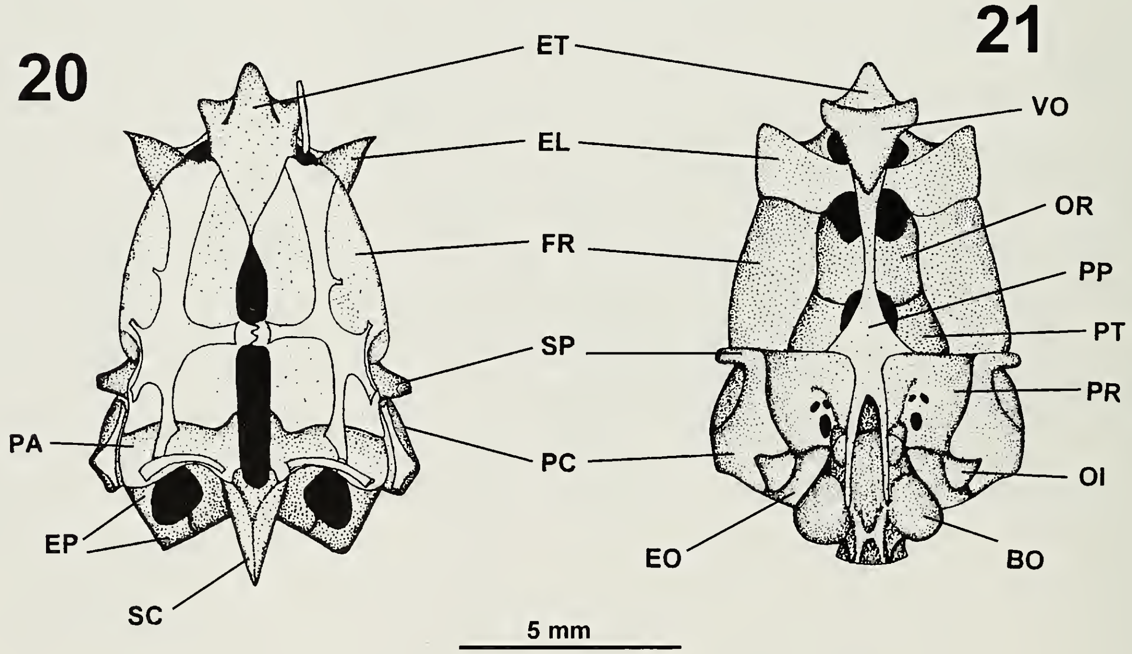

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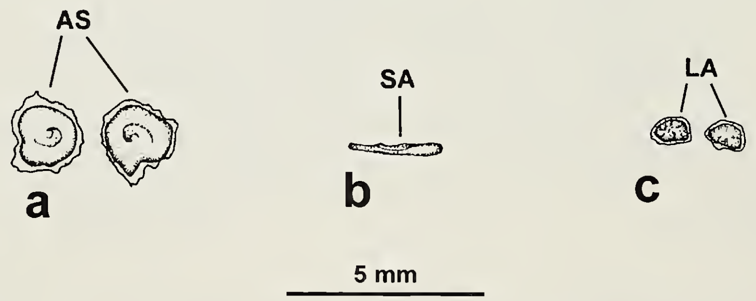

Figs. 17–22. Cranium of *A. mexicanus,* female, SL 74.29 mm. 17, lateral view. 18, Orbitosphenoid, different shapes; 19, Pterosphenoid, different shape; 20, dorsal view; 21, ventral view; 22a, Otolith asteriscus, dorsal view; 22b, Otolith sagitta, dorsolateral view; 22c, Otolith lapillus, dorsal view. Abbreviations.—AS—asteriscus; BO—basioccipital; EL—lateral ethmoid; EO—exoccipital; EP—epioccipital; ET—ethmoid; FR—frontal; LA—lapillus; OI—opisthotic; OR—orbitosphenoid; PA—parietal; PC—pterotic; PP—parasphenoid; PR—prootic; PT—pterosphenoid; RN—rhinosphenoid; SA—sagitta; SC—supraoccipital; SP—sphenotics; VO—vomer.

ulating with the lateral ethmoids. Two foramina providing passages for ramus buccalis of facial nerve. Ventrally, vomer articulating with parasphenoid and dorsally with ethmoid. Ventral surface of vomer without anatomical markings, few present on dorsum.

Frontals (Figs. 1, 17, 20, 21).—Laminar bones comprising a large part of dorsal region of cranium, connected to each other by epiphyseal bar that bridges the cranial fontanels. Each frontal with a ventral keel in medial position. Frontal articulating dorsoposteriorly with parietal, dorsoanteriorly with ethmoid, nasal and lateral ethmoid, and ventrally with orbitosphenoid, pterosphenoid, sphenotics, and pterotic. Each frontal containing canals of accoustico lateralis system. Anterior portions of these canals wide and continuous with nasal canal. Frontal bone with medial canals splitting in two main branches: an epiphysial branch extending medially over the epiphysial bar and opening above the frontal fontanel, and posterior branch connected posteriorly with the parietal and this canal, but not to extrascapular canal. Another branch, smaller than the former two, runs laterally continuing with the pterotic canal. Small side branches of these canals opening on dorsal surface of frontal.

Parietals (Figs. 1, 17, 20).—Rectangular laminar paired bones, without anatomical markings on their ventral and dorsal surfaces. Each one articulating dorsoanteriorly with frontal, posteriorly with epioccipital, dorsoposteriorly with supraoccipital and lateroventrally with pterotic. Parietals separated by the cranial fontanel. Laterosensory canal parietal connecting posterolaterally with extrascapular canal and extending dorsally to cranial fontanel.

Supraoccipital (Figs. 1, 17, 20).—Median bone constituting posterior roof of cranium, articulating dorsoanteriorly with parietals and forming posterior border of median dorsal fontanel, ventrolaterally with epioccipitals, and ventrally with pterotics. In dorsal view, supraoccipital "V" shaped, with a wide anterior base. Dorsal surface with a groove extending posteriorly to end of supraoccipital spine.

Epioccipitals (Figs. 17, 20).—Smooth tubular paired bones, each containing a major portion of the posterior vertical semicircular canal of the auditory and equilibrium systems. Epioccipital articulating dorsally with supraoccipital, posteroventrally with exoccipital and anteroventrally with pterotic. Lateral epioccipital process anteriorly contacting parietal and pterotic, dividing postemporal fossa in two parts.

Exoccipitals (Figs. 17, 21).—Smooth paired bones forming ventral part of posterior cranium, dorsally articulating with epioccipital, ventrally with basioccipital, anteriorly with prootic and anterolaterally with pterotic and opisthotic. Each exoccipital with laminar part enclosing the foramen magnum and ventral spherical part constituting the roof of the otic capsule for lagena.

Opisthotics (Fig. 21).—Small, thin bones, having triangular shape with a curved base, located external to articulation between pterotic, exoccipital and prootic; opisthotic attaching by ligament to ventral process of postemporal bone.

Basioccipital (Figs. 17, 21).—Constituting posterior base of cranium, with one globular part and other laminar. Dorsally articulating with exoccipitals, anteriorly with prootic, ventromedially with parasphenoid and posteriorly with first vertebra. Basioccipital also forming ventral portion of otic capsule for lagena and posterior region of saccular cavity for asteriscus. No anatomical markings on external surface.

Pterotics (Figs. 17, 20, 21).—Paired bones articulating anteriorly with sphenotic, ventromedially with prootic, dorsally with frontal and parietal, and posteriorly with epioccipital. Pterotic with rounded process that projects posteriorly and ventrally, providing insertion for levator operculi muscle. Pterotic articulating with hyomandibular at a groove. Internally, pterotic enclosing a major part of the horizontal semicircular canal. Each pterotic with a "V"-shaped canal of the accoustico lateralis system, canal continuing ventrally to preopercular canal and dorsally to frontal canal. A small foramen present between pterotic and sphenotic. Extrascapular overlapping posterodorsal part of pterotic.

Sphenotics (Figs. 17, 20 21).—Paired bones, quadrangular with rounded edges in lateral view and with a strong rounded process anterodorsally. Sphenotics articulating anteriorly with pterosphenoid, ventrally with prootic, posteriorly with pterotic and dorsally with frontal. Sphenotic not associated with lateral sensory system.

Prootics (Figs. 17, 21).—Complex paired bones. Dorsolaterally articulating with sphenotics and pterotics, medially with prootic on the other side, anteriorly with pterosphenoid, ventrally with parasphenoid, and posteriorly with opisthotic, exoccipital and basioccipital. Prootic with three foramina of different sizes, the auditory foramen largest.

Parasphenoid (Figs. 1, 17, 21).—Longest unpaired bone of cranium, spanning ventral median region of cranium and articulating anteriorly with vomer, dorsoposteriorly with prootics and basioccipitals. Ventrally with a medial quilla joining with suspensor pharyngeals by ligaments. Ventroposteriorly ending in two laminar process.

Pterosphenoids (Figs. 1, 17, 21).—Paired bones, rectangular in lateral view, with smooth edges, forming part of wall and floor of cranial cavity. Together with orbitosphenoid, pterosphenoids constituting medial aspect of ocular cavity. Pterosphenoid articulating dorsally with frontal, laterally with sphenotic, ventrally with parasphenoid, and anteriorly with orbitosphenoid. A small foramen for trochlear nerve present at articulation of orbitosphenoid and pterosphenoid.

Orbitosphenoid (Figs. 1, 17, 21).—Located ventral to middle region of frontal and posterior to ethmoid. Anterodorsally articulating with frontal and posteriorly with pterosphenoid. Ventrally, orbitosphenoid with a process directed toward anterior part of cranium. Orbitosphenoid highly varible in shape, length, and width at intra- and interpopulation levels (Fig. 18), usually resembling a "J" in lateral view. In dorsal view, orbitosphenoid resembling two wings or a "bird in flight" (Mejía-Mojica & Díaz-Pardo 1991).

Rhinosphenoid (Figs. 1, 17).—Small, almost square to irregular medial bone located anteriorly to orbitosphenoid, between lateral ethmoids. Rhinosphenoid ossified in five of our specimens.

Nasals (Fig. 1).—Tubular paired bones, slightly curved with smooth surface, located anterolateral to cranium. Nasal articulating anteriorly with premaxilla, posteriorly with frontal. Each nasal bone containing a branch of the laterosensory system.

Otoliths (Fig. 22a, b, c).—The ovoid lapillus contained in an utricular sac on floor of prootic. The spine-like sagitta contained in saccular recess formed by prootic, basioccipital and exoccipital. The lenticular asteriscus lying in capsule formed by the exoccipital and basioccipital. Asteriscus larger than the other otoliths and bearing small projections around its border.

Antorbital and Infraorbital bones.—This series comprising seven paired elements as follows:

Antorbitals (Fig. 1).—Each bone located ventrolaterally to respective nasal orifice. Antorbital with an elongated triangular shape, the anterior part considerably narrower than the posterior part; however, shape of antorbital varying among specimens. This variation apparently independent of sex (Fig. 3).

Infraorbitals 1 (Figs. 1, 2).—Shape similar to the blade of a scalpel, the ventral border variably prolonged in width and length. First infraorbital partially overlapped by the maxilla.

Infraorbitals 2 (Fig. 1).—Triangular bone with inferior margin usually smooth or sometimes jagged. Posterior portion of bone deeper than anterior portion. Second infraorbital located lateral to anguloarticular and quadrate bones and never overlapping inferior margin of infraorbital 3.

Infraorbitals 3 (Figs. 1, 4).—Largest bone of the series. Shape semicircular. Inferior margin always smooth, lateral surface occasionally with small foramina. Third infraorbital located lateral to quadrate and preopercle, but inferior margin never reaching laterosensory canal of preopercular bone.

Infraorbitals 4 (Figs. 1, 4).—Rectangular bone, shape depending on shape of articulation with infraorbital 3. Anteroventral edge projecting ventrally. Fourth infraorbital located lateral to hyomandibular bone.

Infraorbitals 5 (Figs. 1, 4).—Quadrangular bone with rounded corners. Located dorsal to infraorbital 4 and lateral to hyomandibular.

Infraorbital 6 (Fig. 1).—Thumb-nail shaped bone, posteroventral margin roughly straight at articulation with fifth infraorbital. Sixth infraorbital located lateral to sphenotic and frontal.

All the circumorbital bones smooth and bearing canals for the accoustico lateralis system. Canal of sixth infraorbital connecting with laterosensory canals of pterotic and frontal bones. *Astyanax mexicanus* lacking supraorbital bones.

Upper Jaw

Premaxillae (Figs. 1, 9).—Strong, paired bones articulating dorsally with ethmoid and nasal bones, laterally with maxillae. Premaxilla triangular in dorsal view. Each premaxilla with two teeth rows. In one specimen a replacement row present. Anterior row consisting of four teeth, each one having three, sometimes four, cusps. Posterior row with four to five teeth, each one with three to six cusps. Dorsal surface of premaxilla smooth, ventral surface with a small foramen. One specimen with a tooth malformation in the posterior row (Fig. 11).

Maxillae (Figs. 1, 10).—Thin, paired bones, each articulating anteriorly with premaxilla. Posterior ramus of maxilla overlapping dentary and bearing one or two teeth, each with five to eight cuspids.

Lower Jaw

Dentaries (Figs. 1, 6, 12).—Paired robust bones, each articulating dorsoposteriorly with anguloarticular and retroarticular, posteromedially with coromeckelian bone. Dentary with a single row of four frontal teeth and several posterior ones. First and third frontal teeth similar in size and appearance; second one about the same size or slightly smaller than the first. The fourth smaller than the other three frontal teeth. All of them with five to seven, usually six, cusps. Fifth dentary tooth smaller than the first four, with five or six cusps, usually five. Remaining teeth smaller (five to ten), with one or two cusps. Replacement row of teeth always present but variously developed and positioned, teeth of replacement row directed vertically.

Lateral surface of each dentary with a canal for accoustico lateralis system, associated with three small foramina. Posterior portion of this canal continuous with the anguloarticular canal. Symphyseal and lateral diastemmas absent.

Anguloarticulars (Figs. 1, 6, 12).—Paired bones that form the joint between the dentary and skull, shape similar to a fan with three peaks, middle one longest and pointed, other two rounded. Anguloarticular articulating anteriorly with dentary, ventroposteriorly with retroarticular, posteriorly with quadrate via a condyle, and medially with Coromeckelian bone. Anguloarticular containing a canal of the lateral sensory system that communicates posteriorly with canal of preopercle.

Retroarticulars (Figs. 1, 6, 12).—Paired, triangular bones, equal to or slightly smaller than coromeckelian bone. Retroarticular articulating ventroposteriorly with anguloarticular. Shape and length of retroarticular variable.

Coromeckelian bones (Fig. 12).—Small, paired, oval bones with smooth external surface, located along medial face of anguloarticular. Medial surface of coromeckelian with a median keel.

Opercular Series

Opercles (Figs. 1, 6).—Thin, paired, nearly rectangular bones with smooth surfaces and borders. Opercle articulating anteriorly with hyomandibular via a condyle on the latter, opercle articulating ventrally with subopercle.

Subopercles (Figs. 1, 6).—Thin, paired bones with smooth surfaces and borders articulating dorsally with opercle. Anterior part of subopercle with a small dorsal process.

Interopercles (Figs. 1, 6).—Paired, flat, smooth bones with triangular shape, posterior portion deeper than anterior part. Interopercle articulating dorsally with preopercle.

Preopercles (Figs. 1, 8).—Large, flat, paired bones, the dorsal limb lying between hyomandibular and opercle. Preopercle roughly triangular in shape, with a broad base and thin dorsal limb. A canal of the laterosensory system extending the length of preopercle; anteriorly, the canal continuous with anguloarticular canal, dorsally the canal continuous with pterotic canal.

Mandibular Arch

Hyomandibulars (Fig. 6).—Strong, paired bones with smooth surfaces. Dorsal portion of bone broad with rounded margins, ventral part slender. Hyomandibular articulating dorsally with neurocranium through a fossa in the pterotic and another in the sphenotic. Dorsoposteriorly, hyomandibular articulating with opercle, ventrally with metapterygoid.

Quadrates (Figs. 1, 7).—Paired bones lying above preopercle and articulating anteroventrally with anguloarticular by a condyle. Quadrate L-shaped, with vertical limb shorter than horizontal one. A posteriorly directed process of varying size sometimes present along dorsal margin of horizontal limb. Variation in this process apparently independent of sex.

Symplectics (Fig. 6).—Two smooth rodlike bones, slightly curved or straight, located medial to quadrate bone.

Palatine Arch

Metapterygoids, mesopterygoids, ectopterygoids, palatines and the vertical part of quadrate forming the anterior suspensory mechanism of lower jaw.

Metapterygoids (Fig. 6).—Paired bones of irregular shape with smooth surfaces. A small foramen present on posterior portion of metapterygoid. Posterior portion of bone deeper than anterior part. Two processes of variable size present on dorsal surface of posterior portion of metapterygoid. Metapterygoid articulating dorsoanteriorly with mesopterygoid and dorsoposteriorly with hyomandibular.

Mesopterygoids (Figs. 5, 6).—Paired triangular bones with smooth surfaces. Mesopterygoid articulating anteriorly with palatine, anteroventrally with ectopterygoid, and ventrally with metapterygoid and quadrate.

Ectopterygoids (Figs. 5, 6).—Paired triangular bones adjacent to mesopterygoids. Ectopterygoid narrower than mesopterygoid but of similar surface morphology and thickness.

Palatines (Figs. 5, 6).—Paired bones, square shaped with slightly rounded angles. Palatines articulating anteriorly with maxillary and posteriorly with ectopterygoids and mesopterygoids.

Mesopterygoid, ectopterygoid and palatine bones without teeth.

Hyoid Arch

Interhyals (Figs. 6, 15, 16).—Small, cylindrical, paired bones, lying ventral to hyomandibular and posterior to symplectic. Interhyal located below interopercle, articulating with hyomandibular and symplectic.

Posterior ceratohyals (Fig. 15).—Paired triangular bones with rounded posterior end and smooth borders and surfaces. A foramen located centrally or somewhat closer to the posterior border, associated or not with a canal. Posterior ceratohyal articulating anteriorly with anterior ceratohyal and posteriorly with interhyal. Ventrally posterior ceratohyal supporting fourth branchiostegal.

Anterior ceratohyals (Fig. 15).—Paired bones, rectangular in lateral view, with smooth surfaces. Anterior ceratohyal articulating anteriorly with dorsal and ventral hypohyals, posteriorly with posterior ceratohyal, and, ventrally, supporting first three branchiostegal rays. Third branchiostegal ray overlying and articulating with most posteroventral part of anterior ceratohyal. First and second branchiostegal rays inserted into small grooves on ventral margin of anterior ceratohyal.

Dorsal hypohyals (Fig. 15).—Shallow paired bones overlying and articulating with ventral hypohyal and anterior ceratohyal.

Ventral hypohyals (Fig. 15).—Paired quadrangular bones with rounded angles, articulating with anterior ceratohyals and dorsal hypohyals.

Urohyal (Fig. 14b)—Triangular bone bearing projections on the ventral surface of varying length and number. Urohyal inserting between and connected by ligaments to ventral hypohyals.

Branchial Arches

Basihyal (Fig. 13a).—This rectangular and slightly flattened median bone the anteriormost element of the branchial skeleton. Basihyal located between dorsal hypohyals. In one specimen, first basibranchial malformed (see Fig. 14a).

Basibranchials (Fig. 13a).—Together with the basihyal, these four unpaired bones forming the median spine of the gill-arch skeleton. Anteriormost basibranchial flattened and attached by a ligament to basihyal; second and third basibranchials elongated; and fourth leaf-shaped and smaller than preceding two. A shared basibranchial cartilage uniting all basibranchials.

Hypobranchials (Fig. 13a).—Three paired bones comprising most proximal elements of first three gill arches. First hypobranchial tongue-shaped, articulating with first basibranchial and first ceratobranchial. Second hypobranchial dome-shaped, articulating with second basibranchial and second ceratobranchial. Third hypobranchial saccular-shaped, articulating with third basibranchial and third ceratobranchial. All hypobranchials bearing gill rakers on anterior edge.

Ceratobranchials (Fig. 13a).—Five paired bones that form most of the ventral part of each gill arch. First three ceratobranchials elongated and slightly flattened, each articulating proximally with a hypobranchial and distally with an epibranchial. Fourth ceratobranchial elongated and slightly flattened, articulating proximally with a hypobranchial and distally with fourth epibranchial. First four ceratobranchials bearing gill rakers along anterior and posterior edges. Fifth ceratobranchial modified to form lower pharyngeal bone, which bears several small, scattered, unicuspid teeth on its dorsal surface and gill rakers along the anterior edge.

Epibranchials (Fig. 13a).—Four paired bones forming most of dorsal portion of each gill arch. First two elongated, slightly flattened, and lacking uncinate processes. Third elongated and bearing posteriorly directed uncinate process near distal end of bone; uncinate process articulating with upper pharyngeal teeth. Fourth epibranchial triangular. All epibranchials with small rakers along anterior edge, and first three with gill rakers along posterior edge.

Third and fourth epibranchials supporting upper pharyngeal plate. Upper pharyngeal irregular in shape and with several small, scattered unicuspid teeth on ventral surface.

Suspensory pharyngeals.—Three small, paired bones articulating with first three epibranchials and with parasphenoid. First one triangular, without teeth (Fig. 13b). Second almost rectangular with few unicuspid teeth (Fig. 13c). Third triangular with numerous unicuspid teeth (Fig. 13c).

Gill Rakers.—Total number of anterior gill rakers on first arch 18 to 21, second and third arches 18 to 20, and fourth arch 13 to 18. Five posterior gill rakers on first arch, five to six on second, 14 to 16 on third, and five to six on fourth. Dorsal border of lower pharyngeal with six to ten structures similar to gill rakers. All gill rakers conical in shape and with several short conical spicules arranged irregularly.

Discussion

The skull of *Astyanax mexicanus* is made up of 58 bones, nine of them unpaired (ethmoid, vomer, parasphenoid, supraoccipital, orbitosphenoid, basioccipital, urohyal, basihyal, rhinosphenoid), all others are paired. This number differs from that reported for *Astyanax* "*fasciatus*" (sensu Mejía-Mojica & Díaz-Pardo 1991), because they did not include the rhinosphenoid.

A comparison of the skull between *A. mexicanus* and the descriptions of *A.* "*fasciatus*" sensu Mejía-Mojica & Díaz-Pardo 1991, suggests that they are quite similar. However, differences are present in some bones. The opercle in *A. mexicanus* is almost rectangular and wide, whereas in *A.* "*fasciatus*" it is more rhomboid-like and narrower. The supraoccipital (in dorsal view) is short with a wide base in *A. mexicanus,* whereas in *A.* "*fasciatus*" it is longer with a narrow base. Infraorbital 3 in *A. mexicanus* is semicircular, in in *A.* "*fasciatus*" it is angular. Infraorbital 2 has a wide margin articulating with infraorbital 3 in *A. mexicanus,* whereas this margin is narrower in *A.* "*fasciatus.*"

Also, Mejía-Mojica & Díaz-Pardo (1991) described the posterior ceratohyal in *A.* "*fasciatus*" as having a foramen associated with a canal, whereas in *A. mexicanus* it may or may not be associated with a canal. The number of teeth cusps reported from the mandibular bones are different among the two species. All teeth are pentacuspid in *A.* "*fasciatus,*" whereas in *A. mexicanus* there are 3–4 cusps on teeth in the outer row, 3–6 cusps on teeth of the inner row of the premaxilla, 5–8 cusps on maxillary teeth, and 2–6 on dentary teeth. Finally, the number of gill rakers varies among the two species: in *A. mexicanus* 11 gill rakers are present on the first arch, whereas in *A.* "*fasciatus*" there are 13. The latter count is similar to that of *A. aeneus,* which has 12–14 gill rakers (Schmitter-Soto 1997).

Mejía-Mojica & Díaz-Pardo (1991) described as unique for *A.* "*fasciatus*" the presence of a small plate with teeth on the third suspensory pharyngeal; however, it is not exclusive to this species. We found this plate in almost all populations of *A. mexicanus* studied. Here we provide the first report of teeth on the second suspensory pharyngeal for *A. mexicanus.*

Most other osteological elements of *A. mexicanus* are very similar to those described for *Astyanax* "*fasciatus*" and are not discussed further. In general, osteology of *A.* "*fasciatus*" of Mejía-Mojica and Díaz-Pardo (1991) resembles that of other southern forms previously described by Valdéz-Moreno (1997), e.g., infraorbital 2 with a short base, infraorbital 3 with a dorso-posterior projection and angulate shape, and supraoccipital long (in dorsal view) with a narrow base. Southern forms studied by Valdéz-Moreno (1997) appear to be *A. aeneus,* based on the work of Lozano and Contreras (1991).

The main osteological difference found between the skull of *A. mexicanus* and *Brycon meeki,* a well-described "representative of characid osteology" (Weitzman 1962), is the presence of supraorbital bones in the latter. The possible significance of the presence or absence of the supraorbital in characid fishes was discussed by Weitzman & Malabarba (1998). The shapes of the infraorbitals, antorbital, quadrate and anguloarticular are different in *A. mexicanus* and *B. meeki.* The rhinosphenoid is larger in *B.*

meeki than in *A. mexicanus*. There are three rows of teeth on the premaxilla in *B. meeki*, two in *A. mexicanus*. There are 13–15 teeth on the maxilla is 13 to 15 in *B. meeki*, one or two in *A. mexicanus*. The pterotic process and sphenotic are longer in *B. meeki* than in *A. mexicanus*. The distribution of teeth on the superior pharyngeal (in five rows in *B. meeki*) is not the same in *Astyanax* (irregular). The canals of the accoustico lateralis system in *A. mexicanus* are similar to those of *Brycon meeki*, except the anterior portion of the canal in the frontal bone in the former is wider. *B. meeki* has more anterior gill rakers (31 to 33) than *A. mexicanus* (18 to 21). Finally, *A. mexicanus* has teeth on suspensory pharyngeals 2 and 3 whereas *B. meeki* does not.

A comparison of *A. mexicanus* with other tetragonopterinae, like *Paracheirodon axelrodi* (Schulz, 1956), reveals even more differences: *P. axelrodi* lacks infraorbitals 4, 5 and 6, and major structural differences are evident in infraorbitals 1 and 2, the pterotic, opercle, hyomandibular, sphenotic, rinosphenoid, and orbitosphenoid (Weitzman & Fink 1983).

The figures of the posterior region of skull and pectoral girdle of female *Astyanax mexicanus*, that appeared with no explanations in Weitzman & Fink (1983), are consistent with our observations.

The presence of two rows of teeth on the premaxillae in our specimens agrees with previous reports for the genus by Eigenmann (1921), Géry (1977) and Mejía-Mojica & Díaz-Pardo (1991). We found the number of maxillary teeth to be only one or two; this agrees with data of Eigenmann (1921), Géry (1977) and Mejía-Mojica & Díaz-Pardo (1991) and is within the range (zero to three) given by Contreras & Rivera (1985) for Mexican forms. The last authors followed Gery (1977) in reporting up to seven maxillary teeth for Central American forms. None of the above citations referred specifically to *A. mexicanus*. Alvarez del Villar (1970) considered the maxillary teeth smooth ("no aserrados", sic), and Contreras-Balderas & Rivera (1985) reported teeth tricuspidate for the genus *Astyanax*; we found these teeth with five to eight cusps in *A. mexicanus*.

The number of dentary teeth in our specimens is the same as that reported by Géry (1977). Alvarez (1970) and Mejía & Díaz-Pardo (1991) mentioned that dentary teeth are pentacuspid in *Astyanax*, whereas Contreras & Rivera (1985) indicated that they are tricuspid for the genus. Apparently, number of cusps is variable in this genus, and may be subject to abrasion, so this character should be considered with caution.

Malformations in the premaxillae (Fig. 12) and the fourth infraorbitals (Fig. 5) were detected in two specimens from Río Salado and Río Alamo. Cailliet et al. (1986) described deformations on the jaws and head of other species of fish, related to heredity and/or enviromental factors. However, this is the first time that malformations are reported for *Astyanax*, and the causes were not addressed in this study.

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Literature Cited

Álvarez del Villar, J. 1970. Peces Mexicanos (claves). Secretaría de Industria y Comercio, México, 166 pp.

Bănărescu, P. 1990. Zoogeography of fresh waters. AULA, Verlag Wiesbaden, Germany, 541 pp.

Bocourt, F.M. 1868. Note sur les poissons du genre Tetragonoptére provenant du Mexique et du Guatemala-5 Ser. Sci. Nat. Zool., 9:62.

Buckup, P.A. 1998. Relationships of the Characidiinae and phylogeny of characiform fishes (Teleostei: Ostariophysi). Pp. 123–144 *in* L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena & C. A. S. Lucena, eds., Phylogeny and classification of neotropical fishes. Porto Alegre, Brazil.

Cailliet, G. M., M. S. Love, & A. W. Ebeling. 1986. Fishes: a field and laboratory manual on their structure, identification and natural history. Wadsworth Publishing Company, Belmont, California, 194 pp.

Contreras-Balderas, S., & M. L. Lozano-Vilano. 1998. Problemas nomenclaturales de las formas mexicanas del género *Astyanax* (Pisces: Characidae).—Zoología Informa 38:1–13.

———, & R. Rivera-Teillery. 1985. *Bramocharax (Catemaco) caballeroi* subgen. et. sp. nv., del Lago de Catemaco, Veracruz, México.—Publicaciones Biológicas del Instituto de Investigaciónes Científicas UANL 2(1):7–29.

Eigenmann, H. C. 1921. The American Characidae, part 3.—Memoirs of the Museum of Comparative Zoology 43:209–310.

Espinosa Pérez, H., M. T. Gaspar Dillanes., & P. Fuentes Mata. 1993. Listados faunísticos de México. III. Los peces dulceacuícolas mexicanos. Instituto de Biología, UNAM, México, D.F., 99 pp.

Filippi, F. 1853. Nouvelles espèces de poissons.—Revue Magazine Zoologie 5:164–171

Fink, S. V., and W. L. Fink. 1981. Interrelationships of the ostariophysan fishes (Teleostei).—Zoological Journal of the Linnean Society 72:297–353.

Géry, J.R. 1977. Characoids of the world. Tropical Fish Hobbyst Publications, Neptune City, 672 pp.

Hollister, G. 1934. Clearing and dyeing fish for bone study.—Zoologica 12(10):89–101.

Langeani, F. 1998. Phylogenetic study of the Hemiodontidae (Ostariophysi: Characiformes). Pp. 145–160 *in* L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena and C. A. S. Lucena, eds., Phylogeny and classification of neotropical fishes. Porto Alegre, Brazil.

Lozano-Vilano. M. L., & S. Contreras-Balderas. 1990. *Astyanax armandoi,* n. sp. from Chiapas, México (Pisces, Ostariophysi: Characidae) with a comparison to the nominal species *A. aeneus* and *A. mexicanus.*—Universidad y Ciencia 7(14):95–107.

Mejía-Mojica. H., & E. Díaz-Pardo. 1991. Descripción del cráneo de *Astyanax "fasciatus"* (Pisces: Characidae).—Anales Escuela Nacional de Ciencias Biológicas 34:191–214.

Malabarba, R. L. 1998. Monophyly of the Chaerodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193–234 *in* L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena and C. A. S. Lucena, eds., Phylogeny and classification of neotropical fishes. Porto Alegre, Brazil.

Menezes, A. N. 1969. Systematics and evolution of the tribe *Acestrorhynchini* (Pisces: Characidae).—Arquivos de Zoologia 18:1–150.

Miller, R. R. 1978. Composition and derivation of the native fish fauna of the Chihuahuan desert region.—Transactions of the Biological Research Chihuahuan Desert Region 4:773–802.

Obregón-Barbosa, H., S. Contreras-Balderas, & M. L. Lozano-Vilano. 1994. The fishes of Northern and Central Veracruz, México.—Hydrobiologia 286:79–95.

Paulo-Maya, J. 1994. Análisis morfométrico del género *Astyanax* (Pisces: Characidae) en México. Unpublished M. S. thesis, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, México, 107 pp.

Schmitter-Soto, J. J. 1998. Diagnosis of *Astyanax altior* (Characidae), with a morphometric analysis of *Astyanax* in the Yucatan Peninsula.—Ichthyological Exploration of Freshwaters 8(4):349–358.

Schulz, L. P. 1956. The amazing new fish called the scarlet characin.—New Jersey, Tropical Fish Hobbyst 4(4):41–43.

Schuppa, M. 1984. Morphometrische und meristische Untersuchungen an verschiedenen *Astyanax*—populationen (Characidae) Mexikos. Unpublished thesis, Universität Hamburg, Germany, 94 pp.

Valdéz-Moreno, M. E. 1997. Estudio comparativo osteológico del género *Astyanax* en diversas cuencas de México. Unpublished M.S. thesis, Universidad Nacional Autónoma de México, 139 pp.

Vari, R. P. 1983. Phylogenetic relationships of the families Curimatidae, Prochilodontidae, Anostomidae and Chilodontidae (Pisces: Characiformes).—Smithsonian Contributions to Zoology 378:1–61.

———. 1989a. A phylogenetic study of the Neotropical Characiform family *Curimatidae* (Pisces: Characiformes).—Smithsonian Contributions to Zoology 471:1–71.

———. 1989b. Systematics of the Neotropical Characiform genus *Pseudocurimata* Fernández-Yépez (Pisces: Ostariophysi).—Smithsonian Contributions to Zoology 490:1–71.

———. 1995. The neotropical fish family Ctenoluciidae (Teleostei: Ostariophysi: Characiformes): Supra and Intrafamilial phylogenetic relationships, with a revisionary study).—Smithsonian Contributions to Zoology 564:1–90.

———, & A. S. Harold. 1998. The genus *Creagrutus* (Teleostei: Characiformes: Characidae): Monophyly, relationships, and undetected diversity. Phylogeny and classification of neotropical fishes. Pp. 245–260 *in* L. R. Malabarba, R. E. Reis,

R. P. Vari, Z. M. S. Lucena and C. A. S. Lucena, eds., Phylogeny and classification of neotropical fishes. Porto Alegre, Brazil.

Weitzman, S. H. 1962. The osteology of *Brycon meeki*, a generalized characid fish, with an osteological definition of the family.—Stanford Ichthyological Bulletin 8(1):1–77.

———, & W. L. Fink. 1983. Relationships of the neon tetras, a group of South American freshwater fishes (Teleostei, Characidae), with comments on the phylogeny of the New Word characiforms.—Bulletin Museum of Comparative Zoology 150(6):339–395.

———, & S. V. Fink. 1985. Xenurobryconin phylogeny and putative pheromone pumps in Glandulocaudine fishes (Teleostei: Characidae).—Smithsonian Contributions to Zoology 421:1–121.

———, & L. R. Malabarba. 1998. Perspectives about the phylogeny and classification of the Characidae (Teleostei: Characiformes). Pp. 161–170 *in* L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena and C. A. S. Lucena, eds., Phylogeny and classification of neotropical fishes. Porto Alegre, Brazil.

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Geographic variation in *Poecilia* Bloch and Schneider, 1801 (Teleostei: Poeciliidae), with descriptions of three new species and designation of lectotypes for *P. dovii* Günther, 1866 and for *P. vandepolli* van Lidth de Jeude, 1887

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Abstract.—The South American cyprinodontiform fish species with the vernacular name "mollies" are analyzed and three new species of the genus *Poecilia* are described and figured, viz., *P. boesemani,* n. sp. from Port of Spain, Trinidad, *P. koperi,* n. sp. from coastal areas of Venezuela and Colombia, and *P. wandae,* n. sp. from the Zulia district, Venezuela, west of Lake Maracaibo. Thirteen species of *Poecilia* are presently recognized from the northeastern part of South America and adjacent islands, viz., six mollies (including *P. vivipara* and *P. caucana*), five micropoeciliids, *P. heterandria* and the guppy (*P. reticulata*). Two different populations in both *P. koperi* and *P. wandae* are recognized, based on variation in pigmentation. From the type series of *P. dovii* Günther, 1866 and *P. vandepolli* Van Lidth de Jeude, 1887 lectotypes are selected. Four subspecies of *P. gillii* are recognized as morphologically and geographically distinct populations.

Poecilia reticulata, P. heterandria, P. bifurca, P. parae, P. picta, P. branneri and *P. minima* are not considered herein, whereas *P. laurae* remains a species inquirendae. A geocline in characters of the species of *Poecilia* is recorded and an evolutionary scenario is discussed.

This paper seeks to extend our biogeographic knowledge of the genus *Poecilia* Bloch & Schneider, 1801 and describes three new species from the southern end of the range of this genus. The present study records seven species from the northeastern part of South America. Whereas the number of poeciliid species constitutes a dominant part of the Central American fish fauna, this is not the case in South America. Miller (1983) constructed a key and checklist for the Mexican species, but there are no comprehensive lists for the species of *Poecilia* from Central and South America. Specimens of the species herein described as new, viz., *P. koperi, P. boesemani* and *P. wandae,* were previously identified as either *P. vivipara* Bloch & Schneider, 1801; *P. sphenops* Valenciennes, 1846 (Regan 1913: 1013; Price 1955:18; Boeseman 1960:122); *P. vandepolli* van Lidth de Jeude, 1887 (de Beaufort 1940:111; Schultz 1949:84, 97–99; Feltkamp and Kristensen 1969); or mentioned as 'unidentified species' (Rosen & Bailey 1963:48).

Regan (1906–08) examined variation within the species of *Poecilia* and extended our knowledge of the expression of morphology and pigmentation (Regan 1906–08, fig. 13), as well as the geographic range (from northern Mexico to the Leeward Islands) of the *P. sphenops* complex.

With the discovery of the structures of the gonopodial tip as a taxonomic tool (Eigenmann 1907), Regan (1913) reorganized species groups in the subfamily Poeciliinae.

With respect to the *P. sphenops* complex, he allocated *P. sphenops* to the genus *Mollienesia* on the basis of identical gonopodia of *M. latipinna* and *M. sphenops.* Moreover, the number of dorsal fin rays of *M. formosa* was intermediate between the numbers found in *M. latipinna* and *M. sphenops,* which therefore rendered the character invalid. Although Regan did not mention *P. vandepolli,* the geographic range of his *M. sphenops* still included the Leeward Islands, i.e., the Lesser Antilles.

The importance of the gonopodial tip was also recognized by Hubbs (1924), who used the gonopodium as "the chief distinctive feature of the Poeciliidae (as here delimited)." The *M. sphenops* group was defined by Hubbs (1926) as "the multitude of races allied to, or inseparable from *M. sphenops.*" This group was separated from *M. latipinna* and allies by the number of dorsal fin rays. For *M. sphenops,* Hubbs was "unable to delimit, in either distribution or in characters, any multitude of elementary species making up the *sphenops* complex of Middle America. The problem of determining the relationships of the diverse types, many of which have received specific names, is in prospect a most fascinating study."

The situation remained promising, even after the revision of Rosen and Bailey (1963), who listed a total of 35 nominal species in their synonymy of *P. sphenops.* Schultz and Miller (1971) mentioned: ". . . a thorough study of the whole complex and the type specimens will be required before systematic units and the nomenclature can be convincingly coordinated." Species recognition was aided by dental analyses (Schultz and Miller 1971), i.e., unicuspid and tricuspid species were recognized. Other alpha-taxonomic features (meristic and morphologic characters, body and fin color, even allozyme data) remained confusing. Rivas (1978) remarked that "proportional body measurements are [to be] omitted . . . , there is considerable variation in characters individually, ontogenetically, seasonally, geographically, and environmentally and, therefore, they are of little or no value in distinguishing species (except in relative fin position)." Extensive and detailed investigations (Schultz and Miller 1971, Menzel and Darnell 1973, Miller 1975) resulted in a checklist for the Central American mollies (Miller 1983), which included eight species of Central American short-finned mollies. No species were mentioned from outside this range. Comparisons of the Mexican species to those of Central and South America (Poeser 1992, 1995, 1998) have led to the present study.

Methods

Some 17 lots of *Poecilia vandepolli,* including the type series of *P. vandepolli vandepolli* and *P. v. arubensis,* have been reexamined. From the type series, a lectotype is selected. Meristic data and inner jaw dentition (cf. Schultz and Miller 1971) received special attention. Vernier calipers were used to record distances to 0.1 mm. The average of the measurements and counts are given and compared to a similar study of Feltkamp and Kristensen (1969) and to the data of *P. vivipara* and of *P. gillii.*

In the description of the new species, proportional morphometric values (Table 2) are recorded in thousandths of the standard length (SL), following Miller (1975). The small size of *P. wandae* made measurements difficult to impossible and therefore some were omitted. Meristic characters follow Hubbs and Lagler (1947). In the type series of *P. wandae,* all specimens have damaged caudal fins; therefore, the caudal fin ray count is estimated. Terms concerning the shape of inner jaw dentition follow Garman (1895). Melanophore pigmentation of preserved specimens and gonopodial structures are also recorded (Figs. 1 to 4).

The combined data are used to evaluate relationships between the newly described species. A key to the species is provided in Appendix 1.

The following abbreviations are used in the species diagnosis provided below.

A = anal fin rays
BS = scales around the body
CPD = least depth of the caudal peduncle
CPS = scales around the caudal peduncle
D = number of dorsal fin rays
G = gonopodial ray
LLS = lateral scales
P = pelvic fin rays
PL = predorsal length
PS = predorsal scales
SL = standard length

Systematics

The genus *Poecilia* is diagnosed by the shape of gonopodial ray 4p, which has six to fourteen unserrated distal segments, followed by dorsally serrated subdistal segments (cf. Miller 1975). The genus consists of several ill-defined subgenera. A more detailed analysis is in progress.

In the subgenus *Poecilia,* ventral spine-like serrae are present on the third gonopodial ray. Gonopodial rays 4a and 4p are very similar, as are rays 5a and 5p. The *P. sphenops* species group has terminal segments of gonopodial ray 4a and of gonopodial ray 4p close to each other, giving the gonopodium a sharp appearance. The members of this species group are moderately sized to large, with nuptial specimens usually larger than 35 mm SL. The members of the *P. caucana* species group are defined by the relative thickness of gonopodial ray 4p versus 4a. The tips of these rays are split, making the gonopodium blunt. Nuptial specimens are less than 35 mm SL.

Poecilia vivipara Bloch & Schneider, 1801

Poecilia vivipara Bloch & Schneider, 1801: 452, pl. 86, Fig. 2 (type locality: Surinam).

Poecilia surinamensis Humboldt & Valenciennes, 1821:158 (type locality: Surinam, French Guyana, Brazil).

Poecilia unimaculata Humboldt & Valenciennes, 1821:158 (type locality: Brazil, Rio de Janeiro).

Poecilia schneideri Humboldt & Valenciennes, 1821:159 (type locality: Surinam).

Neopoecilia holacanthus Hubbs, 1924:11 (type locality: Puerto Rico, introduced).

Material.—West Indian Antilles: ZMA 120.384 (22), St. Lucia, freshwater pool, ±1 km west from Fort Vieux, coll. J. H. Stock, 20-II-1974.

Guyana: BMNH 1974. 10. 10. 527–619 (7 out 93), Georgetown, Seawall trench, no date; CAS 59364 (12), Georgetown trenches, C. H. Eigenmann 1908; CAS (SU) 21784 (2), same data as CAS 59364; USNM 66278 (2), same data as CAS 59364; ZMA 100.629 (2), same data as CAS 59364; ZMA 119.912 (3), East Coast Demerara, Turkeyen, drainage canal, coll. M. Tamessar, 28-I-1987; ZMA 119.913 (6), East Coast Demerara, Bel Air, stagnant ditch, coll. M. Tamessar, 28-I-1987; ZMA 119.917 (4), East Coast Demerara, Industry, shallow pool, coll. M. Tamessar, 28-I-1987; ZMA 121.005 (5), Guyana, coll. F. Vermeulen, no date; ZMA 121.007 (15), Guyana, coll. F. Vermeulen, 1992; ZMA 121.009 (5), Guyana, coll. F. Vermeulen, 1992.

Surinam: MNHN B. 932 (5 syntypes of *P. surinamensis*), Surinam River, Levaillant, no date; MNHN 4391 (48 syntypes of *P. surinamensis*), Cayenne, Rousseau, no date; MNHN B. 918 (60), without exact locality, Duvernoy, no date; RMNH 18516 (2), Surinam, coll. J. Th. Noordijk, August 1887; ZMA 105.332 (2), Paramaribo-west, garden canals, coll. H. Nijssen, 12-XII-1966; ZMA 106.757 (16), Marowijne River, coastal plain on Tijgerbank, west of mouth, coll. H. Nijssen, 1-IV-1966; ZMA 115.118 (45), Surinam district, Lagoon 7 & 8, 05°59′N, 54°49′W, coll. M. P. Panday, 22-IV-1974; ZMA 115.121 (20), same data as ZMA 115.118; ZMA 119.908 (6), Surinam River, pool near beach at Braamspunt, coll. I. Kristensen, 14-III-1960; ZMA 121.000 (4), Paramaribo, Mason Street, polluted trench, coll. F. Vermeulen & W. Suyker, 24-III-1991.

French Guiana: USNM 121833 (9), Cayenne, Carriera Guila, S. F. Yolles 1945; USNM 121834 (2), Cayenne, Pont Magie, S. F. Yolles 1945; USNM 121835 (9), Cayenne, Ruisseau de l'institute-eau douce, S. F. Yolles 1945; USNM 149938 (4), Cayenne, S. F. Hildebrand 1945.

Brazil: RMNH 2724 (2 syntypes of *P. unimaculata*), Rio de Janeiro, coll. Delalande, no date; ZMA 100.628 (1), Brazil, coll. Moesch, 1884; ZMA 116.210 (14), Rio Grande do Norte, Rio Açu (Rio Assu), downstream of Macau, coll. R. Boddeke, 10-I-1979.

Diagnosis.—A = 8; D = 7; C = 16–18; LLS = 24–26; CPS = 16. *Poecilia vivipara* may have a midlateral spot or blotch in both sexes, a unique character in the subgenus. The gonopodium has no extruding hooks or spines, gonopodial ray 4a with serrae on dorsal surface.

Description.—Medium sized species, mature males smaller than 50 mm and females smaller than 60 mm. The body is truncate and displays dark stripes on the sides. The caudal and dorsal fins have black markings, with broad yellow margins. The caudal fin has black margins, at the base broader than at the terminal end. There is some variation in the presence or absence of the spot at the side of the body. No extensive records are available of the extent of this variation. In the populations in which it is present, the blotch is also prominent in young specimens. The gonopodium is figured in Miller (1975), the presence of dorsal serrae on ray 4a are unique within the subgenus.

Distribution.—*Poecilia vivipara* is found in coastal habitats from Venezuela to Argentina. It is also found on some islands of the Lesser Antilles.

Remarks.—Garman (1895) diagnosed this species and provided a list of synonyms. He also explained the obvious aberrant figure in the original description. Hubbs (1926) synonymized *Neopoecilia holocanthus*, correcting his misidentification.

Poecilia mexicana Steindachner, 1863

Poecilia mexicana Steindachner, 1863:178, pl. 4, fig. 1, 1a (type locality: Mexico, Orizaba).

Poecilia thermalis Steindachner, 1863:181, plate 4, fig. 3, 3a (type locality: Central America, warm springs).

?*Gambusia* (?) *modesta* Troschel, 1865:105 (type locality: Mexico).

?*Gambusia* (?) *plumbea* Troschel, 1865:106 (type locality: Mexico).

Poecilia chisoyensis Günther, 1866:342 (type locality: River Chisoy, Vera Paz).

Poecilia dovii Günther, 1866:344 (in part; type locality: Mexico; lectotype is *P. gillii*).

Poecilia limantouri Jordan & Snyder, 1900: 116–117, 129–131 (type locality: Tampica, Tamaulipas, Mexico).

Mollienesia sphenops vantynei Hubbs, 1935:11, plate 2, fig. 1 (type locality: Guatemala, Uaxactum, Rio Hondo).

Mollienesia sphenops macrura Hubbs, 1935:12, plate 2, figs. 2–3 (type locality: Guatemala, Rio San Pedro de Martir).

Mollienesia sphenops altissima Hubbs, 1936:239, plate 9, figs. 1–3 (type locality: Mexico, Yucatan Peninsula, Miramar Spring).

Mollienesia sphenops melanistia Hubbs, 1937 (type locality: Mexico, Tamaulipas, Arroyo Marmoleyo).

Material.—Barbados: BMNH 1970.1.29: 1 (1) Barbados, coll. R. Heath, no date; RMNH 24814 (55), rivulet near Three Mills (13°10'N, 59°27'W), coll. I. Kristensen, 13.6.1961; RMNH 24804 (6), rivulet at Three Mills (13°10'N, 59°27'W), coll. I. Kristensen, 13.6.1961; RMNH 24809 (5), rivulet near Three Mills (13°10'N, 59°27'W), coll. I. Kristensen, 13.6.1961.

Diagnosis.—A = 9; D = 9–10; C = 18–22; LLS = 26–27; CPS = 18.

Description.—*Poecilia mexicana* is rather variable in its morphology. This is a truncate, torpedo shaped species in northern Mexico but ranges to high, laterally flattened specimens at the eastern end of the range in the Yucatan Peninsula. While the northern populations possess deeply blue pigmented bodies, alpha-males of the Yucatan populations have a more copper-red body. The fin pigmentation is also varying, from totally black at the base of the fin with an orange outer area (in northern populations) to a black and yellow reticulate pattern (on the Yucatan Peninsula). Between these extremes clinal variation is noted.

In the Barbados material, both males and females exhibit considerable variation in their pigmentation, especially the specimens in RMNH 24804 have many spots on their body (perhaps a basis for why they were separated from the other lots). Females have nine anal fin rays, some females have 10 dorsal fin rays. The membranous hook on gonopodial ray 3 is extremely small, without a bony spine. Several specimens have 20 caudal fin rays, whereas all specimens have 18 scales around the caudal peduncle.

The diagnostic features of *P. mexicana* generally most closely agree with the nominal subspecies *P. gillii gillii* (see below), with the exception of the number of scales around the caudal peduncle (18 versus 16 in *P. gillii*).

Distribution.—*Poecilia mexicana* occurs on the Atlantic coast of Central America, from the Texas border, through Yucatan into Guatemala and Costa Rica. The population found on Barbados is probably derived from escaped aquarium specimens, which is confirmed by their abnormal variability in body pigmentation.

Poecilia gillii
(Kner & Steindachner, 1864)

Xiphophorus Gillii Kner and Steindachner, 1864: in Kner & Steindachner, 1865:25 (type locality: Panama, Rio Chagres); *Poecilia gillii*; Günther, 1868:395; *Poecilia sphenops gillii*; Hubbs, 1953:145.

Poecilia mexicana [non Valenciennes, 1863]; Poeser, 1992:86 (misidentification).

Poecilia thermalis [non Steindachner, 1863] Günther, 1866:341 (type locality: San Salvador, warm springs).

Poecilia dovii Günther, 1866:344 (in part: type locality: Lake of Nicaragua).

Platypoecilus mentalis Gill, 1876:335 (type locality: Isthmus of Panama).

Poecilia Boucardi Steindachner, 1876:386 (type locality: Colon, Panama).

Poecilia cuneata Garman, 1895:179, plate V (type locality: Colombia, Gulf of Uraba, Turbo); *Poecilia sphenops cuneata*; Hubbs, 1926b:77.

Poecilia salvatoris Regan, 1907:65, plate 14, figs. 2–3 (replacement name for *P. thermalis* Günther, 1866).

Platypoecilus tropicus Meek, 1907:146 (type locality: Costa Rica, Turrialba).

Poecilia tenuis Meek, 1907:147 (type locality: Costa Rica, Tiribi).

Poecilia caudata Meek, 1909:209–210 (type locality: Costa Rica, Turrubares).

Poecilia spilonota Regan, 1908:460 (type locality: San José, Costa Rica).

Lembesseia parvianalis Fowler, 1949:267–269 (type locality: Africa, Congo system, Oka).

Mollienesia sphenops petersi Schindler, 1956:1–4, fig. 1 (type locality: Honduras, lake Yojoa).

Material.—Nicaragua: Lectotype of *P. dovii* (BMNH 1863.12.16.77, Lake of Nicaragua, coll. captain J. W. Dow, no date). 5 Paralectotypes of *P. dovii,* (BMNH 1863.12.16.78-92, same data as BMNH 1863.12.16.77).

Costa Rica: 4 Syntypes of *P. spilonota* (BMNH 1907.2.11.44-50, San José, coll. P. Bidley, no date).

Panama: NWM 21608 (1 syntype of *Xiphophorus Gillii*), Rio Chagres, Panama, no further data. MCZ 29433 (10), 1 mile south of Panama City, coll. USFC Steamer Albatross (Alex. Agassiz), 23-X-1904; MCZ 33847 (10), ca. 9°43′N, 79°43′W, between Gorgona and Matachin, collected before 1930; MCZ 54068 (10), small tributary of main stream on left about 0.75 km upriver of bridge, Bayano drainage, probably Rio Canita, Panama, coll. W. L. Fink & K. E. Hartel, 1-IV-1978; USNM 050368 (14), Panama, coll. C. H. Gilbert; USNM 64764 (17), Folks R. Swamp, Cristobal, coll. A. H. Jenning, 4-VIII-1909; USNM 65618 (15), 1 mile south of Panama city, coll. Str. Albatross, 23 X-1904; USNM 78837 (27), Upper Trinidad, coll. Meek & Hildebrand, 7-III-1911; USNM 247529, (24) canals in banana field, Bocas Province, California, coll. Loftin, 2-IX-1962; USNM 247531, (44) Rio Gaurumo, Bocas Province, coll. Loftin, 18-IV-1963; USNM 247432 (10 of 50), Canal zone, behind Fort Clayton, residential area, coll. Loftin & Tyson, 19-IV-1962; USNM 247436, (6) Bocas del Toro, Esendo de Verequas island, coll. J. Legler, 14-V-1962; USNM 247548, (35) San Blas, small river opposite to Mulatupo island, coll. Loftin & Evermann, 2-XII-1962; USNM 247550, (18) San Blas, Rio Acla, coll. Loftin, 16-XII-1962; USNM 293473, (10 of 51) 9°14′N, 78°58′W, Rio Tearbles, Bayano drainage, Panama province, coll. W. C. Sternes et al., 25-II-1985; USNM 293476, (23) 9°28′N, 79°3′W, Comarca Kuna Yala, Rio Mandinga, coll. W. C. Sternes et al., 5-III-1985; USNM 293494 (42), Panama province, Rio Frijoles, above pipeline rd., N. of Gamboa (Rio Chagres drainage, Atlantic side), coll. W. C. Sternes et al., 26-II-1985.

Colombia: 2 Syntypes of *P. cuneata* (MCZ 6458, Turbo, Gulf of Uraba, Colombia, coll. T. Barbour, no date); 3 Syntypes of *P. cuneata* (USNM 120285, same data as MCZ 6458); 5 Syntypes of *P. Boucardi* (MCZ 32959, San Pablo (Aspinwall (Colon), Quebrada San Pablo), coll. Hassler Expedition (Steindachner & Mr. Boucard), VII-1872); BMNH 99.3.15.27-29 (3), Monkey Hill, Colon, coll. Dr. H. Festa, no date.

Additional material from Nicaragua and Panama in Poeser (1992), from El Salvador in Poeser (1995).

Diagnosis.—A = 9; D = 9–10; CPS = 16; LLS = 26–29. In his checklist, Miller (1983) was uncertain if *P. gillii* was different from *P. mexicana*. Therefore, I have included a discussion of this species in the remarks section.

Description.—This species is very similar to *P. mexicana*, with the exception of the number of scales around the caudal peduncle. In *P. mexicana*, 18 scales around the caudal peduncle are common.

Remarks.—All examined type material is consistent with the above meristic data. Over its extensive range, *P. gillii* shows considerable variation in body shape and in dorsal fin color, and moderate variation gonopodial features. These variations appear to reflect intraspecific diversification, justifying taxonomic separation, i.e., division in subspecies. Carr & Giovannoli (1950:17–18) reported the live colors of *P. gillii* and the sympatric *P. marcellinoi* Poeser, 1995 from Honduras: "One male with yellow spots, a black blotch at the caudal base and spotted dorsal and caudal fin, and one female with black spotted sides (=*P. marcellinoi*). One female with yellow spotted sides, and a male with golden-orange blotches, with a black blotch on the dorsal base and rest of fin orange (=*P. gillii*)."

Poecilia gillii salvatoris is reported from El Salvador, where males from most populations are reported to have red dorsal fins (Hildebrand 1925). This prompted Miller (1994) to redescribe *P. salvatoris* Regan, 1907, although all other characters are as found in the present study for *P. gillii*. Poeser (1995) in his redescription of *Poecilia salvatoris* agreed with the diagnosis of *P. salvatoris* by Regan (1908), with the exception of the number of anal fin rays. Regan (1908:104) mentioned 8–9 anal fin rays; however, examination of 14 of his syntypes did not yield any specimen with eight anal fin rays, so Regan's account is judged erroneous. In the preserved material, no trace of red was found in the dorsal fins. The red finned western Central American populations are here considered as a subspecies, viz., *P. gillii salvatoris.*

Villa (1982) provided a key to the genus *Poecilia* in Nicaragua, in which he recognized three species, viz., *P. gillii, P. sphenops*, and "an undescribed species with unicuspid teeth". He mentioned (p. 134, translated from Spanish):

P. gillii: "Unicuspid inner teeth, incomplete supraorbital system, preorbital pores free, 26–28 (modally 27) lateral scales, 16 scales around caudal peduncle, 28–30 (modally 30) vertebrae. Guatemala, El Salvador, to Panama".

P. spec.: "Unicuspid inner teeth, complete supraorbital system, free preorbital pores, 28–30 (modally 29) lateral scales, 18 scales around caudal peduncle, 28–30 (modally 30) vertebrae. Rio Ulya (Honduras), Lagunas Apoyeque and Xiloa, lake Managua and Nicaragua, and Rio Sapoa & Frio, Tilaran region, Costa Rica".

P. sphenops: "Tricuspid inner teeth, incomplete supraorbital pores, preorbital pores covered, 26–28 (modally 27) lateral scales, 16–18 scales around caudal peduncle, 28–30 (modally 29) vertebrae. Guatemala and El Salvador, Atlantic side of Honduras, Nicaragua including the Great Lakes".

Villa's diagnosis of *P. sphenops* fits the description of *P. marcellinoi* (tricuspid inner teeth, 16 scales around the caudal peduncle). While his description of *P. gillii* is accurate, his figure of *P. gillii* shows 9 transverse scales on the caudal peduncle, which is a diagnostic character of *P. mexicana*. I suspect the figures were switched. His undescribed species might very well be *P. mexicana*. The apparently aberrant number of lateral scales (also mentioned by Bussing [1987]) is explained by character displacement (cf. Poeser 1995). The only synonym of *P. sphenops* in Rosen & Bailey (1963) from Nicaragua is *P. dovii* Günther, 1866. *Poecilia dovii* was considered synonymous with *P. sphenops* by Regan (1908). Since the type material of *P. dovii* contained specimens from *P. mexicana* (with 18 scales around the caudal peduncle), as well as from *P. gillii* (with 16 scales around the caudal peduncle), it is only partially alluded to the synonymy of *P. gillii.* In honor of captain J. W. Dow, the lectotype is selected from the lot he collected himself in Nicaragua, which is *P. gillii.* Günther (1866) mentioned that *P. dovii* occurred only in Guatemala and Mexico. However, since the type locality includes Nicaragua, this country should be included in the range of distribution. The specimens from Lake Amatitlàn (BMNH 1865.6.10.13-15) are not registered in the British Museum as syntypes, and these were not studied. The specific status of these types remains to be determined.

Poecilia gillii appears to be nearly the only species of *Poecilia* present in Costa Rica. Meek (1914:116–117) placed all Costa Rican taxa in synonymy with *Platypoecilus tropicus* (=*P. gillii*) as follows: "The inland or fresh-water forms of this species or variety found in Costa Rica are very variable, and as a result several species have from time to time described. . . . The females and many males of these inland forms usually have a black spot at the base of the middle dorsal rays, ... On many specimens from salt and brackish water some of the scales have a dark spot which forms lines along the rows of scales. . . . On many of the males, especially from larger streams, the basal half of the caudal is black, or with black blotches; on some of these the basal half of the dorsal is also black." Specimens with a black basal half of the caudal fin, formerly described as *P. caudata* Meek, 1909, are herein recognized as a subspecies, viz., *P. gillii caudata.*

Bussing (1987) identified most of the Costa Rican populations as *P. gillii.* He gave the following description (translated from Spanish): "Body with yellow spots, in some females these spots are black. Scales in a lateral series 26–28, mostly 27. Three orbital pores in one line. In the males sometimes a large dorsal fin, with black spots or blotches at the base. Caudal fin with spots, blotches or solid black pigmentation. Some males with orange in their caudal fin. Other fins yellow, head and body bluish. Note: some males have a red dorsal. Large species, up to 105 mm." Males possessing a red dorsal fin are *P. gillii salvatoris.* Bussing also recorded *P. mexicana,* in a much lower frequency, i.e., three populations from over fifty in total, widely apart from each other (Bussing 1987:144, map 20). His diagnosis for this species is: "Very much like *P. gillii.* Yellow spots on body, black in some females. 28–30 (modally 29) Lateral scales, and three orbital pores, forming a triangle. Dorsal and caudal spotted, rest of fins yellow. It is also a large species, up to 110 mm." Bussing (1987) illustrated *P. gillii* and *P. mexicana* in his paper, and his diagnoses of *P. gillii* and *P. mexicana* correspond with the account of Villa (1982) (see above). Surprisingly, Bussing did not record any populations of *P. marcellinoi.*

Hubbs (1926, 1953) considered *P. sphenops* in Panama either *P. sphenops cuneata* (cf. Hubbs 1926), or *P. s. gillii* (cf. Hubbs 1953). Examination by me of Panamanian populations confirms earlier findings of profound morphometric differences, as well as constant meristic data, in all Panamanian populations. A conspicuous reduction of the gonopodial spine on ray 5 is noted. In populations near the Costa Rican border (Bocas del Toro district of Panama) the spine is distinct. In populations near Colombia, i.e., the San Blas area, it is reduced or absent, as is found in *P. koperi* (Fig. 4a). This shift in character expression from west to east is not accompanied by meristic changes.

Although some populations contain poorly pigmented, slender specimens, other populations manifest heavily pigmented, stout specimens. Nevertheless, all specimens have nine anal fin rays, nine (or rarely ten in the San Blas district) dorsal fin rays, 16 scales around the caudal peduncle, 18 scales around the body, and 26 to 29 scales in a lateral series. The consistency of these counts suggests that all populations belong to the same species.

Because the missing spine is of taxonomic significance, this form was named *P. gillii cuneata* Garman, 1895. The populations of *P. gillii* from Panama examined in the present study are partly sympatric with *P. marcellinoi* like in El Salvador (Poeser 1995). Poeser (1992) reported a male with an aberrant gonopodium from Nicaragua (GCRL 6697), identified then as *P. mexicana mexicana.* Re-examination of my notes proved that the identification and locality was wrong. The sample containing this male was GCRL 8748, viz., *P. gillii cuneata* from Panama.

Rosen & Bailey (1963) considered *Lembesseia parvianalis* a synonym of *P. sphenops.* However, since *L. parvianalis* has unicuspid inner teeth, Miller (1983) placed it in the synonymy of either *P. mexicana* or *P. gillii.* Based on the original description, in which 8 transverse scales on the caudal peduncle are illustrated, I assign it to the synonymy of *P. gillii.* Fowler's (1949) record is important for its taxonomic value. The *P. sphenops* group, if raised to generic level, would become *Lembesseia* (with *L. surinamensis* (=*P. sphenops*) as type species).

Distribution.—Poecilia gillii is recorded from the Pacific coast of Guatemala to the Atlantic coast of Colombia. In northern regions, from Guatemala to Costa Rica, it is represented by the subspecies *P. gillii salvatoris.* The subspecies *P. gillii caudata* occurs in Costa Rica, whereas *P. gillii gillii* is present in Panama. The South American populations, as well as adjacent populations in Panama, are considered to be *P. gillii cuneata.* The type locality of *P. cuneata* was designated "Turbo, Gulf of Darien" (Garman 1895). Rosen and Bailey (1963) added 'Panama' to this locality. However, study of several maps did not confirm this addition. The nearest village with that name is near the Gulf of Uraba, an extension of, and sometimes also so-called, the Gulf of

Darien, in Colombia. I presume that this is the correct type locality.

Poecilia caucana (Steindachner, 1880)

Girardinus caucanus Steindachner, 1880: 87, plate 4, figs. 4, 5 (type locality: Colombia, Caceres); *Allopoecilia caucana* Hubbs, 1924:11.

Material.—Colombia: UMMZ 186317 (51), Depto. Cordoba, Tierra Alta, Rio Sinu, coll. W. Moberley & K. Adler, 1965.

Venezuela: UMMZ 186931 (54), Rio Monay, coll. F. F. Bond, 1938; UMMZ 186934 (24), Quebrada Goajira, F. F. Bond, 1938; UMMZ 186937 (44), Rio Bucares, coll. F. F. Bond, 1938; USNM 86264 (4), Valera, Trujillo, coll. H. Pitteir, 1923; USNM 121677 (33), Rio Motatan, 4 km above Motatan, coll. L. P. Schultz, 25-III-1942.

Panama: USNM 293444, (7), Rio Meteti, Darien Province, 40 km NNW of Yaviza, coll. W. C. Sterns et al., 24-II-1985; USNM 293574, (10), Rio Peresinico, Darien Province, coll. B. Chernoff, J. Lundberg, L. McDade, 23-II-1985.

Diagnosis.—A = 8; D = 7–8; C = 18–22; LLS = 26–27; CS = 16; CPS = 14. *Poecilia caucana* is a small to medium sized species, characterized by a black band in its dorsal fin. The gonopodium has ray 4p with broader rays than ray 4a.

Description.—This is one of the smaller species of the genus. The largest specimens examined are a female of 37.4 mm SL and a male of 27.2 mm SL. The dorsal fin has a black transverse band at the base. This fin is usually milky white or yellow, although also red fins are reported in aquarium literature. The other fins are unmarked.

The gonopodial characters figured in Rosen and Bailey (1963) are of considerable interest because gonopodial ray 4p is thicker than ray 4a. In addition, the hook on gonopodial ray 5 is weakly developed.

Distribution.—Atlantic slopes of Panama, Colombia and Venezuela.

Poecilia vandepolli van Lidth de Jeude, 1887

Poecilia Vandepolli van Lidth de Jeude, 1887:137, Pl. 2, Figs. 4 and 5 (type locality: Curaçao).

Poecilia Vandepolli arubensis van Lidth de Jeude, 1887:138, Pl. 2, Figs. 6–10 (type locality: Aruba).

Lectotype.—Curaçao: RMNH 5155, adult male, Curaçao, coll. Neervoort and v. d. Poll, no further data.

Paralectotypes.—RMNH 33843 (4), same data as RMNH 5155.

Material.—Aruba: RMNH 5156 (6 syntypes of *P. Vandepolli arubensis*), Aruba, coll. Neervoort and v. d. Poll, no further data. See also tables below, details in Poeser (1992).

Diagnosis.—A = 8–9; D = 7–8; C = 16; LLS = 26–27; CPS = 16. Several specimens have humeral blotches anterior to the position of the lateral side spot as occurs in *P. vivipara.* The gonopodium lacks extrusions on ray 3 and 5p.

Description.—*Poecilia vandepolli* is reported to have specimens with orange on the ventral side of the body, yellow specimens with blue sides and grayish brown specimens in the same population (Feltkamp and Kristensen 1969). Speckled specimens, allegedly only occurring in Venezuelan populations (Feltkamp and Kristensen 1969), also appear on Curaçao. The pigmentation at the base of the dorsal fin forms a blotch, in addition to dark spots. The body may have a humeral blotch, positioned more anteriorly than a similar such patch of color in *P. vivipara.* The females tend to be paler than males.

The gonopodium, figured in Poeser (1992), is like that of *P. vivipara,* with the exception of the serrae on ray 4a. When fully developed, a little membranous bulge is found on gonopodial ray 3, which covers extruding serrae.

Description of the types.—The lectotype is a mature male, 27.3 mm SL. It has 8 dorsal fin rays and 16 scales around the caudal peduncle. Several scales in the lateral series are missing on this specimen and the caudal fin is damaged, so no further meristic data can be given. Gonopodial ray 3 has a long terminal segment, the hood is short. An extremely short extrusion similar to a small hook is present. Gonopodial ray 4a is unmodified, ray 4p has eight unmodified distal segments followed by serrated segments. Gonopodial ray 5a is one segment longer than 5p. Subdistal ventral modifications occur on ray 5a. The largest female paralectotype, 47.5 mm SL, has about 25 scales in a lateral series (this number is not accurate because some scales are missing). It has nine dorsal fin rays and nine anal fin rays, the caudal fin is damaged.

The specimens in the type series from Aruba are much smaller. The largest male, 22.0 mm SL, has a gonopodium like the lectotype, with seven distal unmodified segments on gonopodial ray 4p and no trace of a hook on ray 3. It has 8 dorsal fin rays, 16 scales around the caudal peduncle, and about 24 scales in a lateral series (some scales are missing). The caudal fin is damaged. This male has a pigmented band proximally on the dorsal fin and a pigmented humeral blotch. The largest female (26.5 mm SL) has eight anal fin rays and nine dorsal fin rays. The caudal fin is damaged. Sixteen scales are found around the caudal peduncle and 27 in a lateral series.

To establish morphometric and meristic variations a detailed examination of 15 populations was carried out. Some 12 lots were examined from Aruba, and three lots from Curaçao (Table 1).

Distribution.—*Poecilia vandepolli* occurs naturally in all kinds of waters of the Netherlands West Indies (Aruba, Curaçao, and Bonaire). It is introduced on St. Maarten/St. Martin (Poeser 1992).

Poecilia koperi, new species
Fig. 1, Table 2

Poecilia vivipara (non Bloch & Schneider, 1801); De Beaufort, 1940:111.

Poecilia sphenops (non Valenciennes, 1846); Regan, 1913:1013 (in part).

Poecilia sphenops vandepolli (non Van Lidth de Jeude, 1887); Schultz, 1949:84, 97–99 (in part).

Poecilia sphenops cuneata (non Garman, 1895); Hubbs, 1926:77.

Holotype.—Adult male, UMMZ 223343, Venezuela, Rio Curipe at Higuerote, coll. F. F. Bond, 2-V-1938.

Allotype.—Adult female, UMMZ 223344, same data as UMMZ 223343.

Material.—BMNH 1909.2.25: 53-56 (5), Venezuela, coll. Arnold, no date; UMMZ 200738 (15 of 123), 2 km N of Ocumare, lagoon on flats near mouth of Rio Cumboto, coll. F. F. Bond, 5-I-1938; UMMZ 200740 (15 of 57), Rio Guaiguaza, 3 km W of Porto Cabello, 2 km from mouth of river, coll. F. F. Bond, 15-I-1938; UMMZ 200744 (12), Rio Sanchon, 5 km W of Tavorda, 10 km W of Porto Cabello, coll. F. F. Bond, 26-I-1938; UMMZ 200753 (15 of 430), Lagunita, 5 km W of Coro, Estado Falcon, coll. F. F. Bond, 19-III-1938: UMMZ 200755 (15 of 115), Falcon, Laguna del Rio Capatárida, at mouth, 5 km N of Capatárida, coll. F. F. Bond, 2-III-1938; UMMZ 200760, (15 of 152), Falcon, Coastal lagoons, 15 km N of Maracaibo, coll. F. F. Bond, 6-IV-1938; UMMZ 200761 (13 of 202), same data as UMMZ 223343; UMMZ 200762 (15 of 80), Estado de Miranda, Lagunita de Tacarigua, at Tacarigua, 85 km E of Caracas on the coast, near the boca, coll. F. F. Bond, 3-II-1939; UMMZ 200764 (28), Boca del Rio Cumboto, 2 km NW of Ocumare; ZMA 109.206 (6), La Goajira, Rio Calancala, San Antonio, coll. P. Wagenaar-Hummelinck, 17-I-1937; ZMA 119.909 (30), Paraguana Estangue de Moruy, coll. P. Wagenaar-Hummelinck, 18-II-1937; ZMA 119.910 (15), Paraguana, Estangue de Santa Ana, coll. P. Wagenaar-Hummelinck, 16-II-1937; ZMA 120.885 (4), 2 km N of Barcelona, Rio Guanta, coll. P. Wagenaar-Hummelinck, 1936.

Table 1.—Overview of standard lengths, proportional measurements and meristic data of *Poecilia vandepolli.*

<table>
<tr><th></th><th>SL</th><th>Pred</th><th>CPd</th><th>A</th><th>D</th><th>C</th><th>LLS</th><th>CPS</th></tr>
<tr><td colspan="9">Aruba</td></tr>
<tr><td colspan="9">ZMA 100.600. The fish were caught in a small freshwater stream, Rooi Prins at ‘Plantage Fontein’. The lot contains small specimens, of which the largest male (20.7 mm SL) has an unclear humeral spot. The gonopodium of this male is fully developed. The bodies are olive brown, without any additional pigmentation. Dorsal fin pigmentation lightly spotted, darker in males than in females. (Three additional small males are without a humeral blotch.) Eight females (22–31 mm SL), eight subadults and 30 juveniles complete this lot.</td></tr>
<tr><td>Males</td><td>19.4</td><td>575</td><td>175</td><td>—</td><td>8</td><td>16</td><td>25.5</td><td>15</td></tr>
<tr><td>Females</td><td>26.0</td><td>610</td><td>156</td><td>8.8</td><td>7.5</td><td>15.8</td><td>26.1</td><td>15.6</td></tr>
<tr><td colspan="9">ZMA 100.606. This lot was collected in a freshwater pool at ‘Plantage Fontein’. It contains medium sized specimens, largest males about 35 mm SL with a clear humeral blotch (at scale 5 of LLS) and a large dorsal fin that reaches the base of the caudal fin. The dorsal fin has a large anterior blotch at the base.
In this lot there is a total of six males with humeral blotch, all adults, of which two males do not possess a blotch, 14 females (30-48 mm SL), eight subadult and 30 juveniles.</td></tr>
<tr><td>Males</td><td>34.6</td><td>551</td><td>207</td><td>—</td><td>8.3</td><td>18</td><td>26.3</td><td>16</td></tr>
<tr><td>Females</td><td>43.3</td><td>613</td><td>173</td><td>9</td><td>8</td><td>16.4</td><td>26.5</td><td>16</td></tr>
<tr><td colspan="9">ZMA 100.607 is a sample from a small pool of freshwater at ‘Fontein Plantage’. Only one fully grown male (without blotch) is present, with one fully grown female. It further contains three subadults and five juveniles.</td></tr>
<tr><td>Male</td><td>33.6</td><td>533</td><td>162</td><td>—</td><td>8</td><td>17</td><td>25</td><td>16</td></tr>
<tr><td>Female</td><td>41.9</td><td>616</td><td>159</td><td>9</td><td>8</td><td>17</td><td>27</td><td>16</td></tr>
<tr><td colspan="9">ZMA 100.608, again from a small freshwater pool at ‘Fontein Plantage’. Two males in this sample have a blotch, viz., the largest and the smallest males. One male is without blotch. One large female is present, together with one small female. 12 Juveniles.</td></tr>
<tr><td>Males</td><td>30.9</td><td>581</td><td>200</td><td>—</td><td>8</td><td>17</td><td>26.3</td><td>16</td></tr>
<tr><td>Females</td><td>34.0</td><td>611</td><td>170</td><td>9</td><td>8</td><td>16</td><td>27</td><td>15</td></tr>
<tr><td colspan="9">ZMA 102.212. Pool at the well ‘Rooi Prins’. Males in this lot have faded humeral blotches. The largest males have the dorsal fins to caudal base, with an anterior blotch at the base.</td></tr>
<tr><td>Males</td><td>30.6</td><td>588</td><td>180</td><td>—</td><td>8</td><td>16</td><td>26</td><td>16</td></tr>
<tr><td>Females</td><td>33.1</td><td>653</td><td>171</td><td>9</td><td>7.8</td><td>18</td><td>26</td><td>15.7</td></tr>
<tr><td colspan="9">ZMA 120.413. ‘Spaans Legioen’. 54 Small, dark specimens, of which 22 are males, 25 are females, six subadults and one juvenile. No characteristic coloration can be observed. Dorsal fins and anal fins are damaged.</td></tr>
<tr><td>Males</td><td>23.7</td><td>602</td><td>184</td><td>—</td><td>—</td><td>17.7</td><td>26.3</td><td>16</td></tr>
<tr><td>Females</td><td>26.4</td><td>607</td><td>177</td><td>—</td><td>—</td><td>16</td><td>25.7</td><td>15.7</td></tr>
<tr><td colspan="9">ZMA 120.414. This lot is from ‘Rooi Awa Marga’, which is a slow stream. One small male with a completely developed gonopodium is present, with five small females and five juveniles.</td></tr>
<tr><td>Male</td><td>16.0</td><td>563</td><td>163</td><td>—</td><td>8</td><td>16</td><td>25</td><td>16</td></tr>
<tr><td>Females</td><td>21.6</td><td>602</td><td>153</td><td>8</td><td>7</td><td>16.5</td><td>25.5</td><td>16</td></tr>
<tr><td colspan="9">ZMA 120.415. Salinja master, caught at an abandoned saltpan (24 g Cl/l). The sample contains five males, three females, three subadults and 3 juveniles. The scales of these specimens are white and hard, probably caused by the high salinity.</td></tr>
<tr><td>Males</td><td>24.7</td><td>633</td><td>167</td><td>—</td><td>8</td><td>16</td><td>26</td><td>16</td></tr>
<tr><td>Females</td><td>25.8</td><td>627</td><td>149</td><td>9</td><td>7.5</td><td>15.5</td><td>26</td><td>16</td></tr>
<tr><td colspan="9">ZMA 120.422. Salinja master, east. Again the abandoned saltpan (6 g Cl/l). Nine males, of which the two largest were very dark. These two specimens are not recorded in the table. 19 Females are found, of which one has many irregularly positioned spots. Eight subadults and four juveniles complete this lot.</td></tr>
<tr><td>Males</td><td>22.8</td><td>598</td><td>172</td><td>—</td><td>8</td><td>16</td><td>26</td><td>16</td></tr>
<tr><td>Females</td><td>23.3</td><td>638</td><td>149</td><td>8.7</td><td>8</td><td>15.7</td><td>26.5</td><td>15.8</td></tr>
<tr><td colspan="9">ZMA 120.423. ‘Bron Rooi Prins’ pool. It contains sixteen males, twenty-three females and 4 subadults.</td></tr>
<tr><td>Males</td><td>31.0</td><td>606</td><td>187</td><td>—</td><td>8</td><td>16</td><td>25.3</td><td>16</td></tr>
<tr><td>Females</td><td>35.8</td><td>627</td><td>172</td><td>9</td><td>8</td><td>18</td><td>25.8</td><td>16</td></tr>
</table>

Table 1.—Continued.

	SL	Pred	CPd	A	D	C	LLS	CPS
ZMA 120.425. 'Salinja Balashi'. 9 Males, fifty-eight females, eighteen subadults and 2 juveniles. This population has some extra-ordinary features. The population consists of more or less colorless specimens. The males are few in number, and one specimen seems of intermediary sex, i.e., does not have his gonopodium fully developed while being large enough. The other eight males are normally developed. Many females only have eight anal fins.								
Males	22.0	562	187	—	8	16	25	16
Females	29.3	616	169	8.3	7.8	16.6	26.3	16
ZMA 120.437. 'Fontein pond'. Seven males, six females, five subadults and one juvenile.								
Males	32.5	577	190	—	7.7	16.7	25.7	16
Females	27.5	626	144	9	8	16.7	27.5	16
Curaçao								
ZMA 100.603. Zaquito. A note in bottle reads: males with orange-red dorsal fins, orange-red gill-areas, ventral sides and caudal fins. On the sides 3 to 6 rows of orange-red spots.								
Males	30.7	510	168	—	8	16	25	14.5
Females	29.7	622	163	8.2	7.8	16	25.8	15
ZMA 123.465. 5 km SWS of Willemsstad, from a tidal pool. The complete population was poisoned, and contains more males than females. 48 Males, of which some have more than one humeral blotch. All males are heavily pigmented, i.e., are speckled. Some have rows of black spots on the caudal peduncle. 36 Females, 3 subadults, 1 juvenile.								
Males	38.4	506	171	—	8	16	26.3	17.5
Females	39.4	581	155	8.9	7.9	16	26.6	16.9
ZMA 123.466. Hato. 127 mainly black or dark brown specimens.								
Male	31.3	474	180	—	8	16	26	17
Females	30.2	674	164	8.5	8	16	25.5	16
Averages of Morphometric and Meristic Data								
Aruba								
Males	26.8	580.8	181.2	—	8.0	16.5	25.7	15.9
Females	30.7	620.5	161.8	8.8	7.8	16.5	26.3	15.8
Curaçao								
Males	33.5	496.7	173.0	—	8.0	16.0	25.8	16.3
Females	33.1	625.7	160.7	8.5	7.9	16.0	26.0	16.0

Colombia: BMNH 1899.3.15: 24-26, (2), Colombia, coll. H. Festa, no date.

Diagnosis.—A = 8 (rarely 9); D = 8 (rarely 7); LLS = 25–26; BS = 18; CPS = 16; PS = 11–13

Descriptions.—*Poecilia koperi* has unicuspid inner teeth. The largest specimens examined are a female of 56.2 mm SL and a male of 47.0 mm SL.

Holotype.—The largest male (38.5 mm SL) has a deep body, with depressed sides. The upper part of body exhibits two dark horizontal rows of dark spots, which are less conspicuous ventrally. The body is brown, dorsally darker than ventrally. The caudal fin has black spots on the membrane between the rays. The dorsal fin is pigmented like caudal fin, reaching caudal base. The inner jaw dentition is unicuspid. Proportional body measurements in Table 2.

Meristic data include 26 scales in the lateral series, 12 predorsal scales, 16 scales around caudal peduncle, and 18 scales around body. Pectoral fins exhibit 16 rays, the dorsal 8 fin rays, and the caudal 17 fin rays. The last segment of gonopodial ray 3

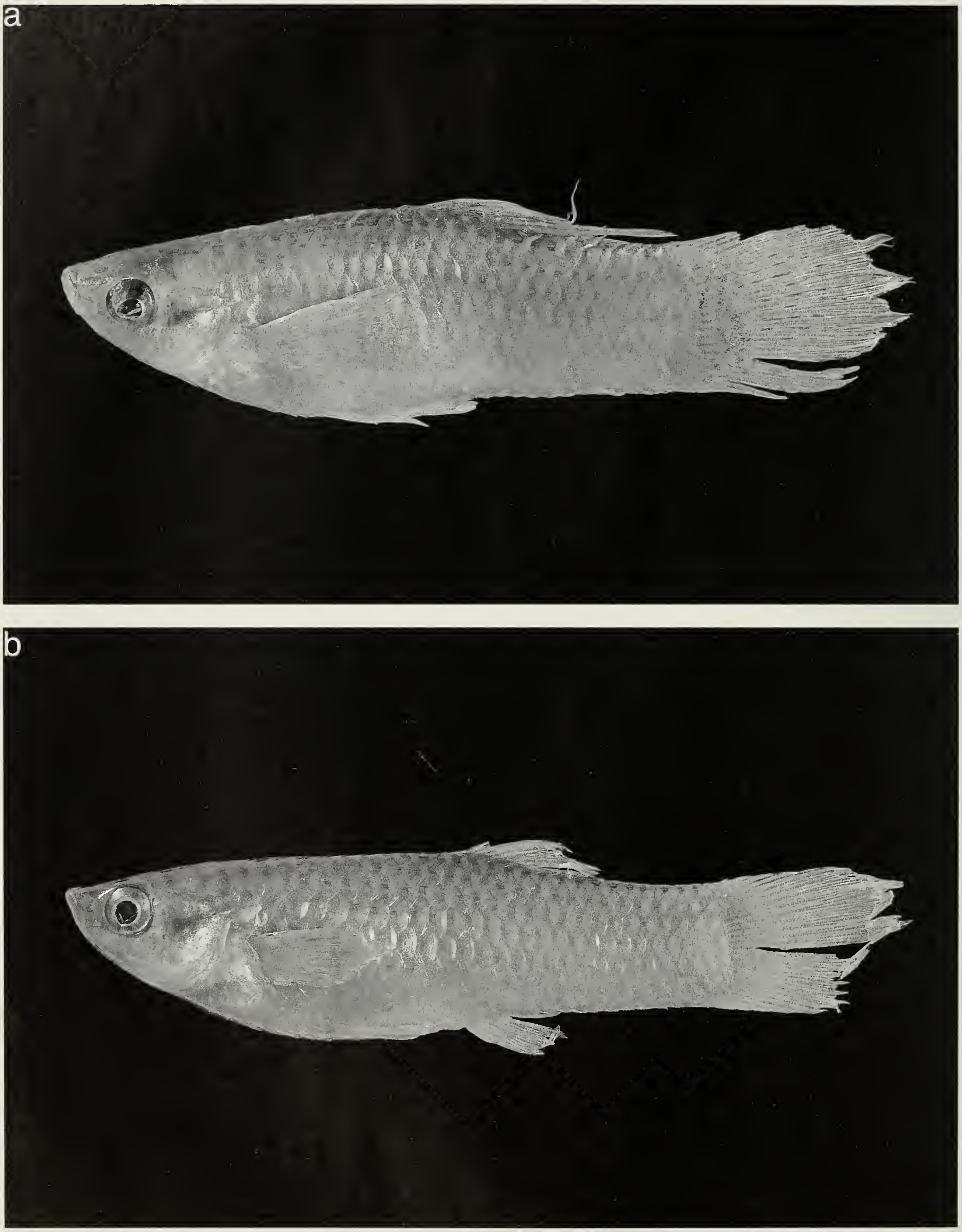

Fig. 1. *Poecilia koperi,* (a) holotype, (b) allotype.

has an extruding spine, two subsequent segments without serrae, nine segments with ventral processes, and the other segments with serrae on both sides (Fig. 4a). Ventrally on ray 3, a hood is present, not reaching the tip. Ray 4a of the gonopodium is without serrae, ray 4p has ten distal unserrated segments, followed by ten segments

Table 2.—Proportional measurements of *P. koperi, P. boesemani* and *P. wandae.* The standard lengths are in millimeters, proportional measurements in thousandths of the standard length.

	Poecilia koperi				*Poecilia boesemani*		*Poecilia wandae*			
	Males	(Holotype)	Females	(Allotype)	(Holotype)	(Allotype)	Males	(Holotype)	Females	(Allotype)
Standard Length (mm)	34.8	38.5	34.1	40.6	43.8	47.8	20.4	18.1	19.9	23.1
Predorsal Length	543	535	592	579	573	586	577	582	606	636
Dorsal Origin to Caudal Base	396	463	294	351	397	402	389	390	371	342
Anal Origin to Caudal Base	495	562	303	346	534	368	549	522	358	381
Body Depth	281	348	214	253	320	326	269	253	270	273
Head Length	242	253	198	219	228	243	243	286	278	199
Head Width	167	191	144	171	210	222	170	165	181	173
Caudal Peduncle Length	468	553	266	282	486	276	530	527	392	312
Caudal Peduncle Least Depth	198	253	138	164	192	174	187	187	158	165
Interorbital Bony Width	132	146	114	134	137	132	114	110	127	126
Mouth Width	92	110	76	84	110	111	74	60	88	91
Snout Length	38	48	29	39	41	50	—	—	—	—
Orbital Length	60	59	48	50	62	56	—	—	—	—
Dorsal Fin Depressed Length	361	452	156	—	295	238	205	220	166	147
Dorsal Fin Basal Length	131	163	80	96	151	138	—	—	—	—
Anal Fin Depressed Length	200	202	126	144	221	157	267	308	179	177
Anal Fin Basal Length	—	—	53	57	—	67	—	—	—	—
Pectoral Fin Length	160	253	160	182	212	195	—	—	—	—
Pelvic Fin Length	96	185	166	105	180	123	229	264	—	117
Caudal Fin Length	215	371	214	239	253	236	—	330	—	173

with dorsal serrae. Rays 5a and 5p do not have spines, and are seven segments shorter than 4p.

Allotype.—The largest female (40.6 mm SL) has spots on the body like those of the holotype, and has fins with indistinct pigmentation. The dorsal fin is short, reaching halfway from the base of the first ray to the caudal fin base. The caudal fin has 16 rays, the anal fin has eight rays. The other meristic counts are like those in the holotype.

Distribution.—*Poecilia koperi* occurs in coastal areas from the Peninsula de Araya, Venezuela to the eastern part of Colombia.

Etymology.—This species is named after my friend Michel Koper, with whom discussions have helped to keep my thinking flexible.

Remarks.—*Poecilia koperi* is a medium sized species of the *Poecilia sphenops* complex (cf. Miller 1983), distinguished from *P. gillii cuneata* only by the reduced number of fin rays in the dorsal and anal fin. From the other subspecies of *P. gillii* it is distinguished by gonopodial characteristics.

Two geographically separated color morphs exist in this species. The pigmentation of the body of specimens east of Coro consists of two or three horizontal rows of spots, which are less conspicuous ventrally. The body becomes darker dorsally, as opposed to the lighter ventral side. The unpaired fins are moderately pigmented, i.e., they only have spots on the membrane between rays. The dorsal fin reaches to the base of the caudal fin. The populations west of Coro, i.e., in the Maracaibo basin, are more intensely pigmented. The males have about 10 distinct vertical stripes from halfway the body to the caudal base. The scales on the body have pigmented margins. The base of the caudal fin is covered with scales, which are irregularly pigmented. The caudal fin has longitudinal spots, the dorsal fin has a median blotch from the base to halfway the fin, distally replaced by dark spots. The females are pigmented like the males, but with fainter stripes on the body. The fins in the females are without spots and the snout is less pointed. Meristic data and the gonopodium are identical in the two populations, although Maracaibo populations never have seven dorsal fin rays, nor nine anal fin rays. The gonopodium has a fleshy hood that nearly reaches the tip. Gonopodial ray 3 has two or three weakly serrated terminal segments. Other segments of ray 3 have ventral serrae and irregular dorsal extrusions. A membranous ventral hook is found on the edge of the last segment. Gonopodial ray 4a is with long unserrated segments. Gonopodial ray 4a possesses seven to eleven unserrated distal segments, others segments have dorsal serrae. This ray is somewhat shorter than ray 4a. Gonopodial rays 5a and 5p have long unserrated segments ending at fourth to seventh segment of ray 4p counting from the tip (Fig. 4a).

Schultz' (1949:97) record of *P. vivipara,* partly based on de Beaufort's (1940) account, is erroneous; re-examination of the specimens mentioned by de Beaufort (1940: 111) in ZMA revealed that this material is *P. koperi.*

Poecilia boesemani, new species
Fig. 2, Table 2

Poecilia sphenops (non Valenciennes, 1846); Regan, 1913:1013 (in part); Price, 1955:18; Boeseman, 1960:122.

Holotype.—RMNH 21543, adult male, Trinidad, Port of Spain, Maraval River, coll. M. Boeseman, 27-VII-1954.

Allotype.—RMNH 32428, adult female, same data as RMNH 21543.

Diagnosis.—A = 8; D = 8–9; LLS = 27; BS = 20; CPS = 16; PS = 13–16.

Description.—Holotype: male, 43.8 mm SL. The body does not have a distinct pattern of pigmentation. The dorsal fin is angular, with dark spots on the membranes between the rays. These spots form two regular horizontal lines. In the caudal fin, a vertical line of similar spots is found on the posterior part. Proportional body measurements in Table 2.

Fig. 2. *Poecilia boesemani,* (a) holotype, (b) allotype.

The dorsal fin has 10 rays, the caudal fin has 18 fin rays. Pectoral fin with 16 rays, 20 scales around the body, 16 scales around the caudal peduncle, 27 scales in a lateral series. The holotype misses one or two predorsal scales, so the exact number is unknown. All head pores are exposed. The gonopodium is like *P. mexicana* (Fig. 4b, see Miller 1975), i.e., with a spine in the membranous hook on gonopodial ray 3. Inner jaw teeth unicuspid or possibly subtricuspid (Garman 1895, Miller 1975).

The female allotype is 47.8 mm SL. The morphology and pigmentation are like that noted in the holotype but without spots in the caudal fin. The anal fin has 8 rays, the dorsal fin contains 9 rays, the pectoral fin has 13 rays. All other counts are identical to those of the holotype.

Distribution.—This species is known only from its type locality.

Etymology.—This species is named after Dr. Marinus Boeseman, emeritus curator of the ichthyological collection of the National Museum of Natural History, Leiden (RMNH), who collected the specimens.

Poecilia wandae, new species
Figs. 3, 4, Table 2

Holotype—USNM 121683, adult male, Venezuela, Maracaibo basin, hot spring, creek tributary to Rio Mechango, 20 km above bridge, coll. L. P. Schultz, 21-III-1942.

Allotype.—USNM 326142, adult female, same data as USNM 121683.

Material.—USNM 121669 (4), Cano, ½ mile W of Sinamaica, coll. L. P. Schultz, 11-III-1942; USNM 121670 (3), Rio Socuy, 3 km above mouth, coll. L. P. Schultz, 24-II-1942; USNM 121671 (42), Cienago del Guanavana, about 10 km N of Sinamaica, coll. L. P. Schultz, 11-III-1942; USNM 121672 (12), Rio San Juan, 12 km S of Rosario, coll. L. P. Schultz, 26-II-1942; USNM 121673 (1), Rio San Ignacio, about 20 km S of Rosario, coll. L. P. Schultz, 26-II-1942; USNM 121674 (1), Rio Negro, below mouth of Rio Yasa, coll. L. P. Schultz, 2-III-1942; USNM 121675 (27), Lago Tule, about 75 km W of Maracaibo, coll. L. P. Schultz, 1-III-1942; USNM 326143 (261), same data as USNM 121683.

Diagnosis.—D = 5–7; A = 6–8; C = (probably) 14–16; LLS = 24–26; PS = 11–13; BS = 16; CPS = 14. This species is very much like *P. caucana,* differing only in regards to the reduced meristic and gonopodial characteristics.

Description.—*Poecilia wandae* is a small species, with mature males ranging from 13 to 22 mm SL. Most specimens have a brownish body with 7 to 10 vertical stripes extending from the caudal peduncle to halfway along the body. In some specimens a longitudinal stripe over the lateral line is present. The dorsal fin has a median basal blotch and a black margin, whereas the other fins are unmarked. *Poecilia wandae* has an elongated body with a compressed head. Females have fewer vertical stripes than the males. Gonopodial ray 3 at the tip with 1 or 2 unserrated elements, all other segments of this ray are serrated on both sides (Fig. 4c). The fleshy hood reaches the tip. Gonopodial ray 4a has long, unserrated segments, with the last segment pointing downwards, while 4p has 7–8 square unserrated elements at the tip and the distal segment pointing upwards. The tip is split. Gonopodial rays 5a and 5p are unserrated and do not reach the tip. Gonopodial ray 5p has a retrorse spine, which is more weakly developed at the end of ray 5a.

Description of the types.—The holotype is a male, 20.6 mm SL. The body has seven vertical stripes that extend from the middle of the body to the middle of the caudal peduncle. This is combined with a reticulate pigmentation pattern that is dorsally darker than ventrally. The dorsal fin reaches halfway from the base of its last ray to the base of the caudal fin. The caudal fin is clear, whereas the dorsal fin has a median basal blotch and has a dark margin. The female allotype is 23.1 mm SL. Pigmentation and scale counts are like those noted on the holotype. It has six dorsal fin rays and eight anal fin rays. The caudal fin rays are broken.

The meristic data are like those recorded for *P. caucana.* There are 25 scales in a lateral series, no more than 14 scales around the caudal peduncle and 16 scales around the body. Unfortunately, the caudal fins and the dorsal fins are damaged. *Poecilia wan-*

Fig. 3. *Poecilia wandae,* (a) holotype, (b) allotype.

dae resembles *P. caucana* in gonopodial characters. Gonopodial ray 3 has the first two segments unserrated; all other segments are serrated on both sides. The fleshy palp covers the tip. Gonopodial ray 4a has unserrated segments, with the last segment bending down. Gonopodial ray 4p has seven unserrated distal segments, the last segment bends upwards, splitting the tip. Gonopodial rays 5a and 5p are unserrated, both

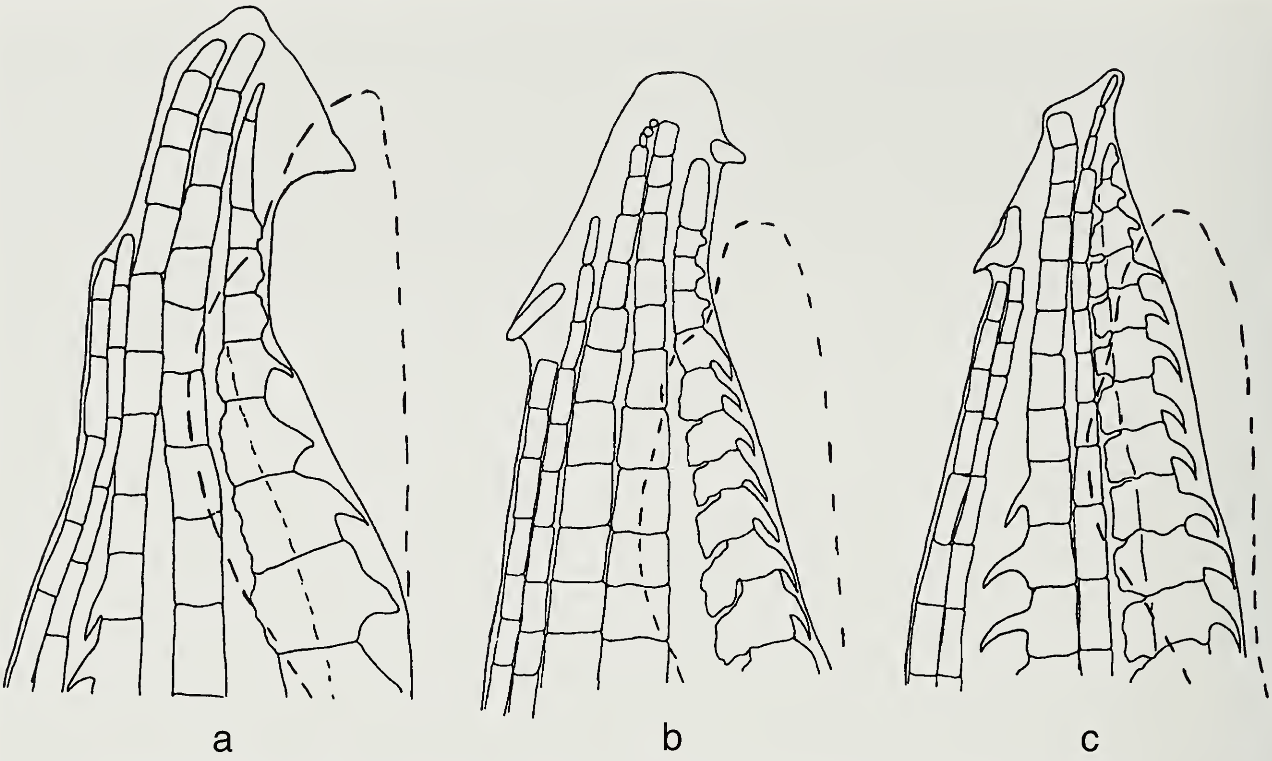

Fig. 4. Tips of gonopodia of (a) *Poecilia koperi,* (b) *Poecilia boesemani,* (c) *Poecilia wandae.*

do not reach the tip. Gonopodial ray 5p has a spinous retrorse extremity. Proportional body measurements in Table 2.

Distribution.—This species is known from several river systems west of the Maracaibo basin.

Etymology.—This species is named after Vanda Marisa Freitas de Leite, who wishes to be called Wanda.

Remarks.—Some specimens collected from the population of the Rio San Juan/Rio Negro drainage are pale, without any specific marking with the exception of two specimens. One female has a distinct black spot on the caudal base and another spot on the left side of the body under the dorsal fin. Another female had a similar spot on the left side at the upper margin of the caudal base. The number of specimens available, however, was too limited to decide whether these latter populations are either specifically distinct, or only color morphs of *P. wandae.*

Discussion

The South American species of *Poecilia* inhabit mostly peripheral habitats, i.e., coastal areas or islands. *Poecilia sphenops* and *P. vandepolli* do not occur on the Venezuelan mainland (Poeser 1992; present study), despite earlier reports (Schultz 1949, Feltkamp and Kristensen 1969). In the present paper, seven species from the northeastern part of South America are recorded. One of these species, *P. gillii* (Kner and Steindachner, 1864), also occurs in Central America, and one species, *P. vivipara,* extends from the Orinoco drainage and the Lesser Antilles south to Argentina. The re-examination of *P. vandepolli* confirmed past observations concerning character variation in this species, whereas examination of the Colombian and Venezuelan populations of mollies confirmed earlier conclusions (Poeser 1992) that the Venezuelan population are neither *P. sphenops* nor *P. vandepolli.* One of the new species described herein, *P. wandae,* is related to *P. caucana* based on its morphological and gonopodial characteristics.

Venezuela is divisible into four distinct biogeographical regions, viz., the Maracaibo basin, mainland Venezuela, the drainage of the Rio Orinoco, and the adjacent islands

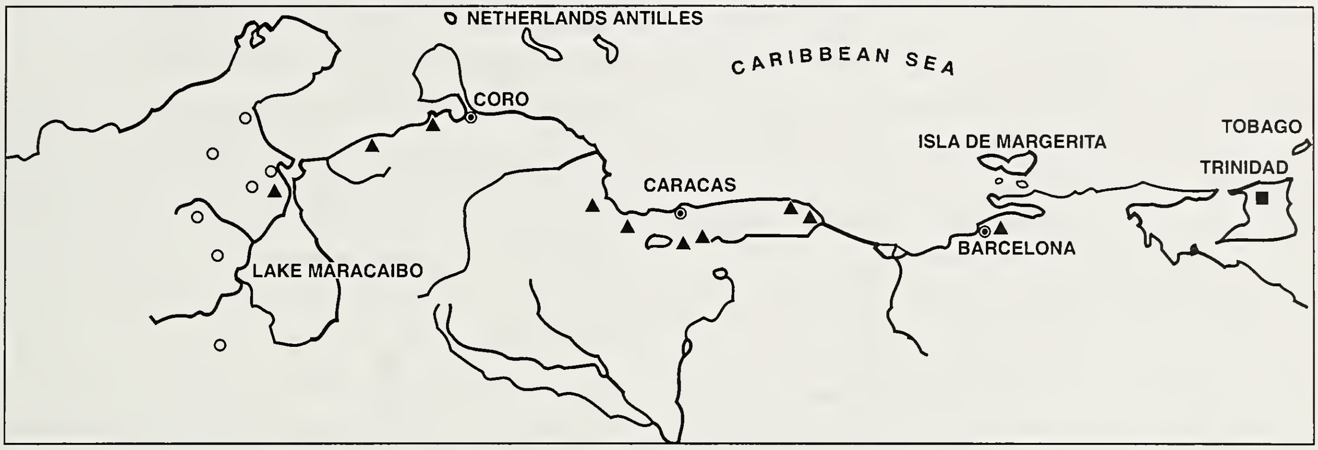

Fig. 5. Map of Venezuela. The locations of UMMZ material (=*P. koperi*) are noted with black triangles, the USNM material (=*P. wandae*) are open circles, the RMNH material (=*P. boesemani*) is a black square.

of the Lesser Antilles. Only one of the examined species occurs in more than one district, viz., *P. caucana* (along the Atlantic coast from Panama to the delta of the Rio Orinoco). In the Rio Orinoco, *P. vivipara* finds its northernmost mainland extension. *Poecilia vandepolli* and *P. boesemani* are endemic species located on islands adjacent to Venezuela. Comparisons with Central American mollies reveals that the species of *Poecilia* manifest a clinal reduction in body size and a decrease in meristic characters from north to south. *Poecilia mexicana,* naturally occurring on the Atlantic side of Mexico, has unicuspid inner teeth, nine dorsal fin rays, nine anal fin rays, 18 scales around the caudal peduncle, and two spines at the tip of the gonopodium (Table 3). Miller (1983) could not distinguish *P. mexicana* from *P. gillii,* and genetic data of *P. mexicana* from Vera Cruz and from Costa Rican populations (labeled "*P. gillii*") are virtually identical (Brett & Turner 1983, p. 136: cluster map of NEI identity values).

Why then separate *P. mexicana* from *P. gillii*? Villa (1982) and Bussing (1987) both mentioned two species fitting the descriptions given in the present paper. Although 29 scales in a lateral series are not typical for *P. mexicana* (cf. Menzel and Darnell 1973), Bussing (1987) nevertheless considered populations with this character as *P. mexicana.* The alternative hypothesis would be that *P. gillii* is a subspecies of *P. mexicana* with 16 scales around the caudal peduncle. The populations with 29 scales in a lateral series (Villa 1982; Bussing 1987) should then be considered another (possibly new) species.

Poecilia gillii has been reported to exceed 100 mm SL (Bussing 1987). The body size of the investigated specimens was always much less than 100 mm SL. In contrast to its variable body shape (Meek 1914, Meek and Hildebrand 1916), the meristic data are fairly constant. From El Salvador (Poeser 1995), through Nicaragua (Villa 1982) and Costa Rica (Bussing 1987) to Panama and Colombia (present study), *P. gillii* constantly displays nine anal fin rays, nine or ten dorsal fin rays, 16 scales around the caudal peduncle, and on average 27 scales in a lateral series. The only significant change in diagnostic characteristics is a reduction of the spine found on gonopodial ray 5p. The observed differences in gonopodial structures I regard as subspecific variation within *P. gillii.*

The next species in the Central to South American cline is *P. koperi,* found in Venezuela. *Poecilia koperi* differs from *P. gillii* in the number of dorsal and anal fin rays (8 versus 9 in *P. gillii*). The reduction of the gonopodial spine on ray 5p is complete in *P. koperi.* The next species south, *P. vivipara,* continues the trend of reduction, exhibiting 7 dorsal fin rays and a lack of all gonopodial extremities. In addition, *P. vi-*

Table 3.—Clinal variation in meristic data and gonopodial characters in 5 examined taxa, from north to south.

Species	Range	A	D	CPS	Gonopodial tip
P. mexicana	Atlantic coast from Texas to Costa Rica	9	9 or 10	18	spine on ray 3, spine on ray 5
P. gillii gillii	Pacific coast from Guatemala to Panama	9	9 or 10	16	spine on ray 3, spine on ray 5
P. g. cuneata	Panama and the Atlantic coast of Colombia	9	9 or 10	16	spine on ray 3
P. koperi	Colombia and Venezuela	8	8	16	spine on ray 3
P. vivipara	Venezuela to Argentina	8	7	16	no gonopodial spines

vipara has a median positioned humeral blotch and serrae on gonopodial ray 4a, unique characters in the subgenus, but not in the genus. In the subgenus *Lebistes* sensu Rosen and Bailey (1963), *P. reticulata* also has serrae on gonopodial ray 4a, *P. bifurca* exhibits the lateral body spot, and *P. picta* exhibits both the serrae on ray 4a and the lateral body spot.

An exception to these clinal variations is seen in *P. boesemani,* which occurs on Trinidad. *Poecilia boesemani* has a reduced body size, less anal fin rays and a reduced number of scales around the caudal peduncle than seen in *P. mexicana,* whereas the number of dorsal fin rays and the gonopodial characters are similar in these two species. Based on the last two similarities, Price (1955:7, 18) and Boeseman (1960: 122) presumed that *P. boesemani* was merely an introduced aquarium strain with the vernacular name 'Liberty molly'. *Poecilia boesemani* resembles western populations of *P. sphenops* in fin pigmentation and general morphology (Schultz and Miller 1971). The inner jaw dentition, however, is unicuspid versus tricuspid in *P. sphenops. Poecilia boesemani* differs from most Central American species in the number of anal fin rays (8 versus 9 in the other species), in the number of scales around the caudal peduncle (mostly 18 in the other species) and in female pigmentation (rows of black spots in *P. sphenops* and in *P. mexicana*). *Poecilia boesemani* more closely resembles *P. butleri,* another widely distributed Mexican species, in the number of anal fin rays; it differs, however, in dorsal fin pigmentation (distinct basal blotch in *P. butleri* [cf. Schultz and Miller, 1971]). Furthermore, *P. boesemani* and *P. butleri* are geographically the most separated species. *Poecilia boesemani* differs from *P. koperi* and *P. vandepolli* in the presence of distal spines on both gonopodial rays 3 and 5. Boeseman's (1960, p. 122) observation that "it lacks a distal retrorse segment on gonopodial ray 5", is erroneous (Fig. 4b). *Poecilia vandepolli,* occurring on the Dutch Lesser Antilles, also has a reduced body size, less dorsal fin rays, 16 scales around the caudal peduncle, and gonopodial characteristics like those seen in *P. vivipara.* It also has a humeral blotch, although it is found more anteriorly on the body than in *P. vivipara.*

The clinal variation is evident in *P. caucana* and *P. wandae. Poecilia wandae* is superficially like *P. caucana,* resembling it in size, scale counts, pigmentation, and gonopodial structures. It differs, however, in the number of anal fin rays (6–8 versus always 8 in *P. caucana*), dorsal fin rays (5–7 versus 7 or 8 in *P. caucana*), and in the absence of a membranous hook on gonopodial ray 3. The gonopodia of both species agree in several internal structures (Rosen & Bailey 1963:62, fig. 25B). Rosen & Bailey (1963) reported that this 'undescribed species', viz., *P. wandae,* was osteologically like *P. caucana,* as well as the Hispaniolan species of *Poecilia,* viz., *P. elegans, P. dominicensis* and *P. hispaniolana,* and "the smaller species of the *P. sphenops* group". Unfortunately, they did not specify to which species in the *P. sphenops* group they were referring. The occurrence of such similarities in widely separated species suggests that the osteological evidence could represent a primitive state. Furthermore, based on its gonopodial structures, it was suggested that *P. caucana* is related to the species of *Limia* of Hispaniola, and to the Central South American species of *Pamphorichthys* (Rosen 1975, Rauchenberger 1989). This would than place the origin of *P. caucana* and *P. wandae* from an ancestral species in South America at 80 to 70 Mya. (Pitman et al. 1990: fig. 2.5C). During this period, Hispaniola was situated between North and South America, as part of the great Arc of Proto-Greater Antilles. The morphological differences, i.e., the diversion from the "molly-geocline", as well as the osteological and gonopodial characteristics linking *P. caucana* and *P. wandae* with Hispaniolan and South Brazilian species, suggest a separate origin for these two species. The overall similarities in gonopodial structures, however, warrant their present inclusion in *Poecilia.*

Under a dispersalist scenario, one may conclude that members of the genus *Poecilia* entered South America after the completion of the Andean uplift and the formation of the Panamanian landbridge, i.e., about 4 Mya. (Pitman et al. 1990: fig. 2.5 F). This rapid dispersal and speciation resulted in subsequent differentiation from the Central American species of *Poecilia.* This hypothesis is confirmed by a molecular phylogeny presented by Breden et al. (1999), who concluded that *P. vivipara* was significally different from the species of the *P. sphenops* complex in Central America. Breden et al. (1999) suggested a separate taxonomic status for the *P. sphenops* complex and allocate these species, together with the broad finned mollies (cf. Miller 1983), in the subgenus *Mollienesia* (sensu Miller 1975). Rodriguez (1997) proposed a similar taxonomy based on a phylogenetic analysis of morphological characters. However, all three studies (Miller 1975, Rodriguez 1997, Breden et al. 1999) did not investigate the clinal variation in characters found in the present study. The suggestion of a separate taxonomic status for *P. vivipara* will be the subject of further investigations.

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Literature Cited

Beaufort, L. F. de. 1940. Freshwater fishes from the Leeward group, Venezuela and eastern Colombia.—Studies of the Fauna Curaçao, Aruba, Bonaire, and the Venezuelan islands 2(7):109–114.

Boeseman, M. 1960. The fresh-water fishes of the Island of Trinidad.—Studies of the Fauna of Curaçao and other Caribbean Islands 10(48):72–153.

Breden, F., M. B. Ptacek, M. Rashed, D. Taphorn, & C. A. Figueiredos. 1999. Molecular phylogeny of the life-bearing fish genus *Poecilia* (Cyprinodontiformes: Poeciliidae).—Molecular Phylogenetics and Evolution (12)2:95–104.

Brett, B. L. H., & B. J. Turner. 1983. Genetic divergence in the *Poecilia sphenops* complex in Middle America.—Biochemical Systematics and Ecology 11(2):127–137.

Bussing, W. A. 1987. Peces de las aquas continentales de Costa Rica.—2. Edicion, San Juan, Costa Rica: Editorial de la Universidad de Costa Rica: 1–271.

Carr Jr., A. F., & L. Giovannoli. 1950. The fishes of the Choluteca drainage of Southern Honduras.—Occasional Papers of the Museum of Zoology, University of Michigan (523):1–38, Pl. I&II.

Feltkamp, C. A., & I. Kristensen. 1969. Ecological and morphological characters of different populations of *Poecilia sphenops vandepolli* (Cyprinodontidae).—Studies of the Fauna of Curaçao 31:102–130.

Fowler, H. W. 1949. Results of the two Carpenter African Expedition, 1946–1948, part 2.—The fishes.—Proceedings of the Academy of Natural Sciences of Philadelphia 101:233–275.

Garman, S. 1895. The Cyprinodonts.—Memoires of the Museum of Comparative Zoology 19(1):1–179, Plates I–XII.

Günther, A. 1866. A catalogue of the fishes in the British museum.—London (6):1–368.

Hildebrand, S. F. 1925. Fishes of the republic of El Salvador, Central America.—U.S. Bulletin of the Bureau of Fisheries, Washington 41(985): 237–287.

Hubbs, C. L. 1926. Studies of the fishes of the order Cyprinodontiformes VI.—Miscellaneous Publications of the Museum of Zoology of Michigan, 16(1):1–87.

———. 1953. Geographic and systematic status of the fishes described by Kner and Steindachner in 1863 and 1865 in Panama and Ecuador.—Copeia 1953(3):141–148.

Hubbs, C. L., & K. F. Lagler. 1947. Fishes of the Great Lakes region.—Cranbrook Institute of Science 26:i–xi, 1–186.

Meek, S. E. 1914. An annotated list of fishes known to occur in the fresh waters of Costa Rica.—Publications of the Field Colombian Museum, zoological series 10(10):101–134.

Meek, S. E., & S. F. Hildebrand. 1916. The fishes of the freshwaters of Panama.—Publications of the Field Colombian Museum, zoological series 10(15):217–374.

Miller, R. R. 1975. Five new species of Mexicana poeciliid fishes of the genera *Poecilia, Gambusia,* and *Poeciliopsis.*—Occasional Papers of the Museum of Zoology, University of Michigan (672):1–44.

———. 1983. Checklist and key to the Mollies of Mexico (Pisces: Poeciliidae: *Poecilia,* subgenus *Mollienesia*).—Copeia 1983(3):817–821.

———. 1994. Origin and classification of the Liberty Molly.—Tropical Fish Hobbyist (42)6:104, 106, 108.

Pitman, W. C., S. Cande, J. La Brecque, & J. Pindell. 1990. Fragmentation of Gondwana: the separation of Africa from South America. Pp. 15–34 *in* Peter Goldblatt, ed., Biological relationships between Africa and South America. Proceedings of the 37th Annual Systematics Symposium.—Botanical Gardens 1990.

Poeser, F. N. 1992. Re-establishment and redescription of *Poecilia vandepolli* Van Lidth de Jeude, 1887 (Pisces: Poeciliinae), with comments on related species.—Studies of the Natural History of the Caribbean Region 71:59–74.

———. Nonrandom variation in *Poecilia marcellinoi* n. sp. and *P. salvatoris* Regan, 1907 in El Salvador (Pisces; Poeciliidae).—Bijdrage tot de Dierkunde 64(4):239–252.

———. 1998. The role of character displacement in the speciation of Central American members of the genus *Poecilia* (Poeciliidae).—Italian Journal Zoology 65, Suppl.: 145–147.

Price, J. L. 1955. A survey of the freshwater fishes of the Island of Trinidad.—Journal of the Agricultural Society of Trinidad & Tobago (863):1–28.

Regan, C. T. 1908. Pisces. *In* F. Godman, DuC., and O. Salvin, Biologia Centrali-Americana. London, Ser. III, pt. 193: 1–203, plates 1–24.

———. 1913. A revision of the cyprinodont fishes of the subfamily Poeciliinae.—Proceedings of the Zoological Society of London 1913(1):977–1018, pl. 99–101.

Rodriguez, C. M. 1997. Phylogenetic analysis of the tribe Poeciliini (Cyprinodontiformes: Poeciliidae).—Copeia (4):663–679.

Rosen, D. E., & R. M. Bailey. 1963. The poeciliid fishes (Cyprinodontiformes), their structure, zoogeography and systematics.—Bulletin of the American Museum of Natural History 126(1):1–176.

Schultz, L. P. 1949. A further contribution to the ichthyology of Venezuela.—Proceedings of the United States National Museum 99:1–211.

Schultz, R. J., & R. R. Miller. 1971. Species of the *Poecilia sphenops* complex (Pisces: Poeciliidae) in Mexico.—Copeia 1971(2):282–290.

Villa, J. 1982. Peces Nicaragüenses de agua dulce.—Coleccion Cultural Banco Americana; Serie: Geografia y Naturaleza, 3:i–xiv, 1–253.

Appendix 1.—Key to the species of the subgenus *Poecilia* (sensu Rosen and Bailey, 1963), south of Mexico.

1a.	Inner jaw dentition tricuspid	*P. marcellinoi*
1b.	Inner jaw dentition unicuspid	2
2a.	Number of scales around the caudal peduncle 18	*P. mexicana*
2b.	Number of scales around the caudal peduncle less than 18	3
3a.	Number of scales around the caudal peduncle 16	4
3b.	Number of scales around the caudal peduncle 14	100
4a.	Number of anal fin rays 9	5
4b.	Number of anal fin rays 8	7
5a.	Body never with humeral blotch, never with 8 anal fin rays	6
5b.	Body often with humeral blotch, sometimes with 8 anal fin rays	*P. vandepolli*
6a.	Gonopodial tip with spiny hooks on ray 3 and ray 5p	*P. gillii gillii*[a]
6b.	Gonopodial tip with spiny hook only on ray 3	*P. gillii cuneata*
7a.	Gonopodial tip with spiny hooks on ray 3 and ray 5p	*P. boesemani*[b]
7b.	Gonopodial tip without hooks or spines	8
8a.	Gonopodial ray 4a never with dorsal serrae	*P. koperi*
8b.	Gonopodial ray 4a with dorsal serrae	*P. vivipara*
9a.	Number of anal fin rays 8	*P. caucana*
9b.	Number of anal fin rays less than 8	*P. wandae*

[a] Specimens with a red dorsal fin are diagnosed *P. g. salvatoris,* unicuspid specimens with a caudal blotch are *P. g. caudata.*

[b] Miller (1983) reported *P. butleri* from El Salvador, fitting this description. However, he omitted the diagnostic characteristics for these populations.

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On the occurrence of the vestimentiferan tube worm *Lamellibrachia luymesi* van der Land and Nørrevang, 1975 (Annelida: Pogonophora) in hydrocarbon seep communities in the Gulf of Mexico

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Abstract.—*Lamellibrachia luymesi* van der Land & Nørrevang, 1975 is recorded from shallow-water hydrocarbon seep communities along the Louisiana slope in the Gulf of Mexico. It is typically the most abundant tube worm species in these shallow-water communities, sometimes with individuals occurring in aggregations numbering in the thousands. Tubes extend deeply into the sediment, and apical portions may project above the sea floor a distance of one meter or greater. This study documents intraspecific variation for a number of important morphological features of *L. luymesi,* such as the number of sheath lamellae, the number of branchial lamellae, the length and width of the obturaculum and vestimentum, the ratio of obturacular length to vestimental length, the ratio of vestimental diameter to vestimental length, and features of the tube. Comparisons of these features are made with other species of *Lamellibrachia.* The record of *L. luymesi* on the Louisiana slope extends the geographic range of this species from the southern North Atlantic Ocean into the northern Gulf of Mexico.

Subsequent to the description of the first species of *Lamellibrachia, L. barhami,* by Webb (1969), van der Land & Nørrevang (1975) described a second species, *L. luymesi,* and discussed the possible relationships that vestimentiferans in general have with the Annelida, Polychaeta, and Pogonophora. Following their original description, van der Land & Nørrevang (1977) provided an in-depth description of the anatomy and histology of *L. luymesi.* Both the original description and the subsequent anatomical and histological account were based on a single male specimen collected off the coast of Guyana in about 500 m of water.

The record of *L. luymesi* off the coast of Guyana remained as the only documented vestimentiferan species from the Atlantic Ocean until Paul et al. (1984) reported the presence of vestimentiferan tube worms in 3000 m of water at the base of the Florida Escarpment in the Gulf of Mexico which were later named *Escarpia laminata* by Jones (1985). A second Atlantic species of *Lamellibrachia, L. victori,* was described by Mañé-Garzón & Montero (1985), based on two specimens collected in about 300 m of water off Uruguay. Since the description of *L. victori,* no additional confirmed records of either Atlantic species of *Lamellibrachia* have been published. However, beginning in 1985 (Kennicutt et al. 1985), numerous records of a *Lamellibrachia* sp., occurring along the Louisiana slope in the Gulf of Mexico, have been reported (see synonymy below).

The purpose of the present study is to confirm the identity of the *Lamellibrachia* sp. that occurs along the Louisiana slope as

L. luymesi and to provide an account of the intraspecific variation it displays with regard to certain important diagnostic morphological characters.

Systematics

As discussed in Gardiner et al. (2001), the systematic relationships of vestimentiferans remain unsettled. In order to maintain consistency with other recent descriptions of vestimentiferans and broader discussions of pogonophoran morphology and phylogeny (Southward et al. 2002, 2003), we consider vestimentiferans as comprising a subclass within the class Pogonophora of the phylum Annelida.

Materials and Methods

Specimens were collected by the manned submersible *Johnson-Sea-Link I (JSL I)* from two hydrocarbon seep sites on the Louisiana slope in the Gulf of Mexico and brought to the surface in a temperature-insulated container. On board ship, specimens were immediately fixed in their tubes in 10% buffered formalin in seawater. In the laboratory, tubes were sliced open with the aid of a Dremel Moto-Tool high speed drill, and specimens were extracted, rinsed in distilled water and transferred to 70% ethanol.

For scanning electron microscopy (SEM), materials were dissected from selected specimens, dehydrated in a graded ethanol series, critical-point dried, using carbon dioxide, and sputter coated with gold-palladium. Material was examined in either a Topcon ABT-60 or a JEOL JSM-5200 scanning electron microscope. Negatives of figures were scanned at 600 dpi, and plates were constructed using Adobe Photoshop 7.0 (Adobe Systems, Inc., San Jose, California, USA).

Subclass Vestimentifera Webb, 1969
Family Lamellibrachiidae Webb, 1969
Genus *Lamellibrachia* Webb, 1969

Type species.—*Lamellibrachia barhami* Webb, 1969, by monotypy.

Diagnosis.—Vestimentiferan worms with tapering tubes and bodies. Anterior obturacular region provided with branchial plume; orientation of branchial lamellae relative to obturaculum axial and parallel; branchial filaments of obturacular plume of one type; plume covered by variable number of peripheral sheath lamellae; anterior face of obturaculum bare, lacking crust or secreted structures; paired internal excretory ducts opening by single, dorsal medial excretory pore. Anteroventral margin of vestimentum discontinuous, posteroventral margin of vestimentum broadly discontinuous, lobes usually not overlapping. Opisthosome with variable number of segments; chaetigerous segments with chaetae usually in single row; chaetae with variable number of teeth in anterior and posterior groupings. Tube hard, tapered, usually with variable number of collars anteriorly, becoming smooth posteriorly (Webb 1969; van der Land & Nørrevang 1975, 1977; Jones 1985; Southward 1991).

Lamellibrachia luymesi van der Land & Nørrevang, 1975
Figs. 1–8

Lamellibrachia luymesi van der Land & Nørrevang, 1975:86–101, Figs. 1–7; 1977:1–102, pls. 1–26.—Jones, 1985: 128.—Southward, 1991:872–874, table 2.

Lamellibrachia sp.—Kennicutt et al., 1985: 351, 352, table 1.—Childress et al., 1986: 1307.—Brooks et al., 1987:1139, table 1.—MacDonald et al., 1989:235–245, Fig. 3A–D.—Fisher et al., 1990:1095, table 1.—MacDonald et al., 1990:246, Fig. 2.—Childress & Fisher, 1992:382.—Williams et al., 1993:439, 440, table 1.—Carney, 1994:150.—Scott & Fisher, 1995:107, 109, table 2.—Young et al., 1996:514–516, Figs. 1a, 2b, d, e, m.—Feldman et al., 1997:271, 272, 275, Fig. 2, tables 1, 2.—Fisher et al., 1997:85, 88, 90, 91, table 1.—Miura et al., 1997: 455.—Julian et al., 1999:2245–2256.—

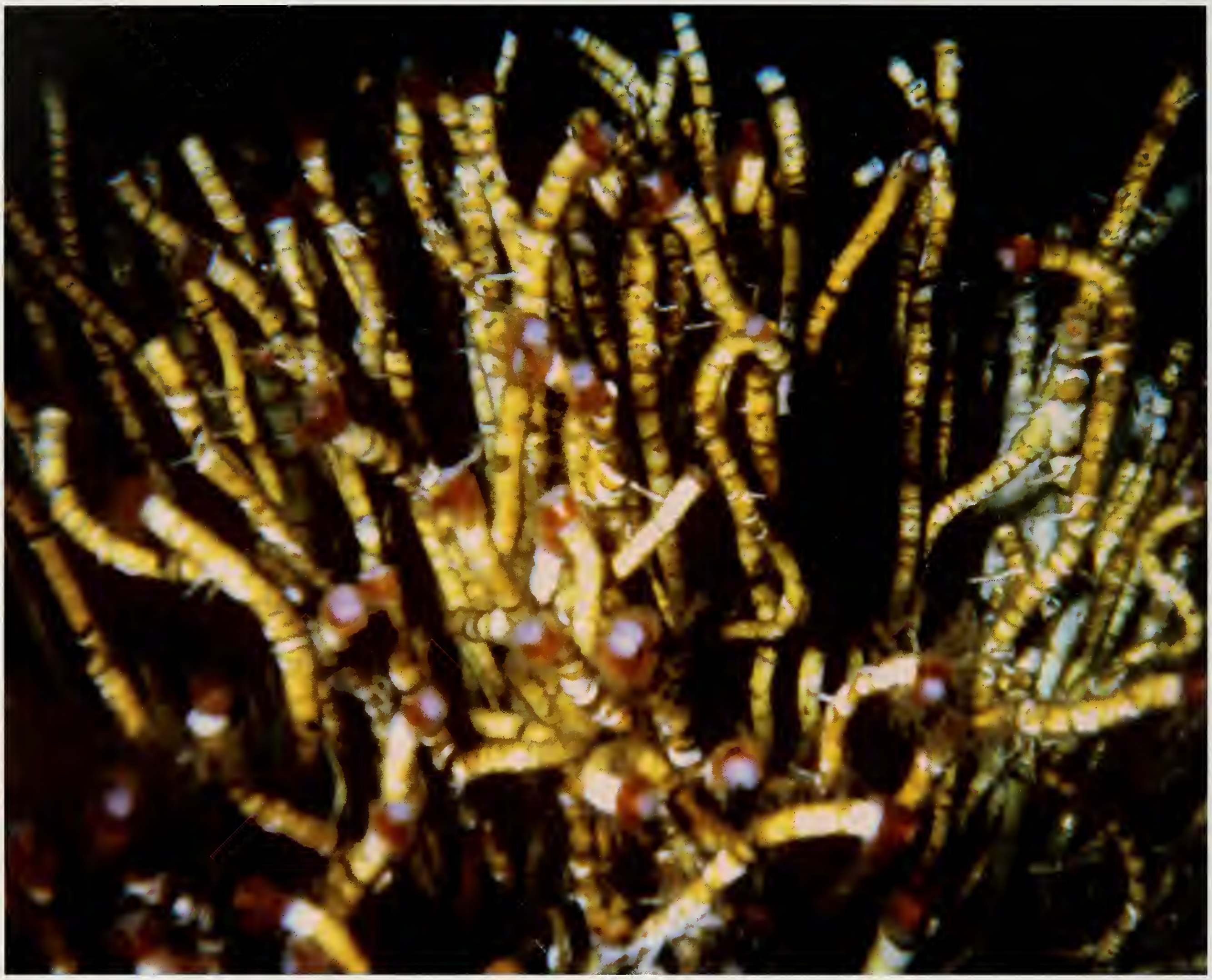

Fig. 1. In situ photograph of portion of large cluster of *Lamellibrachia luymesi* at Bush Hill hydrocarbon seep community. No scale.

Southward, 1999:196, Fig. 5.2, 5.4, 5.5.—Tyler & Young, 1999:196–198, 200–204, table 3.—Schulze, 2001:1–9, Figs. 1F, 2A, 4E, table 1.—Southward et al., 2002:1194.

Lamellibrachia barhami [not *Lamellibrachia barhami* Webb, 1969].—Fisher et al., 1988:232.

Undescribed species of *Lamellibrachia.*—Southward, 1991:872.

Lam.(GoM).—Williams et al., 1993:440, 443, Figs. 1–3, table 1.

L. sp.—Fisher, 1995:307, table 4.

Lamellibrachiid.—Fisher et al., 1997:86, 87, Figs. 1, 2.

Lamellibrachia sp. nov. 2.—Nelson & Fisher, 2000:4, 8, 10, Figs. 2, 3.

Lamellibrachia.—Salvini-Plawen, 2000: 133, 134.

Lamellibrachia cf. *luymesi.*—Freytag et al., 2001:13408–13412.—Gardiner et al., 2001:705.—Bergquist et al., 2002:89–98, Fig. 1.—McMullin et al., 2003: 8–31, Figs. 1, 2, 4, 5, tables 1, 2.

Material examined.—Twenty specimens, Green Canyon hydrocarbon seep community, 27°44.1′N, 91°15.3′W, *JSL I* dive 3523, 25 Jun 1993, 540 m, coll. C. R. Fisher; 8 specimens, Green Canyon hydrocarbon seep community, 27°44.1′N, 91°15.3′W, *JSL I* dive 3525, 26 Jun 1993, 540 m, coll. E. Nix; 12 specimens, Bush Hill hydrocarbon seep community, 27°47′N, 91°31.5′W, *JSL I* dive 3530, 28 Jun 1993, 540 m, coll. J. J. Childress. Selected specimens of this material are deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C.

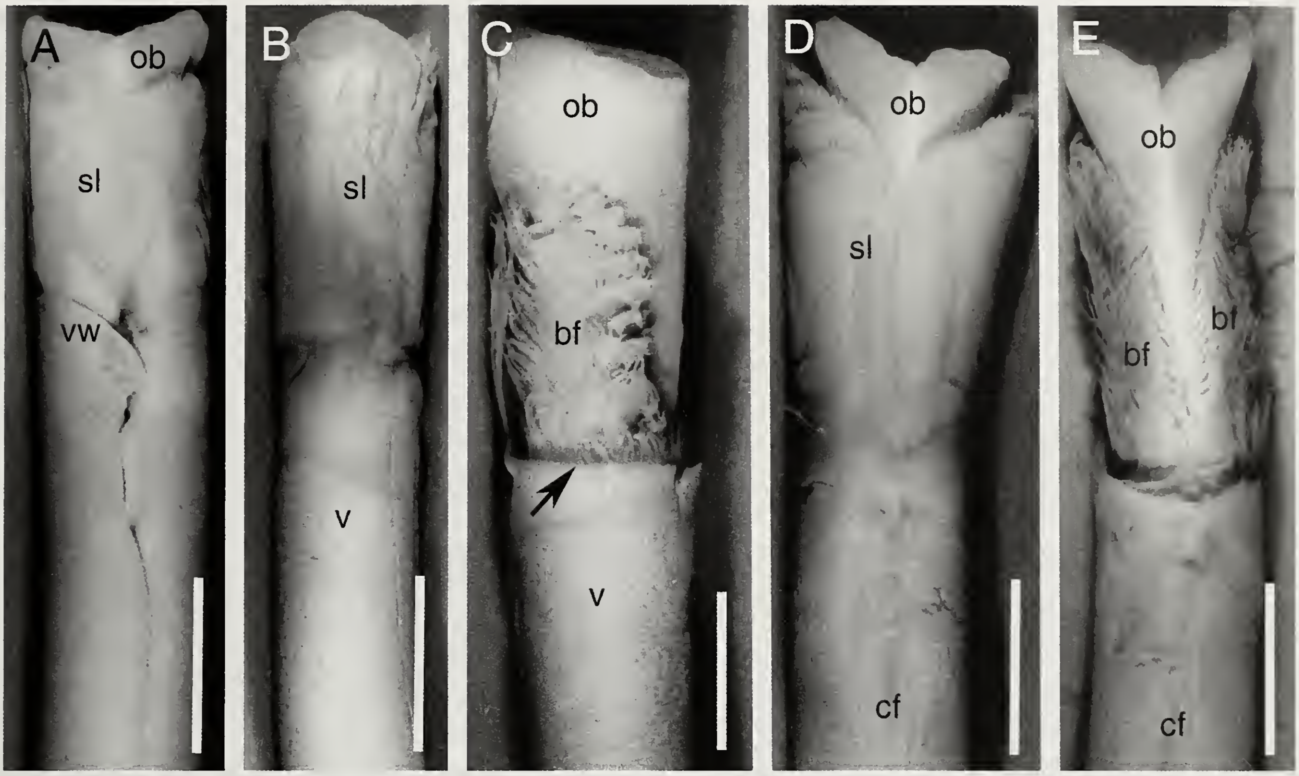

Fig. 2. *Lamellibrachia luymesi,* light micrographs of selected specimens. A, dorsal view of obturacular region showing sheath lamellae not extending to anterior face of obturaculum, together with portion of vestimental region with folded vestimental wings. B, left lateral view of obturacular region showing sheath lamellae nearly covering obturaculum, together with portion of vestimental region. C, right lateral view of obturacular region with sheath lamellae removed to show branchial filaments. Note extent of bare surfaces on obturaculum. Arrow indicates vestimental sheath around base of obturacular region. D, ventral view of obturacular region and portion of vestimental region. E, ventral view of obturacular region with sheath lamellae removed from both sides, exposing branchial filaments. bf, branchial filaments; cf, ciliated field; ob, obturaculum; sl, sheath lamellae; v, vestimental region; vw, vestimental wing. Scale bars: A, B, D, E = 5 mm; C = 3 mm.

Description.—Measurements of selected specimens (length by diameter, in mm; obturacular: vestimental: trunk: opisthosomal regions; + = incomplete; − = change in diameter; — = missing); (USNM 1007801): 9.4 by 4.5: 43 by 4: 142+ by 3.1: —; (USNM 1007803): 14.9 by 4.6: 56 by 4.7: 100+ by 2.3: —; (USNM 1007805): 16.3 by 5: 61.6 by 5.2: 110+ by 3.5: —; (USNM 1007807): 10.4 by 4.5: 51.5 by 4.2: 117+ by 3.4: —; (USNM 1007809): 7.8 by 4.4: 50.3 by 4.6: 115+ by 4.9: —. Measurements of selected tubes (length by diameter, in mm; + = incomplete, − = change in diameter): (USNM 1007801): 1340+ by 6.4–1.3; (USNM 1007802): 1560+ by 7.6–2.5; (USNM 1007804): 1405+ by 8.9–0.9; (USNM 1007806): 1230+ by 10.2–0.7; (USNM 1007808): 1190+ by 6.4–1.2.

Anterior face of obturaculum bare, without crust or secreted structures (Figs. 1, 2A–E). Obturaculum with 15–22 pairs of branchial lamellae ($\bar{X} = 17.8 \pm 1.8$; $n = 10$), composed of single type of filament (Fig. 2C, E), fused for most of length; free ends of filaments with two rows of pinnules and two rows of ciliated cells (Fig. 3A, B), pinnules on some filaments of unequal size (Fig. 3B); branchial lamellae typically covered by 4–8 sheath lamellae on each side of branchial crown ($\bar{X} = 5.3 \pm 1.1$; $n = 30$); number of sheath lamellae not directly correlated with size of specimen (Pearson's correlation); filaments of sheath lamellae lacking pinnules and cilia, almost completely fused, with very short free tips (Fig. 3C, D); sheath lamellae sometimes not extending to apical region of obturaculum (Fig. 2A, D). Distal surfaces of obturaculum of

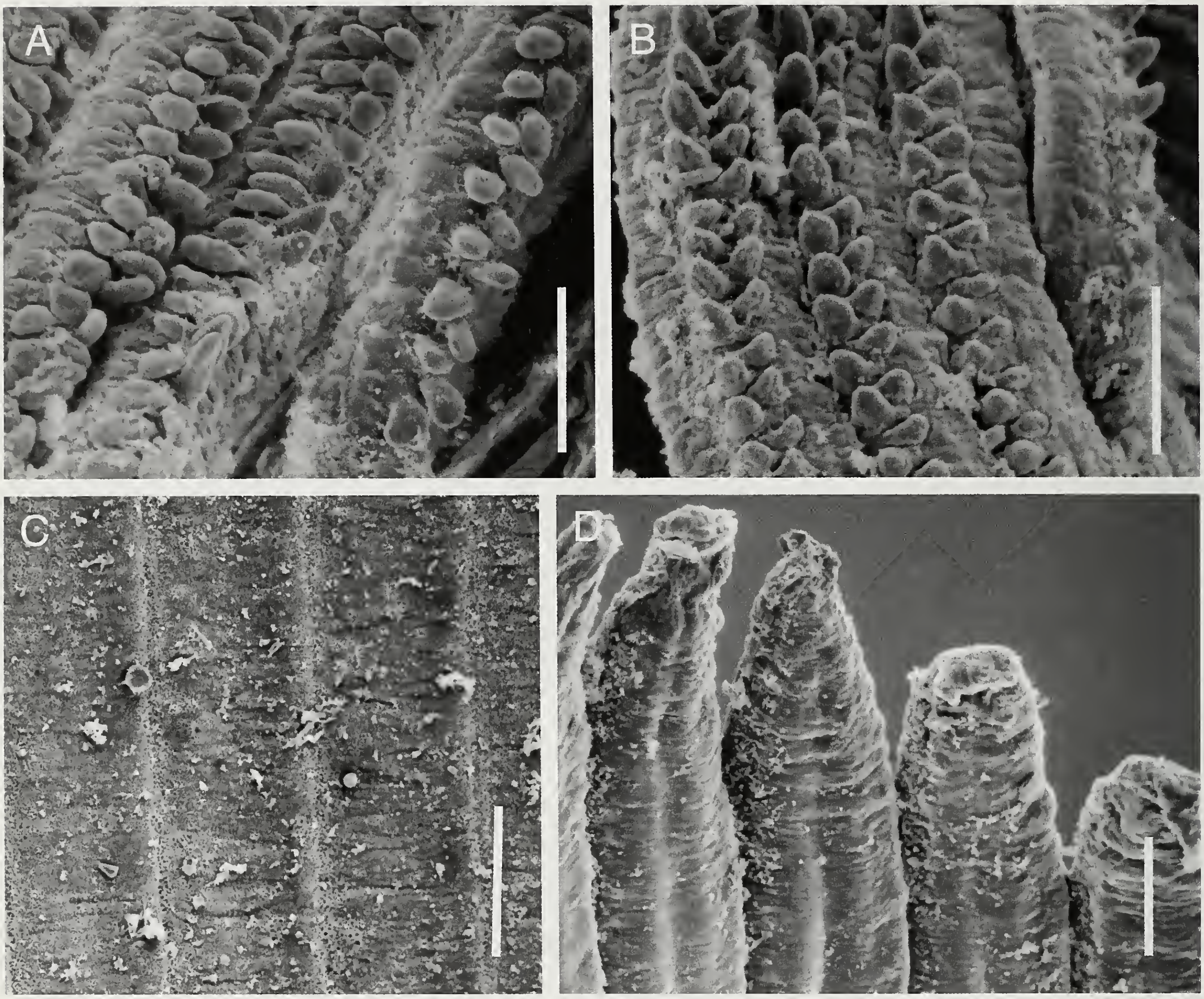

Fig. 3. *Lamellibrachia luymesi,* SEM. A, branchial filaments with pinnules of equal size. B, branchial filaments with pinnules of somewhat unequal size. C, inner face of fused filaments of sheath lamella. Note absence of pinnules and cilia. D, apical region of filaments of sheath lamella. Scale bars: A–C = 75 μm; D = 100 μm.

preserved specimens usually not concealed by branchial lamellae (Fig. 2C–E); obturaculum lenticular in cross-section (Fig. 4), lacking dorsal groove, with poorly developed ventral ridge distally; paired internal excretory ducts opening by single pore on dorsal surface at base of obturaculum; length of obturaculum from 6.6 to 16.3 mm ($\bar{X}$ = 10.8 ± 2.4 mm; n = 40); diameter of obturaculum from 3.4 to 5 mm; ($\bar{X}$ = 4.5 ± 0.6 mm; n = 40); ratio of obturacular length to vestimental length variable, 1:2.6 to 1:6.7 (n = 40). Anterior margin of vestimentum forming short sheath around base of obturaculum (Fig. 2C, arrow), with shallow mid-ventral incision usually with overlapping lobes; posteroventral margin of vestimentum discontinuous, with posteroventral lobes of variable size and separated by large gap (Fig. 5A, B); length of vestimentum from 26.9 to 61.6 mm ($\bar{X}$ = 47.2 ± 8.9 mm; n = 40); diameter of vestimentum from 3.7 to 5.2 mm ($\bar{X}$ = 4.3 ± 0.6 mm; n = 40); ratio of vestimental diameter to vestimental length highly variable, 1:6.2 to 1:16.4 (n = 40); ventral surface of vestimentum with ciliated field, wider in middle region, bluntly to sharply tapered at anterior and posterior ends (Figs. 2D, E, 5A, B); plaques associated with epidermis ventrally and laterally, increasing in density in posterior one-half of vestimentum (Fig. 5A, B, arrowheads); males with paired dorsal ciliated grooves extending from gonopores

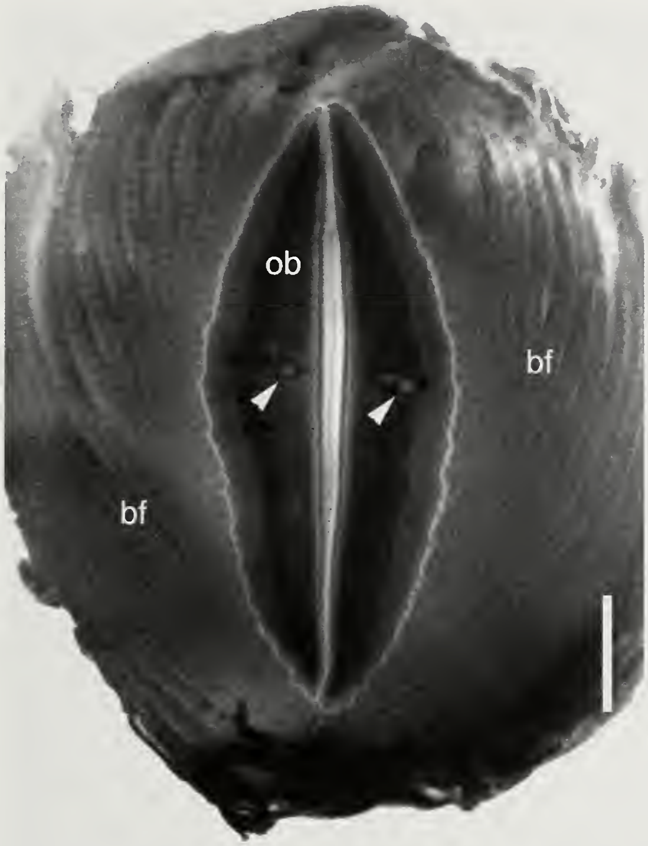

Fig. 4. *Lamellibrachia luymesi.* Light micrograph of cross section through middle region of branchial plume. Arrowheads indicate obturacular blood vessels. bf, branchial filaments; ob, obturaculum. Scale bar = 1 mm.

to near anterior end of vestimentum, diverging anteriorly (Fig. 5C). Trunk very long in adult specimens, tapering to less than 1 mm posteriorly; epidermis with numerous associated plaques 36–45 μm in diameter (Fig. 6). Opisthosome of selected specimen with 26 segments (Fig. 7A), 17 anterior segments each with chaetae occurring in single row, separated middorsally and midventrally by narrow band of epidermis lacking chaetae (Fig. 7B, C), and 9 posterior segments without chaetae; chaetae with teeth in anterior and posterior groupings; anterior grouping usually with 5 teeth in 2 rows, posterior grouping more variable, with 3–4 rows of 3–5 teeth (Fig. 7D). Tube hard, cream-colored to lightly yellowed tan with some dark banding anteriorly in living specimens (Fig. 1), becoming more darkly colored in preserved specimens; tube tapering posteriorly, diameter of aperture from 3.4 to 9.7 mm ($\bar{X}$ = 6.5 ± 1.5 mm, n = 44), with variable number of weakly to moderately developed collars anteriorly (Fig. 8A, B), becoming smooth in middle and posterior regions.

Distribution.—Presently known in the Atlantic Ocean from the type locality in 500 m of water off Guyana (8°01′N, 57°24′W) and in the Gulf of Mexico at several localities along the Louisiana slope in 500–650 m of water, including Green Canyon and Bush Hill hydrocarbon seep communities.

Remarks.—Several external morphological features have been used to distinguish between species of *Lamellibrachia,* including features of the branchial crown, proportions of body regions, and features of the tube (see Table 1). One of the most conspicuous features of the branchial crown is the presence of a number of sheaths composed of fused filaments, i.e., sheath lamellae, that enclose the inner branchial lamellae. Specimens of *L. luymesi* examined for this study usually possess 4 to 8 sheath lamellae on each side of the branchial crown, but most specimens have a different number of sheath lamellae on each side. Typically, one side will have 1 or 2 lamellae greater in number than the opposite side, although no pattern of preference is apparent in the specimens examined in this study. A few specimens have only 2 or 3 sheath lamellae on one side of the branchial crown. Close examination of the these specimens, however, always revealed damage to the branchial crown, and it is likely that some lamellae were torn away when the preserved specimens were removed from their tubes.

The number of pairs of sheath lamellae reported for the holotype of *L. luymesi* falls within the range recorded for specimens from the Gulf of Mexico and, therefore, supports their identification as *L. luymesi.* The majority of specimens with undamaged obturacula examined in the present study (23 of 30 specimens) exhibit a number of sheath lamellae intermediate between species with potentially fewer pairs (*L. barhami* and *L. satsuma*) and *L. columna* with

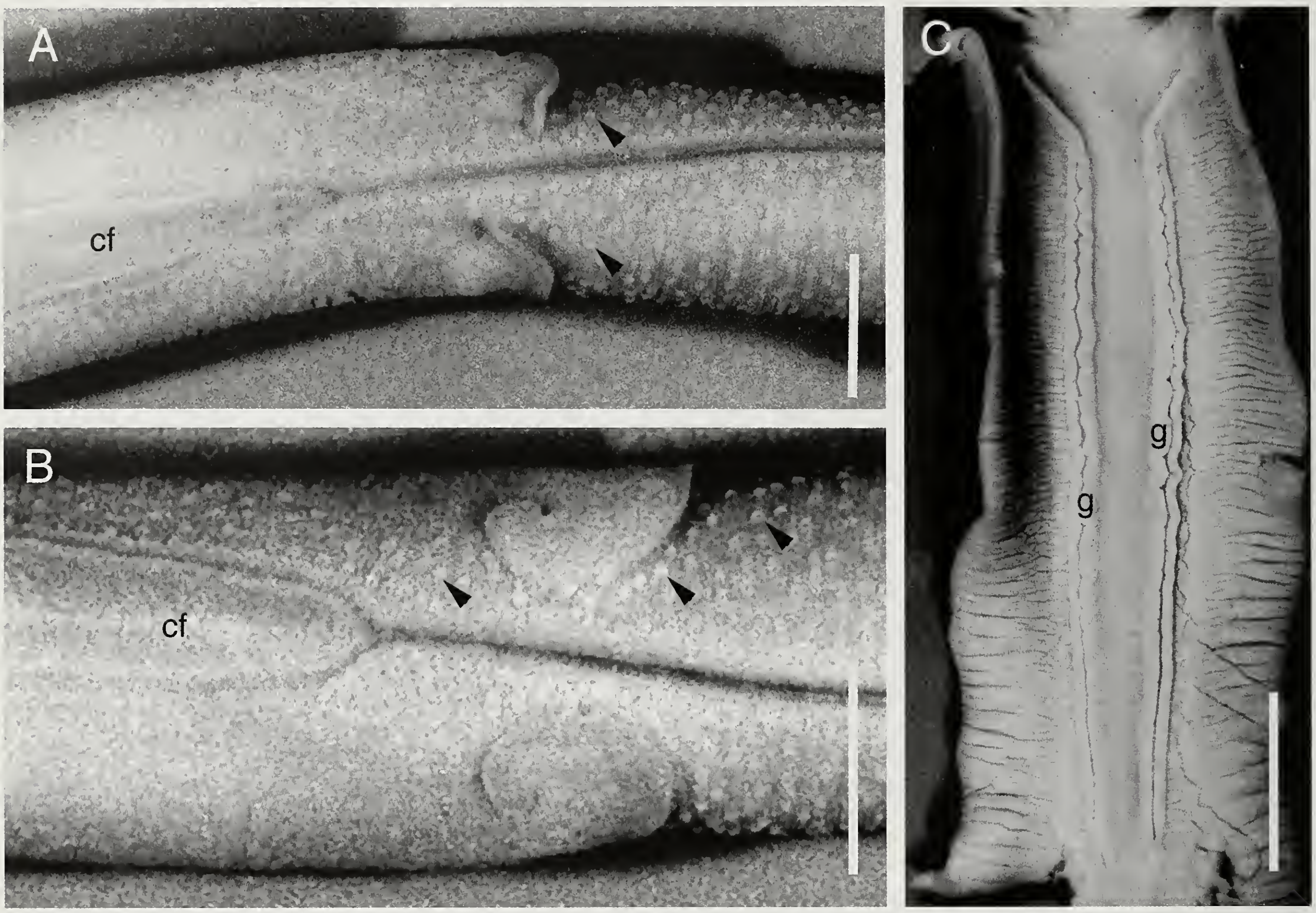

Fig. 5. *Lamellibrachia luymesi,* light micrographs of selected specimens. A, B, posterior end of vestimental region showing discontinuous posteroventral margin of vestimentum with variously developed lobes. Arrowheads indicate plaques on body wall. cf, ciliated field. C, dorsal view of vestimentum of male showing well-developed ciliated grooves (g) leading from gonopores to anterior end of vestimentum. Scale bars: A, B = 2 mm; C = 4 mm.

its higher number (Table 1). Number of pairs of sheath lamellae, therefore, is a useful character to distinguish *L. luymesi* from these other species. However, the number of sheath lamellae of the type material of *L. victori* falls within the range of *L. luymesi* so this character does not distinguish these two species.

Unlike the number of sheath lamellae, the number of branchial lamellae does not differ significantly so this feature is not a useful characteristic to distinguish between species (Table 1). Only *L. barhami* is reported to possess a number of branchial lamellae outside the range exhibited by specimens of *L. luymesi* examined in this study (see Webb 1969). However, Jones (1985) states that *L. barhami* can possess up to 25 pairs of branchial lamellae so it is likely that this species exhibits a range in number that is more consistent with other species of *Lamellibrachia.*

Although lengths and proportions of body regions are affected by a certain degree of contraction at the time of preservation, some interesting trends can be observed between species of *Lamellibrachia.* Among the five species of *Lamellibrachia* currently described, *L. columna* is the largest species and *L. satsuma* is potentially the smallest species (see Table 1). Lengths of the obturacular and vestimental regions of *L. barhami* overlap somewhat with those of *L. luymesi,* but the latter species exhibits a broader range of lengths for both regions and is generally overall the larger of the two species. The obturacular length reported for *L. victori* falls within the range of *L. luymesi* examined for this study, but its vestimental length is slightly greater than the

Fig. 6. *Lamellibrachia luymesi,* SEM. Portion of body wall of trunk region showing numerous plaques (p) and openings of pyriform glands (arrows). Scale bar = 100 μm.

maximum measured for *L. luymesi* (Table 1). Since the vestimental length of *L. victori* is based on a measurement taken from a single specimen, this difference is probably not significant.

Three species of *Lamellibrachia* for which multiple specimens have been examined, i.e., *L. barhami* (Webb 1969, Jones 1985), *L. luymesi* (present study), and *L. satsuma* (Miura et al. 1997), demonstrate generally similar ranges for the ratio of obturacular length to vestimental length (Table 1). Ratios calculated for the type material of *L. luymesi* and *L. victori* fall within the range observed for specimens of *L. luymesi* from the Gulf of Mexico.

When comparing ratios of vestimental diameter to vestimental length, *L. columna* and *L. luymesi* have generally similar values at the lower end of the range, but specimens of *L. luymesi* from the Gulf of Mexico exhibit a somewhat broader range overall (Table 1). Although the value calculated for the holotype of *L. luymesi* is slightly outside the range of specimens from the Gulf of Mexico, the value for that of *L. victori* falls within the range of *L. luymesi* from the Gulf of Mexico.

Van der Land & Nørrevang (1975, 1977) provide illustrations of the dorsal surface of the anterior region of the trunk of the holotype of *L. luymesi* that show a number of transverse grooves in the epidermis (they mistakenly state that these grooves occur on the ventral surface in their 1977 study; see p. 12). Southward (1991), however, questioned the taxonomic value of these grooves, suggesting that they may represent a contraction artifact. Specimens of *L. luymesi* from the Gulf of Mexico examined for this study vary greatly with regard to this feature. Some specimens possess numerous shallow grooves, whereas others have a few deep grooves, whereas still others lack grooves completely. We agree with Southward (1991) that these grooves, when present, represent an artifact of contraction produced at the time of preservation.

The opisthosome and opisthosomal chaetae are known for three species of *Lamellibrachia, L. luymesi* (present study), *L. columna* (Southward 1991) and *L. satsuma* (Miura et al. 1997). Although Webb (1969) discussed and illustrated what he thought was the opisthosome (= opisthomere in Webb) of four specimens of *L. barhami,* the absence of chaetae and external signs of segmentation cast doubt on his observations (also see Jones 1981). Southward (1991) suggested that the opisthosomal chaetae of vestimentiferans might display specific differences. Based on the limited chaetal material examined to date (one opisthosome each for *L. luymesi* and *L. satsuma,* and two for *L. columna*), significant specific differences among these species are not apparent. Chaetae possess teeth in anterior and posterior groupings in the following arrange-

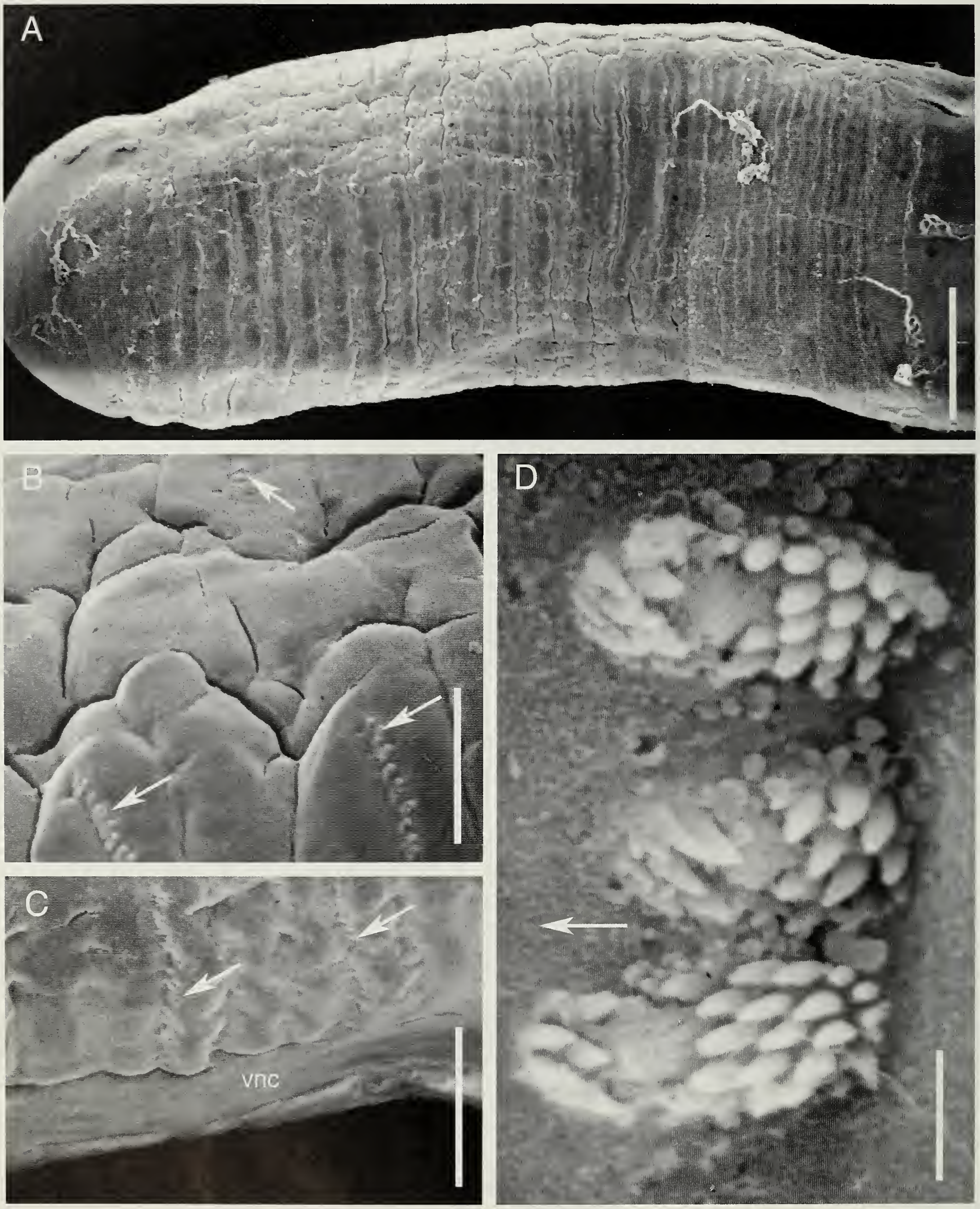

Fig. 7. *Lamellibrachia luymesi,* SEM of opisthosomal region. A, overview of opisthosome of selected specimen. B, dorsolateral view of two chaetigerous segments showing chaetae occurring in single rows (arrows) and middorsal area lacking chaetae. C, ventrolateral view of two chaetigerous segments showing chaetae (arrows) and position of internal ventral nerve cord (vnc). D, enlargement of chaetae. Arrow indicates anterior direction. Scale bars: A = 300 μm; B = 50 μm; C = 75 μm; D = 2 μm.

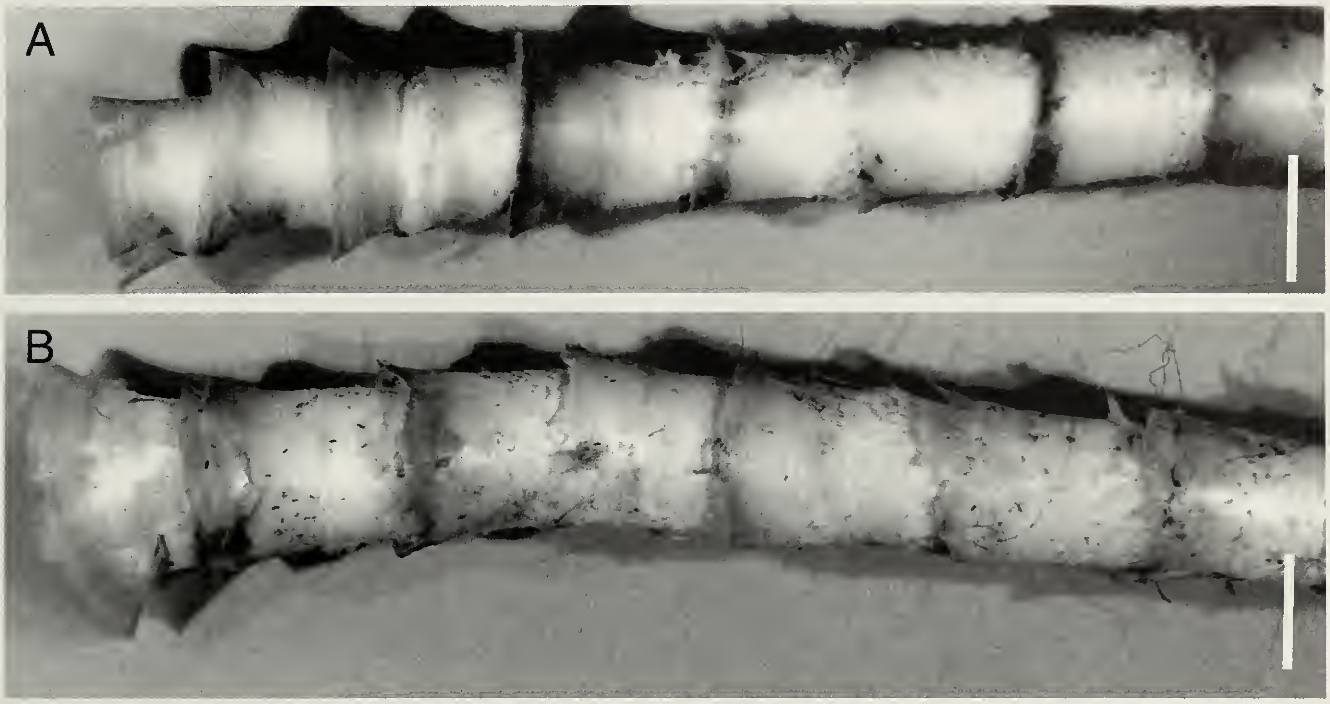

Fig. 8. *Lamellibrachia luymesi.* A, B, light micrographs of anterior ends of tubes showing growth collars. Scale bars = 5 mm.

ments for *L. luymesi, L. columna,* and *L. satsuma,* respectively: anterior groupings—5 teeth in 2 rows, 2–7 teeth in 1–2 rows, 6–9 teeth in 2 rows; posterior groupings—3–4 rows of 3–5 teeth, 3–5 rows of 3–4 teeth, 3–4 rows of 3–4 teeth. Some differences in the number of teeth in each grouping and the number of rows in which they occur exist between these species. However, additional material should be examined to quantify better any possible differences in chaetal characteristics of these and other species of *Lamellibrachia.*

With the possible exception of the maximum tube length provided for *L. satsuma,* tube lengths of all species listed in Table 1 are of incomplete tubes so the full extent of possible tube length in most species of *Lamellibrachia* is uncertain at this time. For *L. luymesi* in the Gulf of Mexico, tube lengths may actually exceed 2 m (SLG, SH, pers. obs.). Based on the absence of discoloration in the posterior region of the tube, van der Land & Nørrevang (1975, 1977) suggested that the tube of the holotype of *L. luymesi* was not buried in sediment. In contrast, specimens of *L. luymesi* in the Gulf of Mexico may have one-half or more of their tube length buried in sediment (SLG, SH, pers. obs.). Van der Land & Nørrevang (1975, 1977) acknowledged that the tube of the holotype of *L. luymesi* was incomplete posteriorly. Based on our observations of *L. luymesi* in the Gulf of Mexico, we believe that the tube of the holotype was broken at the time of collection, leaving a posterior portion buried in sediment.

The presence of collars on the anterior region of tubes is a common feature among vestimentiferans so it is not a particularly useful character to distinguish between species. It is interesting to note, however, that among the five described species of *Lamellibrachia, L. columna* is unique in lacking such collars on its tubes (Southward 1991).

Status of Lamellibrachia victori.—In her comparison of species of *Lamellibrachia* known at the time, Southward (1991) concluded that *L. columna* and *L. barhami* were distinct from each other and that both species were different from *L. luymesi* and *L. victori.* She further noted, however, that *L. luymesi* and *L. victori* could not be clearly distinguished from each other, but the limited material available for each species at the time hindered comparisons. Although

Table 1.—Comparison of certain diagnostic characters for species of *Lamellibrachia*.

	n	Number of sheath lamellae	Number of branchial lamellae	Obturaculum length (mm)	Vestimentum length (mm)	Obturaculum length: vestimentum length	Vestimentum diameter: vestimentum length	Tube length (mm; max)	Tube diameter (mm; aperture)
L. luymesi Gulf of Mexico specimens	40	4–8[a]	15–22	6.6–16.3	26.9–61.6	1:2.6 to 1:6.7	1:6.2 to 1:16.4	1560	3.4–9.7
L. luymesi, holotype van der Land & Nørrevang, 1975	1	6	19[b]	13	63	1:4.8	1:4.5	687	10
L. barhami Webb, 1969	>15[c]	2–4	25	4.5–12.2	23–36.5	1:2.5 to 1:7.8	1:2.9 to 1:6.7	1546	7.5–9
L. victori Mañé-Garzón & Montero, 1985	2	7	18[d]	13	65	1:5	1:8	240	15
L. columna Southward, 1991	14	8–16	21[e]	15–42	60–120	1:2.2 to 1:4.5	1:6.5 to 1:13	820	14–20
L. satsuma Miura, Tsukahara & Hashimoto, 1997	82	0–4[f]	up to 19	1.8–9.8	7.2–24	1:2.1 to 1:8.3	—	1000	2.5–8.7

[a] Undamaged specimens.

[b] Approximate number from Fig. 18 in van der Land & Nørrevang (1977).

[c] Four type specimens from Webb (1969) and numerous specimens from Jones (1985).

[d] Approximate number from Fig. 6 in Mañé-Garzón & Montero (1985).

[e] Approximate number from Fig. 5B in Southward (1991).

[f] Zero in juvenile specimens.

no publications to date indicate that new material of *L. victori* has been collected, abundant new material of *L. luymesi* from the Gulf of Mexico has been examined in the present study, allowing for a better understanding of the morphological variation it exhibits for a number of external features (see Table 1). Results of this study corroborate Southward's (1991) conclusion that *L. luymesi* is distinct from other species of *Lamellibrachia,* except for *L. victori.* For all features listed in Table 1, values for the type material of *L. victori* fall within the range of *L. luymesi* (holotype and Gulf of Mexico specimens), except for length of the vestimentum and aperture diameter of the tube. Because values for these features of *L. victori* are taken from a very limited number of specimens, it is difficult to know their significance with regard to recognizing *L. victori* as a valid species of *Lamellibrachia.* It is likely, however, that the difference in vestimental length is not significant. To resolve this issue, new material must be obtained from the area where the type material of *L. victori* was collected and compared with *L. luymesi.* Until such a study is completed, *L. victori* remains questionably distinct from *L. luymesi.*

Discussion

Presently, ten genera of vestimentiferan tube worms have been described, including *Lamellibrachia* Webb, 1969, *Riftia* Jones, 1981, *Escarpia* Jones, 1985, *Oasisia* Jones, 1985, *Ridgeia* Jones, 1985, *Tevnia* Jones, 1985, *Alaysia* Southward, 1991, *Arcovestia* Southward & Galkin, 1997, *Seepiophila* Gardiner, McMullin & Fisher, 2001, and *Paraescarpia* Southward, Schulze & Tunnicliffe, 2002. With five described species, *Lamellibrachia* contains the largest number of species of these genera. *Escarpia* contains two recognized species, whereas all other genera are monotypic. Among these genera, *Lamellibrachia* also demonstrates the broadest geographic range with two described species occurring in the western Pacific Ocean (*L. columna* and *L. satsuma*), one species in the eastern Pacific Ocean (*L. barhami*), and two species in the western Atlantic Ocean, including the Gulf of Mexico (*L. luymesi* and *L. victori*). Dando et al. (1992) found tubes of vestimentiferan worms in a shipwreck in 1160 m of water in the eastern Atlantic Ocean off Vigo, Spain. They indicated that the appearance of the tubes resembled that of tubes of *L. barhami,* but they were unable to confirm the identity of the species because fully intact worms were not available. Williams et al. (1993), however, were able to obtain degraded tissue from these tubes. In their analysis of the 28S rRNA nuclear gene, they demonstrated that this tissue consistently grouped with species of *Lamellibrachia* also examined in their study. This finding supports the suggestion that the tubes belong to a species of *Lamellibrachia,* thereby confirming the presence of *Lamellibrachia* in the eastern Atlantic Ocean. Recently, *Lamellibrachia* was reported from the southeastern Mediterranean Sea off Crete and Turkey in about 1700 to 2000 m of water (Olu-Le Roy et al. 2001). Currently, no vestimentiferan species are known to occur in the Indian Ocean (see Van Dover et al. 2001).

The two Atlantic species of *Lamellibrachia* are presently known only from cold seep regions on continental margins. It is of interest to note that two Pacific species, i.e., *L. barhami* and *L. satsuma,* have been collected from vent and seep sites, whereas a third described Pacific species, *L. columna,* is recorded only from vent sites (Southward & Galkin 1997, Tunnicliffe et al. 1998, Kojima et al. 2001). In a study based on a partial nucleotide sequence of the cytochrome oxidase I mitochondrial gene (COI) of specimens of *Lamellibrachia* collected from ten sites in the western Pacific, Kojima et al. (2001) recognized four tentative undescribed species, in addition to specimens identified as *L. satsuma.* Of these four undescribed species, two were collected from vent sites only, one was found exclusively in seep sites, and one occurred in vent and seep sites.

Among species of *Lamellibrachia* presently described, morphological characters of the specimens examined in this study are consistent with those of *L. luymesi* and *L. victori.* If these two species are shown to be identical in the future, *L. luymesi* has priority. However, the type locality of *L. luymesi* off Guyana and localities in the northern Gulf of Mexico where specimens were collected for the present study are separated by a distance of approximately 4000 km with localities of intermediate populations not currently known. Based on sequence similarity of the COI mitochondrial gene, McMullin et al. (2003) report that populations of a species of *Lamellibrachia,* which occur over a distance of 6000 km along the west coast of North America, represent a single species, i.e., *L. barhami.* Using similar evidence, McMullin et al. (2003) also indicate that *Paraescarpia echinospica* exhibits a geographic range of at least 4500 km in the western Pacific Ocean. Based on morphological similarity, we suggest that *L. luymesi* is distributed over a wide geographic range in the western Atlantic Ocean.

Lamellibrachia luymesi co-occurs in the Gulf of Mexico with two additional vestimentiferan worms, *Seepiophila jonesi,* which is sympatric with *L. luymesi* in certain seep communities (see Gardiner et al. 2001), and *Escarpia laminata* which was originally recorded from deep water at the base of the Florida Escarpment (Paull et al. 1984, Jones 1985). In addition to the seep sites reported in this study, a species of *Lamellibrachia* occurs along the Louisiana slope in the Gulf of Mexico in a large number of other seep sites (see references in synonymy above for coordinates), extending along a distance of at least 480 km and depths of 550 to 650 m of water. An analysis of the COI gene of specimens taken from populations of *Lamellibrachia* along this distance of the Louisiana slope, including the seep sites used for this study, shows genetic distances indicative of intraspecific variation (McMullin et al. 2003). Morphological similarity of specimens examined in this study, together with the evidence from the analysis of the COI gene, support the suggestion that a single species of *Lamellibrachia,* i.e., *L. luymesi,* inhabits hydrocarbon seep communities along the Louisiana slope in the Gulf of Mexico.

Acknowledgments

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Literature Cited

Bergquist, D. C., I. A. Urcuyo, & C. R. Fisher. 2002. Establishment and persistence of seep vestimentiferan aggregations on the upper Louisiana slope of the Gulf of Mexico.—Marine Ecology Progress Series 241:89–98.

Brooks, J. M., et al. 1987. Deep-sea hydrocarbon seep communities: evidence for energy and nutritional carbon sources.—Science 238:1138–1142.

Carney, R. S. 1994. Consideration of the oasis analogy for chemosynthetic communities at Gulf of

Mexico hydrocarbon vents.—Geo-Marine Letters 14:149–159.

Childress, J. J., & C. R. Fisher. 1992. The biology of hydrothermal vent animals: physiology, biochemistry, and autotrophic symbioses. Pp. 337–441 *in* M. Barnes, A. D. Ansell, & R. N. Gibson, eds., Oceanography and Marine Biology An Annual Review, vol. 30. Biddles Ltd, King's Lynn and Guilford, England, 627 pp.

———, ———, J. M. Brooks, M. C. Kennicutt, II, R. Bidigare, & A. E. Anderson. 1986. A methanotrophic marine molluscan (Bivalvia: Mytilidae) symbiosis: mussels fueled by gas.—Science 233:1306–1308.

Dando, P. R., A. J. Southward, E. C. Southward, D. R. Dixon, A. Crawford, & M. Crawford. 1992. Shipwrecked tube worms.—Nature 356:667.

Feldman, R. A., M. B. Black, C. S. Cary, R. A. Lutz, & R. C. Vrijenhoek. 1997. Molecular phylogenetics of bacterial endosymbionts and their vestimentiferan hosts.—Molecular Marine Biology and Biotechnology 6:268–277.

Fisher, C. R. 1995. Toward an appreciation of hydrothermal-vent animals: their environment, physiological ecology, and tissue stable isotope values. Pp. 297–316 *in* S. E. Humphris, R. A. Zierenberg, L. S. Mullineaux, & R. E. Thomson, eds., Seafloor hydrothermal systems: physical, chemical, biological, and geochemical interactions. Geophysical Monographs Series 91:1–466.

———, J. J. Childress, & N. K. Sanders. 1988. The role of vestimentiferan hemoglobin in providing an environment suitable for chemoautotrophic sulfide oxidizing endosymbionts.—Symbiosis 5:229–246.

———, M. C. Kennicutt, II, & J. M. Brooks. 1990. Stable carbon isotopic evidence for carbon limitation in hydrothermal vent vestimentiferans.—Science 247:1094–1096.

———, I. A. Urcuyo, M. A. Simpkins, & E. Nix. 1997. Life in the slow lane: growth and longevity of cold-seep vestimentiferans.—Marine Ecology 18:83–94.

Freytag, J. K., P. R. Girguis, D. C. Bergquist, J. P. Andras, J. J. Childress, & C. R. Fisher. 2001. A paradox resolved: sulfide acquisition by roots of seep tubeworms sustains net chemoautotrophy.—Proceedings of the National Academy of Sciences 98:13408–13413.

Gardiner, S. L., E. McMullin, & C. R. Fisher. 2001. *Seepiophila jonesi*, a new genus and species of vestimentiferan tube worm (Annelida: Pogonophora) from hydrocarbon seep communities in the Gulf of Mexico.—Proceedings of the Biological Society of Washington 114:694–707.

Jones, M. L. 1981. *Riftia pachyptila*, new genus, new species, the vestimentiferan worm from the Galápagos Rift geothermal vents (Pogonophora).—Proceedings of the Biological Society of Washington 93:1295–1313.

———. 1985. On the Vestimentifera, new phylum: six new species, and other taxa, from hydrothermal vents and elsewhere.—Bulletin of the Biological Society of Washington 6:117–158.

Julian, D., F. Gaill, E. Wood, A. J. Arp, & C. R. Fisher. 1999. Roots as a site of hydrogen sulfide uptake in the hydrocarbon seep vestimentiferan *Lamellibrachia* sp.—The Journal of Experimental Biology 202:2245–2257.

Kennicutt, M. C., II, J. M. Brooks, R. R. Bidigare, R. R. Fay, T. L. Wade, & T. J. McDonald. 1985. Vent-type taxa in a hydrocarbon seep region on the Louisiana slope.—Nature 317:351–353.

Kojima, S., S. Ohta, T. Yamamoto, T. Miura, Y. Fujiwara, & J. Hashimoto. 2001. Molecular taxonomy of vestimentiferans of the western Pacific and their phylogenetic relationship to species of the eastern Pacific. I. Family Lamellibrachiidae.—Marine Biology 139:211–219.

Land, J. van der, & A. Nørrevang. 1975. The systematic position of Lamellibrachia [sic] (Annelida, Vestimentifera). Pp. 86–101 *in* A. Nørrevang ed., The phylogeny and systematic position of Pogonophora. Zeitschrift für zoologische Systematik und Evolutionsforshung, Sonderheft 1, 143 pp.

———, & ———. 1977. Structure and relationships of *Lamellibrachia* (Annelida, Vestimentifera).—Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter 21(3):1–102.

MacDonald, I. R., G. S. Boland, J. S. Baker, J. M. Brooks, M. C. Kennicutt, II, & R. R. Bidigare. 1989. Gulf of Mexico hydrocarbon seep communities II. Spatial distribution of seep organisms and hydrocarbons at Bush Hill.—Marine Biology 101:235–247.

———, N. L. Guinasso, Jr., J. F. Reilly, J. M. Brooks, W. R. Callender, & S. G. Gabrielle. 1990. Gulf of Mexico hydrocarbon seep communities: VI. Patterns in community structure and habitat.—Geo-Marine Letters 10:244–252.

Mañé-Garzón, F., & R. Montero. 1985. Sobre una nueva forma de verme tubicola Lamellibrachia victori [sic] n.sp. (Vestimentifera)–Proposicion de un nuevo phylum: Mesoneurophora.—Revista de Biologia del Uruguay 8:1–28.

McMullin, E. R., S. Hourdez, S. W. Schaeffer, & C. R. Fisher. 2003. Phylogenetics and biogeography of deep-sea vestimentiferan tubeworms and their bacterial symbionts.—Symbiosis 34:1–41.

Miura, T., J. Tsukahara, & J. Hashimoto. 1997. *Lamellibrachia satsuma*, a new species of vestimentiferan worms (Annelida: Pogonophora) from a shallow hydrothermal vent in Kagoshima Bay, Japan.—Proceedings of the Biological Society of Washington 110:447–456.

Nelson, K., & C. R. Fisher. 2000. Absence of cospeciation in deep-sea vestimentiferan tube worms and their bacterial endosymbionts.—Symbiosis 28:1–15.

Olu-Le Roy, K., M. Sibuet, G. Levitre, S. Gofas, & A. Fiala-Médioni. 2001. Cold seep communities in the deep Mediterranean Sea (South of Crete and Turkey): faunistic composition and spatial distribution.—Program and abstracts. Second International Symposium on Deep-sea Hydrothermal Vent Biology. Brest, France. [Abstract, p. 208].

Paull, C. K., et al. 1984. Biological communities at the Florida Escarpment resemble hydrothermal vent taxa.—Science 226:965–967.

Salvini-Plawen, L. V. 2000. What is convergent/homoplastic in Pogonophora?—Journal of Zoological Systematics & Evolutionary Research 38:133–147.

Schulze, A. 2001. Comparative anatomy of excretory organs in vestimentiferan tube worms (Pogonophora, Obturata).—Journal of Morphology 250:1–11.

Scott, K. M., & C. R. Fisher. 1995. Physiological ecology of sulfide metabolism in hydrothermal vent and cold seep vesicomyid clams and vestimentiferan tube worms.—American Zoologist 35: 102–111.

Southward, E. C. 1991. Three new species of Pogonophora, including two vestimentiferans, from hydrothermal sites in the Lau Back-arc Basin (Southwest Pacific).—Journal of Natural History 25:859–881.

———. 1999. Development of Perviata and Vestimentifera (Pogonophora).—Hydrobiologia 402: 185–202.

———, & S. V. Galkin. 1997. A new vestimentiferan (Pogonophora: Obturata) from the hydrothermal vent fields in the Manus Back-arc Basin (Bismarck Sea, Papua New Guinea, Southwest Pacific Ocean).—Journal of Natural History 31: 43–55.

———, A. Schulze, & S. L. Gardiner. 2003. Pogonophora: form and function (Annelida).—Hydrobiologia (in press).

———, ———, & V. Tunnicliffe. 2002. Vestimentiferans (Pogonophora) in the Pacific and Indian Oceans: a new genus from Lihir Island (Papua New Guinea) and the Java Trench, with the first report of *Arcovestia ivanovi* from the North Fiji Basin.—Journal of Natural History 36:1179–1197.

Tunnicliffe, V., A. G. McArthur, & D. McHugh. 1998. A biogeographical perspective of the deep-sea hydrothermal vent fauna.—Advances in Marine Biology 34:353–442.

Tyler, P. A., & C. M. Young. 1999. Reproduction and dispersal at vents and cold seeps.—Journal of the Marine Biological Association, United Kingdom 79:193–208.

Van Dover, C. L., et al. 2001. Biogeography and ecological setting of Indian Ocean hydrothermal vents.—Science 294:818–823.

Webb, M. 1969. *Lamellibrachia barhami,* gen. nov., sp. nov. (Pogonophora), from the Northeast Pacific.—Bulletin of Marine Science 19:18–47.

Williams, N. A., D. R. Dixon, E. C. Southward, & P. H. W. Holland. 1993. Molecular evolution and diversification of the vestimentiferan tube worms.—Journal of the Marine Biological Association, United Kingdom 73:437–452.

Young, C. M., E. Vázquez, A. Metaxas, & P. A. Tyler. 1996. Embryology of vestimentiferan tube worms from deep-sea methane/sulfide seeps.—Nature 381:514–516.

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Four new genera of leucosiid crabs (Crustacea: Brachyura: Leucosiidae) for three new species and nine species previously in the genus *Randallia* Stimpson, 1857, with a redescription of the type species, *R. ornata* (Randall, 1939)

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Abstract.—A study of the leucosiid genus *Randallia* Stimpson, 1857, led to the description of four new genera: *Tanaoa,* for *R. distincta* Rathbun, 1893, *R. pustulosa* Wood-Mason, in Wood-Mason & Alcock, 1891, and a new species, *T. nanus*; *Tokoyo* for *R. eburnea* Alcock, 1896, and a new species, *T. cirrata*; *Toru* for *R. granuloides* Sakai, 1961, *R. trituberculata* Sakai, 1961, *R. pila* Tan, 1996, *R. mesjatzevi* Zarenkov, 1990, and a new species, *T. septimus*; and *Urashima,* for *R. lamellidentata* Wood-Mason, 1892, and *R. pustuloides* Sakai, 1961. *Randallia* is restricted to its type species, *R. ornata* (Randall, 1839), and provisionally 12 other species currently placed in this genus pending further revision. All new genera are diagnosed and species assigned to them described or redescribed and illustrated; extended synonymies are given, and a key for species identification is provided. The type species, *R. ornata,* is redescribed.

The genus *Randallia* Stimpson 1857a was established for *Ilia ornata* Randall, 1839, a leucosiid crab known from the Pacific and Gulf coasts of California (Stimpson, 1857a). The chaotic leucosiid systematics and the fact that Stimpson (1857a:85; 1857b:471) gave but a cursory description, allowed for a miscellaneous assortment of leucosiid crabs to be relegated to that genus. Several authors (Doflein 1904, Serène & Soh 1976, Tan 1996) regarded *Randallia* as a heterogenous genus in need of revision. Yaldwyn & Dawson (1976) sorted *Randallia* species into four ill-fitting "species groups" according to rugosity of the carapace and length of chelipeds, while disregarding the variation in the segmentation of the male abdomen, structure of the first male pleopod, and other morphological features. Though 30 species have been hitherto assigned to *Randallia,* doubts remained as to their systematic position (Ovaere 1989).

A study of the extensive collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C., together with other major collections has enabled re-examination of many type specimens and much of the published material, and led to a reevaluation of *Randallia.* As result, the genus is herein restricted to its type species, *R. ornata* (Randall 1839), known from the eastern Pacific, and 12 other species provisionally retained in *Randallia* s. s. pending further revision (Table 1). Of the other 17 species hitherto assigned to *Randallia* s. l., *R. angelica* Garth, 1940 was synonymized with *R. ornata* (Randall, 1839), by Hendrickx (1997). *Randallia japonica* Yokoya, 1933 was declared a junior synonym of *R. eburnea* Alcock, 1896, by Sakai (1934). Four species were transferred to other genera: *R. coronata* Alcock & Anderson, 1894 to *Pariphiculus* Alcock, 1896, by Alcock (1896); *R. lanata* Alcock, 1896 and *R. villosa* Chen, 1989 to *Ihleus* Ovaere, 1989, by Ovaere (1989); and *R. mirabilis*

Table 1.—Generic assignment of species hitherto attributed to _Randallia_ Stimpson, 1857a (* species herein provisionally retained in _Randallia_ s. s., pending further revision).

*_R. agaricias_ Rathbun, 1898.
*_R. americana_ (Rathbun, 1893)
R. angelica Garth, 1940: synonymized with _R. ornata_ (Randall, 1839) (see Hendrickx 1997).
*_R. bulligera_ Rathbun, 1898
R. coronata Alcock & Anderson, 1894: reassigned to _Pariphiculus_ Alcock, 1896 (see Alcock 1896)
*_R. curacaoensis_ Rathbun, 1922
R. distincta Rathbun, 1893: placed in _Tanaoa,_ new genus
*_R. eburnea_ Alcock, 1896: placed in _Tokoyo,_ new genus
*_R. glans_ Alcock, 1896
*_R. gilberti_ Rathbun, 1906
*_R. granulata_ Miers, 1886
R. granuloides Sakai, 1961: placed in _Toru,_ new genus
R. japonica Yokoya, 1933: synonymized with _R. eburnea_ Alcock, 1896 (see Sakai 1934)
*_R. laevis_ (Borradaile, 1916)
R. lamellidentata Wood-Mason, 1892: placed in _Urashima,_ new genus
R. lanata Alcock, 1896: reassigned to _Ihleus_ Ovaere, 1989 (see Ovaere 1989)
R. mesjatzevi Zarenkov, 1990: placed in _Toru,_ new genus
*_R. minuta_ Rathbun, 1935
R. mirabilis Zarenkov, 1969: reassigned to _Raylilia_ Galil, 2001 (see Galil 2001)
*_R. nana_ Zarenkov, 1990
R. ornata (Randall, 1839): type species of _Randallia_ Stimpson, 1857a
R. pila Tan, 1996: placed in _Toru,_ new genus
*_R. pustulilabris_ Alcock, 1896
R. pustuloides Sakai, 1961: placed in _Urashima,_ new genus
R. pustulosa Wood-Mason, in Wood-Mason & Alcock, 1891: placed in _Tanaoa,_ new genus
R. serenei Richer de Forges, 1983: is placed in synonymy with _Tanaoa distinctus_ (Rathburn, 1893)
*_R. speciosa_ Chen, 1989
R. trituberculata Sakai, 1961: placed in _Toru,_ new genus
R. villosa Chen, 1989: reassigned to _Ihleus_ Ovaere, 1989 (see Ovaere 1989)
R. vitjazi Zarenkov, 1994: placed in synonymy with _Tanaoa pustulosus_ (Wood-Mason, in Wood-Mason & Alcock, 1891)

Zarenkov, 1969 to _Raylilia_ Galil, 2001, by Galil (2001). Four new genera are herein established for three new species, and nine species previously in _Randallia_ s. l. _Randallia serenei_ Richer de Forges, 1983, and _Randallia vitjazi_ Zarenkov, 1994, were recognized as junior synonyms of previously described species. _Randallia_ s. s. differs from the newly established genera in having the antennular operculum entirely sealing the antennular aperture, the anterior margin of efferent branchial channel trilobate, and the male abdominal segments 3–5 fused. All species in the new genera are described or redescribed and illustrated, extended synonymies given, and a key for their identification is provided. The type species, _R. ornata,_ is also redescribed.

Abbreviations used are: btw, between; coll., collector; CP, chalut à perche (beam trawl); CH, chalut (trawl); DW, Waren dredge; I., Island; Is., Islands; Lt., Light; Pt., Point; Stn, station. The French expedition BATHUS was named after the Greek word for deep, _bathys._ The other French expeditions are identified by acronyms: BORDAU, a contraction of "bordure d'Australo-indienne plateau"; CHALCAL, "chalutage New Caledonia"; HALIPRO, "halieutique profonde"; KARUBAR, a contraction of the names of Kai, Aru and Tanimber Islands; MUSORSTOM was organized jointly by the Muséum national d'Histoire naturelle and the Office de la Recherche Scientifique et Technique Outre-Mer (ORSTOM).

The length of each specimen was measured along the vertical median line of the carapace, excluding intestinal spine.

The material used remains deposited in the following museums: National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM); The National Natuurhistorische Museum, Leiden (formerly Rijksmuseum van Natuurlijke History) (NNM); Museum national d'Histoire naturelle, Paris (MNHN); The Natural History Museum, London (NHM); Australian Museum, Sydney (AMS); National Institute of Water & Atmospheric Research, New Zealand (NIWA); National Taiwan Ocean University, Keelung (NTOU); Queensland Museum, Brisbane (QM); South African Museum, Cape Town (SAM); Senckenberg Museum, Frankfurt (SMF); Western Australian Museum, Perth (WAM); Zoological Museum, Amsterdam (ZMA); and Zoological Museum, Moscow University (ZMMU).

Randallia ornata (Randall, 1839)
Figs. 1A, 3A, B

Ilia ornata Randall, 1839:129.

Guaia ornata Gibbes, 1850:186.

Randallia ornata Stimpson, 1857a:85; 1857b:471, pl. 20 fig. 3; 1860:69.—Rathbun, 1898:613; 1904:170; 1937:172, pl. 49, figs 1–2.—Holmes, 1900:100.—Weymouth, 1910:18, pl. 1, fig. 3.—Baker, 1912:102.—Schmitt, 1921:188, fig. 116.—Serène, 1954:491.—Garth, 1960: 111; 1966:10.—Richer de Forges, 1983: 634 (tab.).—Austin, 1985:646.—Bonfil & Carvacho, 1989:83, fig. 4a.—Hendrickx, 1990:45; 1992:7; 1995:129; 1997:163, fig. 114.

Randallia angelica Garth, 1940:54; pl. 11, figs 1–2.—Serène, 1954:492.—Richer de Forges, 1983:634 (tab.).—Rodríguez de la Cruz, 1987:120.

Not *Randallia ornata* Boone, 1930:59, pl. 12 [= *R. bulligera* Rathbun *fide* Garth 1966:10].

Type material.—Paratypes of *Randallia angelica* Garth, 1940: Puerto Refugio, Angel de la Guardia I., R/V *Velero*, Stn 541-36, 110 m, 4 Mar 1936, ♂ 19.5 mm, ♀ 18.5 mm (USNM 139772).

Material examined.—United States. California, San Francisco, 1880, coll. D. S. Jordan, 2 ♀ 30.2, 38.3 mm (USNM 3115). San Francisco Bay, R/V *Albatross*, Apr 1914, ♂ 44.0 mm (USNM 55532). Golden Gate, 21 Jun 1915, ♀ ovig. 39.8 mm (USNM 66506). Monterey Bay, Santa Cruz Lighthouse, R/V *Albatross*, Stn 4560, 18 m, 11 Jun 1904, ♂ 30.2 mm (USNM 66505). Santa Barbara, 1880, coll. D. S. Jordan, 4 ♂ 48.8–54.4 mm, 4 ♀ ovig. 30.2–33.4 mm (USNM 3101). Mugu Bay, Ventura Co., Aug 1923, coll. E. P. Chace, ♂ 25.2 mm, ♀ ovig. 27.4 mm (USNM 57284). Santa Cruz I., R/V *Albatross*, 7 Feb 1889, ♀ 40.0 mm (USNM 17394). San Pedro I., Mar 1931, ♂ 26.3 mm (USNM 21791). Long Beach, coll. H. N. Lowe, 2 ♂ 28.9, 41.9 mm, 2 ♀ 33.5, 35.5 mm (USNM 46684). Newport Bay, 16 Jan 1939, coll. S. A. Glasell, 4 ♂ 19.8–33.5 mm, ♀ 18.7 mm (USNM 207834). Santa Catalina I., R/V *Anton Dohrn*, 30 Dec 1912, 2 ♂ 16.4, 26.2 mm, ♀ 18.2 mm (USNM 50115). Catalina harbour, 23 Jun 1916, ♂ 15.6 mm, ♀ ovig. 17.6 mm (USNM 66488). SW Catalina harbour, 23 Jun 1916, ♀ 19.4 mm (USNM 66496). San Nicolas I., R/V *Albatross*, Stn 4422, 57 m, 13 Apr 1904, ♀ 21.4 mm (USNM 66504). San Diego Bay, R/V *Albatross*, 1 Mar 1904, ♀ 33.4 mm (USNM 66507).

Mexico. Lower California, Playa Maria Bay, 24–26 Aug 1896, coll. A.W. Anthony, 8 ♂ 31.3–53.3 mm, 5 ♀ ovig. 25.7–37.7 mm (USNM 19521). Corona del Mar, 13 m, Jul 1935, coll. G. E. MacGinitie, ♂ 48.8 mm (USNM 89739). Mar 1948, coll. G. E. MacGinitie, ♀ ovig. 30.8 mm (USNM 89742). Balboa, 0–27.5 m, coll. S. H. Glassell, 4 ♂ 11.9–27.3 mm, 4 ♀ 18.1–35.3 mm (USNM 207834).

Redescription.—Dorsal surface of carapace smooth, minutely shagreened anteriorly. Frontal lobes triangulate, anteriorly granulate. Anterolateral margin with subhepatic granulate tubercle, 3 or more pear-

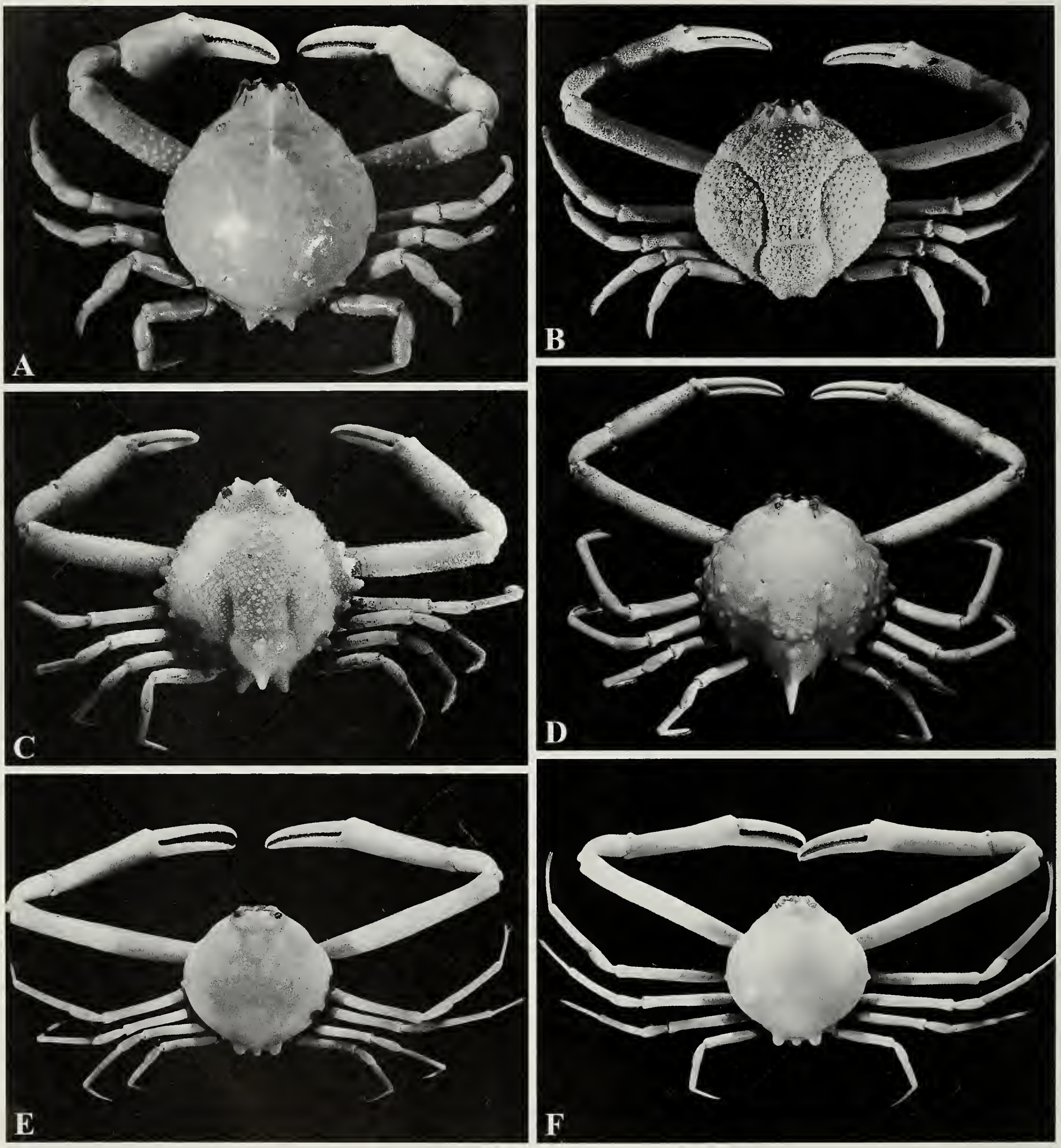

Fig. 1. A, *Randallia ornata* (Randall, 1839): ♂ cl 30.2 mm, dorsal view, California, Monterey Bay, R/V *Albatross,* Stn 4560, USNM 66505; B, *Tanaoa distinctus* (Rathbun, 1893): ♂ cl 40.5 mm, dorsal view, Banc Tuscarora, MUSORSTOM 7, Stn DW 556, MNHN; C, *Tanaoa nanus,* new species: holotype, ♂ cl 12.7 mm, dorsal view, Vanuatu, MUSORSTOM 8, Stn CP 1053, MNHN; D, *Tanaoa pustulosus* (Wood-Mason, in Wood-Mason & Alcock, 1891): ♂ cl 35.8 mm, dorsal view, Btw Negros, Siquijor, R/V *Albatross* Stn 5538, USNM; E, *Tokoyo cirrata,* new species: holotype, ♂ cl 13.0 mm, dorsal view, Vanuatu, MUSORSTOM 8, Stn CP 1086, MNHN; F, *Tokoyo eburnea* (Alcock, 1896): ♂ cl 14.8 mm, dorsal view, Japan, Tosa Bay, SMF 22577.

liform granules on epibranchial margin. Posterolateral margin with small, triangular denticle. Posterior margin bearing 2 dorsoventrally flattened triangular denticles laterally, pearliform granules medially. Hepatic region tumid, topped by 1 or more pearliform granules. Intestinal region slightly inflated, bearing a granule (Fig. 1A).

Anterior margin of efferent branchial channel granulate, with 3 subequal lobes.

Fig. 2. A, *Toru granuloides* (Sakai, 1961): ♂ cl 23.0 mm, dorsal view, Loyalty Is, MUSORSTOM 6, Stn DW 456 (MNHN); B, *Toru pilus* (Tan, 1996): ♂ cl 10.8 mm, dorsal view, Vanuatu, MUSORSTOM 8, Stn CP 1047 (MNHN); C, *Toru septimus*, new species: holotype. ♂ cl 13.1 mm, dorsal view, Loyalty Is., Stn DW 421 (MNHN); D, *Toru trituberculatus* (Sakai, 1961): ♂ cl 13.0 mm, dorsal view, Japan, Mimase (SMF); E, *Urashima lamellidentatus* (Wood-Mason, 1892): holotype. ♂ cl 11.9 mm, dorsal view, Andaman Is. (NHM 1896.9.8.7); F, *Urashima pustuloides* (Sakai, 1961): ♂ cl 32.8 mm, dorsal view, Taiwan, I-Lan county (MNHN B26326).

Third maxilliped anteriorly setose, granulose.

Cheliped merus 0.75 as long as carapace, set with pearliform granules; carpus with few granules distally on upper margin; propodus swollen, smooth but for minutely granulate upper margin; fingers, longer than palm, set with longitudinal granulate ridges. Pereiopodal carpi 1–4 with upper margin distally granulose; upper margin of propodi

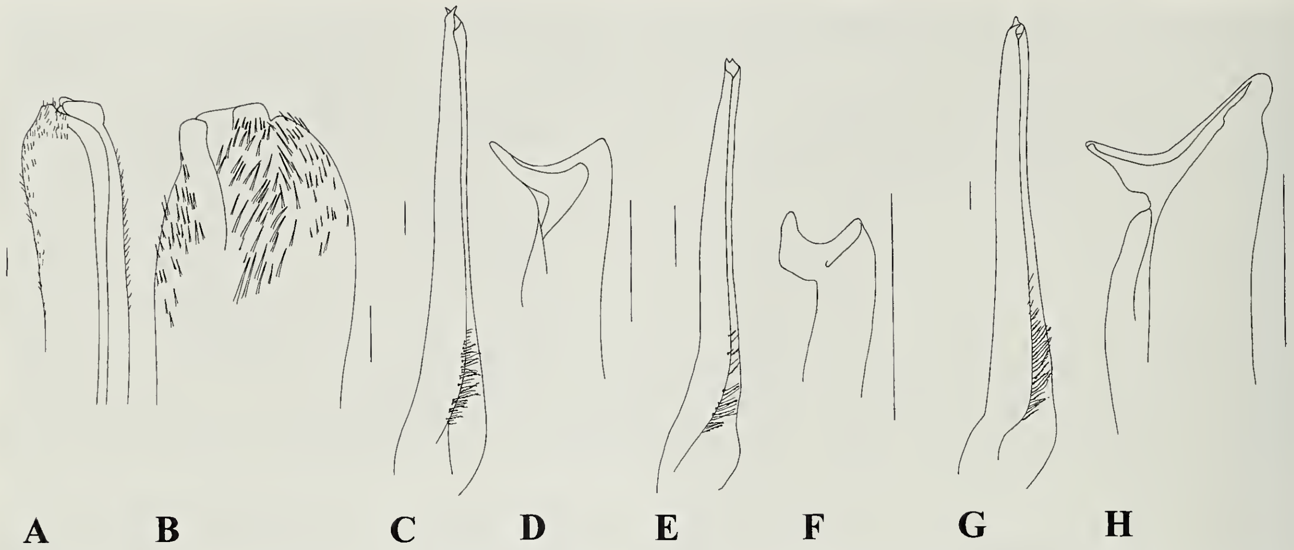

Fig. 3. A, B, *Randallia ornata* (Randall, 1839), ♂ cl 30.2 mm, California, Monterey Bay, R/V *Albatross,* Stn 4560 (USNM 66505): A, first pleopod; B, apex of first pleopod. C, D, *Tanaoa distinctus* (Rathbun, 1893), ♂ cl 40.5 mm, Banc Tuscarora, MUSORSTOM 7, Stn DW 556, (MNHN): C, first pleopod; D, apex of first pleopod. E, F, *Tanaoa nanus,* new species, ♂ cl 13.7 mm, Indonesia, Tanimbar I., KARUBAR, Stn CP 39 (MNHN): E, first pleopod; F, apex of male first pleopod. G, H, *Tanaoa pustulosus* (Wood-Mason, in Wood-Mason & Alcock, 1891), ♂ cl 34.0 mm, Japan, Tosa Bay (NHM 1961.6.5.38/39): G, first pleopod; H, apex of first pleopod. Scales = 1 mm.

1–4 bearing medially granulate ridge; lower margin of fifth pereiopodal merus, propodus granulate.

Thoracic sternites, abdomen minutely pitted. Male first pleopod slightly sinuous, dorso-ventrally flattened, tip thickened, with dense tuft of setae subapically on internal margin (Figs. 3A, B).

Color.—"Carapace variegated with sanguineous spots, confluent anteriorly; chelipeds variegated with red" (Rathbun 1937: 172). "Ground color of carapace olive buff almost covered anteriorly with dots of chrome yellow. Large, regular designs vinaceous russet, smaller patches paler and more orange. Posterior spines white. Cheliped yellow to pale buff, merus covered with carrot red, carpus and manus with a coarse netting of the same color. Merus of ambulatory legs pale yellowish white at base blending into intense scarlet on distal portion. Remaining segments yellowish white; dactyl yellow tipped." (Garth 1940: 55).

Distribution.—Eastern Pacific: Pacific and Gulf coasts of California, 10–185 m.

Remarks.—Randall's (1839) specimens are no longer extant (Rathbun 1937:172). According to Garth (1940) *R. angelica* differs from *R. ornata* in degree of granulation, more prominent frontal teeth and more pronounced angle of front with hepatic margin. Two decades later Garth (1960) considered it a synonym of *R. ornata,* and yet six years later (Garth 1966) reversed himself again and considered *R. angelica* a "Gulf of California cognate" of *R. ornata.* Hendrickx (1997:163), who examined specimens collected off the Pacific and Gulf of California coasts, maintained that *R. angelica* is but a synonym of *R. ornata.*

Examination of large series of specimens, including Garth's paratypes, revealed intraspecific variability in granulation. Smaller specimens (cl < 25 mm) tend to bear coarser, denser granules on the carapace and legs. The differences in granulation enumerated by Garth (1940:56) as characteristic of *R. angelica* fall within the range of variation observed for *R. ornata.*

The 12 species provisionally assigned to *Randallia* s. s. differ from *R. ornata* in a number of characters. *Randallia americana* (Rathbun, 1893), *R. glans* Alcock, 1896, *R.*

agaricias Rathbun, 1898 and *R. speciosa* Chen, 1989 differ from *R. ornata* in having a bilobate margin to the efferent branchial channel. *Randallia granulata* Miers, 1886, *R. gilberti* Rathbun, 1906, and *R. nana* Zarenkov, 1990 differs from *R. ornata* in having segments 3–6 of male abdomen fused in addition to the bilobate margin to efferent branchial channel. *Randallia pustulilabris* Alcock, 1896, *R. laevis* (Borradaile, 1916) and *R. minuta* Rathbun, 1935 differ from *R. ornata* in having the antennular operculum sealing only the bottom half of antennular aperture. *Randallia bulligera* Rathbun, 1898 differs from *R. ornata* in its male first pleopod having a petaloid tip. *Randallia curacaoensis* Rathbun, 1922 differs from *R. ornata* in having the sixth abdominal segment in the male bearing proximally a triangular denticle. As previously mentioned, these species are herein retained in *Randallia* s. s. pending further revision, rather than leave them as *incertae sedis.*

Tanaoa, new genus

Diagnosis.—Carapace subcircular, globose. Front narrow, uptilted, bilobed. Eyes small, retractible. Outer orbital margin trisutured, V-shaped gap proximally on ventral margin. Antennules obliquely folded, basal antennular segment squat, operculiform, sealing lower antennular aperture. Antennae small, slender, basal antennal segment inserted in orbital hiatus. Postorbital region concave. Branchial, intestinal regions swollen, demarcated by grooves, 2 pairs of pits along cardiobranchial grooves. Posterior margin of carapace narrow, bidentate.

Third maxilliped exopod not quite sealing efferent branchial channel. Third maxilliped exopod slightly shorter than endopod; merus of endopod subtriangular, shorter than subrectangular ischium. Anterior margin of efferent branchial channel produced, bilobed, separated by narrow groove from lower orbital margin.

Chelipeds long, slender, equal. Cheliped with merus and palm subcylindrical; fingers nearly as long as upper margin of palm, inner margins denticulate. Pereiopods 1–5 slender, short; all but last dactyl shorter than propodi; upper surface of pereiopodal dactyls setose, tips corneous.

Fourth thoracic sternite swollen laterally. Male abdominal sulcus deep, nearly reaching buccal cavity, anterior margin raised, prominently granulate. Male abdomen triangular, abdominal segments 3–6 fused, basio-lateral regions of fused segments inflated, anterior margin bearing denticle. Telson slender, one-third as long as fused segments, not reaching tip of abdominal sulcus. Walls of abdominal sulcus carinate along sternal sutures 2–4. Female abdominal segments 4–6 fused, swollen, shield-like. Telson ogival, fitting between third maxillipeds, posteriorly sinuous.

Male first pleopod elongate, slightly sinuous, attenuate; bearing minute preapical process perpendicular to tip (Fig. 4a, b); second pleopod short, distally scoop-like.

Type species.—*Randallia pustulosa* Wood-Mason, in Wood-Mason & Alcock, 1891. Gender: feminine.

Species.—*Tanaoa distinctus* (Rathbun, 1893), *Tanaoa nanus,* new species, *Tanaoa pustulosus* (Wood-Mason, in Wood-Mason & Alcock, 1891).

Etymology.—In the myths of the Marquesas islanders, Tanaoa is the god of darkness, confined to the depths of the ocean. The name *Tanaoa* is to be considered as an arbitrary combination of letters and heretofore takes the gender masculine.

Remarks.—*Tanaoa,* new genus, differs from *Randallia* s. s. as follows: antennular operculum seals only the lower antennular aperture; the third maxilliped exopod and efferent branchial channel gape anteriorly; the anterior margin of the efferent branchial channel is bilobate; male abdominal segments 3–6 are fused; and the male first pleopod is distally attenuate, bearing a preapical process. In contrast, in *Randallia* s. s. the antennular operculum seals entirely the antennular aperture; the third maxilliped exopod seals the efferent branchial channel; the anterior margin of the efferent branchial channel is trilobate; the sixth segment of the male abdomen is free; and the male first pleopod is distally club-shaped.

Tanaoa distinctus (Rathbun, 1893), new combination
Figs. 1B, 3C, D

Randallia distincta Rathbun, 1893:257; 1906:890, pl. 16, fig. 2, 3, text-fig. 44.—Ihle, 1918:312.—Serène, 1954:492; 1968:45.—Yaldwyn & Dawson, 1976: 97.—Richer de Forges, 1983:634(tab), 636, 638.

Randallia serenei Richer de Forges, 1983: 634, figs 1–4.—Poupin & Richer de Forges, 1991:211.

Type material.—Holotype of *Randallia distincta* Rathbun, 1893: Hawaiian Is., Oahu I., R/V *Albatross* Stn 3472, 21°12′N, 157°49′W, 4 Dec 1891, 540 m, ♀ 20.4 mm (USNM 17516). Holotype of *Randallia serenei* Richer de Forges, 1983: Tahiti. Port Phaeton, 400–500 m, 1978, coll. B. Richer de Forges, 2 ♂ 40.3, 41.8 mm (MNHN B8735).

Material examined.—Marquesas Is., Tahuata I., 430 m, 13 Sep 1987, ♂ 32.5 mm, ♀ 31.0 mm (MNHN); 9°54.5′S, 139°08.2′W, 350 m, 1 Sep 1990, coll. J. Poupin, 2 ♂ 31.0, 40.0 mm, 2 ♀ 31.8, 43.7 mm (MNHN). Eiao I., 7°58.5′S, 140°44.5′W, 415 m, 19 Jan 1991, coll. J. Poupin, 6 ♂ 39.7–44.3 mm, 10 ♀ 22.6–42.9 mm (MNHN). MUSORSTOM 9, Stn CP 1169, 8°59′S, 140°05′W, 391–408 m, 24 Aug 1997, ♂ 32.2 mm (MNHN). Stn CP 1191, 8°46′S, 140°07′W, 390–400 m, 26 Aug 1997, ♂ 41.7 mm (MNHN). Stn CP 1251, 9°47′S 139°38′W, 500–650 m, 2 Sep 1997, ♂ 40.0 mm (MNHN). Stn CP 1268, 7°56′S 140°43′W, 285–320 m, 4 Sep 1997, ♂ 43.6 mm, ♀ ovig. 39.1 mm (MNHN). Stn CP 1270, 7°56′S 140°43′W, 497–508 m, 4 Sep 1997, ♂ 30.3 mm, ♀ 31.5 mm, 1 juv. (MNHN). Stn CP 1276, 7°52′S 140°37′W, 800–805 m, 5 Sep 1997, ♂ 21.3 mm (MNHN). Stn CP 1281, 7°48′S 140°21′W, 450–455 m, 7 Sep 1997, ♀ 31.5 mm (MNHN). Stn DW 1287, 7°54′S, 140°40′W, 163–245 m, 7 Sep 1997, ♂ 42.6 mm (MNHN).

Tuamotu Archipelago. 18°04.2′S, 141°01.8′W, 500 m, 2 Jun 1990, coll. J. Poupin, ♂ 43.0 mm, ♀ ovig. 42.7 mm (MNHN). Makemo, 300–600 m, 4 Jun 1988, coll. J. Poupin, ♀ 32.5 mm (MNHN).

Society Is., 15°48′S, 154°32′W, 500–700 m, 21 Jul 1988, coll. J. Poupin, ♂ 40.6 mm (MNHN). Tahiti. Port Phaeton, 400–500 m, 6 Oct 1978, coll. B. Richer de Forges, ♂ 40.3 mm (MNHN B8734). Bora-Bora I., 400–700 m, 23 Jul 1988, coll. J. Poupin: ♂ 39.5 mm (MNHN). Taravao, 17°47′S, 149°21′W, 500–600 m, 11 Dec 1988, coll. J. Poupin, 3 ♂ 30.8–39.5 mm, ♀ 40.7 mm (MNHN).

Hawaiian Is. Maui I., W Puniawa Pt, R/V *Albatross* Stn 4079, 21°01.40′N, 156°22.50′W, 261–326 m, 21 Jul 1902 ♂ 42.5 mm, ♀ ovig. 39. 7 mm (USNM 29883). R/V *Albatross* Stn 4082, 21°04.35 N, 156°21.10′W, 402–435 m, 21 Jul 1902 3 ♂ 20.9–30.8 mm, 2 ♀ 32.3, 43.6 mm (USNM 29884). Oahu I., SW Diamond Head Lt, R/V *Albatross* Stn 3813, 483–335 m, 28 March 1902, ♂ 30.4 mm (USNM 29872). SW Diamond Head Lt, R/V *Albatross* Stn 3818, 536–540 m, 31 Mar 1902, ♂ 20.5 mm (USNM 29873). Oahu, SW Kahuku Pt, R/V *Albatross* Stn 4115, 21°41.5′N, 158°08.5′W, 357–441 m, 25 Jul 1902, ♀ 29.8 mm (USNM 29885). Off Honolulu, 27–40 m, Feb–Mar 1962: ♀ ovig. 41.6 mm (WAM c24429). Hawaii I., Kawaihae Lt., R/V *Albatross* Stn 4044, 20°03.15′N, 155°55.20′W, 426–362 m, 11 Jul 1902, ♂ 43.0 mm, ♀ 32.7 mm (USNM 29882). Pailolo Channel, btw Maui, Molokai Is., R/V *Albatross* Stn 3883, 21°09.15′N, 155°34.15′W, 507–520 m, 16 Apr 1902, 2 ♂ 12.6, 18.6 mm, ♀ 19.8 mm (USNM 29878). Pailolo Channel, btw Maui, Molokai Is., R/V *Albatross* Stn 3865, 468–518 m, 10 Apr 1902, 4 ♂ 13.3–20.7 mm, ♀ 13.1 mm (USNM

29877). Molokai I., R/V *Albatross* Stn 3836, 21°00.05N, 157°08.20′W, 435–467 m, 3 Apr 1902, 2 ♀ 20.2, 18.3 mm (USNM 29874).

Western Samoa. Upolu I., Apia, 250–846 m, 5–16 Sep 1980, coll. D. Popper, ♂ 43.5 mm, ♀ 30.8 mm (NNM 35234).

Wallis Is. MUSORSTOM 7, Stn DW 525, 13°11′S, 176°15′W, 500–600 m, 13 May 1992, ♀ 42.2 mm (MNHN).

Banc Tuscarora. MUSORSTOM 7, Stn DW 556, 11°49′S, 178°18′W, 440 m, 19 May 1992, ♂ 40.5 mm (MNHN).

New Zealand. 34°24.0′S, 173°10.3′E, 472 m, 21 Mar 1982, ♂ 35.9 mm (NIWA).

Guam. Agana Bay, 303 m, 28–9 Aug 1975, coll. L. Eldredge, ♀ 24.9 mm (MNHN B8737).

Redescription.—Dorsal surface of carapace covered with pearliform granules, interspaced with smaller granules, granules more pronounced posteriorly. Frontal lobes triangulate, minutely and closely granulate. Third maxilliped prominently granulose. Subhepatic margins of carapace somewhat inflated, 3 low granulate tubercles on epibranchial margin, more pronounced in juveniles. Hepatic, branchial, and intestinal regions demarcated by shallow grooves. Intestinal region bearing small tubercle posteriorly, tubercle reduced in larger specimens; conical, upcurved in juveniles. Posterior margin bearing 2 stubby protrusions laterally (Fig. 3C, D).

Cheliped and pereiopods 1–5 closely granulate throughout. Cheliped merus in adult male nearly as long as carapace; fingers nearly as long as upper margin of palm. Pereiopodal dactyls tomentose anteriorly.

Thoracical sternites granulate. Fused abdominal segment in male triangular, bearing transverse ridge, with preapical median denticle. Telson slender, third as long as fused abdominal segments. Female abdomen granulate, granules larger, closer proximally, low denticle medially on distal margin. Male first pleopod with transverse digitate process preapically (Fig. 1B).

Distribution.—Pacific Ocean: Marquesas Is., Tuamotu Archipelago, Society Is., Hawaiian Is., Samoa, Banc Tuscarora, Wallis Is., New Zealand, Guam; 27–805 m.

Remarks.—Rathbun (1893:257) described *Randallia distincta* from a juvenile female specimen, but on examining additional material collected by the *Albatross,* observed that adult specimens differ from juveniles in lacking tubercles on the branchial margins, denticles on the posterior margin, and a spine on the intestinal region (Rathbun 1906:890). Richer de Forges (1983:634) based his description of *R. serenei* on adult specimens, but noted (1983: 638) that a juvenile from Guam differs from the adults in possessing "les gros granules du bord latéral et le granule de l'aire intestinal". Richer de Forges (1983:638), distinguished *R. serenei* from *R. distincta* in having more rounded tubercules on the posterior margin of the carapace and pronounced branchio-cardiac grooves, though admitting "Pour mieux décrire chacune de ces espèces, il serait nécessaire une gamme de taille de chaque espèce". Examination of the type series of *R. distincta* and *R. serenei,* and numerous additional specimens, including the male first pleopod, has shown that the latter is a junior synonym of the former. The specimen collected off New Zealand has slimmer, longer chelipeds than the other specimens examined.

Tanaoa nanus, new species
Figs. 1C, 3E, F

Randallia pustulosa: Ihle, 1918:246 (not *Randallia pustulosa* Wood-Mason, in Wood-Mason & Alcock, 1891).

Type material.—Holotype: Vanuatu. MUSORSTOM 8, Stn CP 1053, 16°29.23′S, 167°58.70′E, 536–519 m, 1 Oct 1994, coll. B. Richer de Forges, ♂ 12.7 mm (MNHN B.28510). Paratype: Indonesia: 1°17.5′N, 118°53′E, N of Kaniungan, *Siboga* Stn 90, 281 m, 21 Jun 1899, ♂ 14.7 mm (ZMA 242432).

Material examined.—Vanuatu. MUSOR-

STOM 8, Stn CP 1027, 17°53.05′S, 168°39.35′E, 550–571 m, 28 Sep 1994, coll. B. Richer de Forges, ♀ 13.5 mm (MNHN). Stn CP 1047, 16°53.62′S, 168°10.49′E, 486–494 m, 30 Sep 1994, coll. B. Richer de Forges, ♂ 9.5 mm (MNHN). Stn CP 1052, 16°32.37′S, 168°00.29′E, 561–564 m, 1 Oct 1994, coll. B. Richer de Forges, ♂ 12.3 mm (MNHN). Stn CP 1054, 16°27.95′S, 167°57.44′E, 522–527 m, 1 Oct 1994, coll. B. Richer de Forges, ♂ 13.1 mm, ♀ ovig. 12.4 mm (MNHN). Stn CP 1055, 16°30.11′S, 167°55.13′E, 572–580 m, 1 Oct 1994, coll. B. Richer de Forges, ♀ ovig. 15.3 mm (MNHN). Stn DW 1072, 15°39.89′S, 167°19.61′E, 622–625 m, 4 Oct 1994, coll. B. Richer de Forges, ♂ 10.9 mm (MNHN). Stn CP 1089, 15°08.82′S, 167°17.23′E, 494–516 m, 6 Oct 1994, coll. B. Richer de Forges, ♂ 10.9 mm, ♀ ovig. 12.4 mm (MNHN). Stn CP 1111, 14°51.09′S, 167°14.00′E, 1210–1250 m, 8 Oct 1994, coll. B. Richer de Forges, ♀ ovig. 14.1 mm (MNHN). Stn CP 1124, 15°01.72′S, 166°56.51′E, 532–599 m, 9 Oct 1994, coll. B. Richer de Forges, 2 ♀ ovig. 16.2, 17.1 mm (MNHN).

Wallis I. MUSORSTOM 7, Stn DW 523, 13°12′S, 176°16′W, 455–515 m, 13 May 1992, 1 juv. (MNHN).

New Caledonia. HALIPRO 1, Stn CP 867, 21°26′S, 166°18′E, 720–950 m, 22 Mar 1994, coll. B. Richer de Forges, ♂ 10.4 mm, ♀ 15.6 mm (MNHN). BATHUS 4, Stn DW 911, 18°57.80′S, 163°08.47′E, 566–558 m, 5 Aug 1994, coll. B. Richer de Forges, ♀ 12.5 mm (MNHN). Stn DW 915, 18°51.26′S, 163°16.72′E, 580–575 m, 5 Aug 1994, coll. B. Richer de Forges, 3 ♂ 9.9–10.4 mm (MNHN). Stn DW 920, 18°45.33′S, 163°17.16′E, 610–620 m, 6 Aug 1994, coll. B. Richer de Forges, ♂ 8.5 mm (MNHN).

Indonesia: Tanimbar I., KARUBAR, Stn CP 39, 7°47′S, 132°26′E, 477–466 m, 28 Oct 1991, ♂ 13.7 mm, ♀ 14.4 mm (MNHN). Stn CP 59, 8°20′S, 132°11′E, 405–399 m, 31 Oct 1991, 2 ♂ 12.4, 12.5 mm, 2 ♀ ovig. 12.0, 14.6 mm (MNHN). Stn CP 70, 8°41′S, 131°47′E, 413–410 m, 2 Nov 1991, ♂ 10.6 mm (MNHN).

Description.—Dorsal surface of carapace covered with pearliform granules, interspaced with smaller granules. Frontal lobes rounded, closely granulate. Subhepatic margins of carapace somewhat swollen, median subhepatic tubercle followed, in young specimens, by smaller tubercle. Hepatic region bearing granulate tubercle. Anterolateral margin posteriorly set with 3 granulate tubercles, posteriormost tubercle largest. Posterolateral margin bituberculate, posterior tubercle larger. Posterior margin bearing 2 conicalal tubercles laterally. Branchial, intestinal regions demarcated by deep grooves. Intestinal region swollen, bearing granulate tubercle anteriorly, long, upcurved spur posteriorly (Fig. 1C).

Anterior margin of efferent branchial channel deeply sutured. Third maxilliped granulose.

Cheliped and pereiopods 1–5 closely granulate throughout. Cheliped merus in adult male 0.75 as long as carapace, in female 0.66 carapace length; fingers as long as upper margin of palm.

Thoracical sternites in male boldly granulate. Telson slender, third as long as fused abdominal segments. Male first pleopod with lamellate process preapically (Figs. 3E, F).

Etymology.—From the Latin *nanus,* small, minute.

Distribution.—Indo-Pacific Ocean: Wallis I., Vanuatu, New Caledonia, Indonesia; 281–1250 m.

Remarks.—*Tanaoa nanus* differs from *T. pustulosus* in its much smaller size, its coarsely granulated carapace, and the lamellate preapical process of the first male pleopod.

Tanaoa pustulosus (Wood-Mason, in Wood-Mason & Alcock, 1891), new combination

Figs. 1D, 3G, H

Randallia pustulosa Wood-Mason, in Wood-Mason & Alcock, 1891:266; 1892:

pl. 5, fig. 4.—Alcock, 1896:196; 1899: 27.—Doflein, 1904:42, pl. 14, fig. 1–6 (part).—Serène, 1954:491.—Sakai, 1976: 99, pl. 30, fig. 2.—Yaldwyn & Dawson, 1976:95, figs 2–5.—Serène & Vadon, 1981:119, 124.—Richer de Forges, 1983: 634 (tab.).—McLay, 1988:100, fig. 20.—Chen, 1989:217, fig. 15, pl. 4, fig. 1.—Tan, 1996:1054.—Ikeda, 1998:82, pl. 19, fig. 1a–d.—Ng et al., 2001:10.—Chen & Sun, 2002:342, fig. 151, pl. 3.1.

Randallia vitjazi Zarenkov, 1994:104, pl. 5, pl. 8Б.

Not *Randallia pustulosa*: Ihle, 1918:246 [= *T. nanus*, new species].

Material examined.—Fiji. MUSORSTOM 10, Bligh Water, Stn CC 1331, 17°02.4′S, 178°01.8′E, 694–703 m, 8 Aug 1998, 7 ♂ 21.5–30.1 mm, 1 juv. (MNHN). Stn CC 1332, 16°56.2′S, 178°07.9′E, 640–687 m, 8 Aug 1998, 2 ♂ 28.5, 28.3 mm, 9 juvs. (MNHN). Stn CC 1337, 17°03.4′S, 177°47.2′E, 635–670 m, 9 Aug 1998, ♂ 27.8 mm, 1 juv. (MNHN). Stn CP 1342, 16°46.0′S, 177°39.7′E, 650–701 m, 10 Aug 1998, 2 ♂ 28.7, 21.4 mm (MNHN). Stn CP 1346, 17°19.6′S, 178°32.4′E, 673–683 m, 11 Aug 1998, ♂ 30.5 mm, ♀ 29.9 mm (MNHN).

New Caledonia. CHALCAL 2, Stn DW 75, 24°39.31′S, 168°39.67′E, 600 m, 29 Oct 1986, ♂ 19.6 mm, ♀ 30.5 mm (MNHN B21210). HALIPRO 1, Stn CP 867, 21°26′S, 166°18′E, 720–850 m, 22 Mar 1994, 1 juv. 15.8 mm (MNHN). BATHUS 4, Stn CP 911. 18°57.80′S, 163°08.47′E, 566–558 m, 5 Aug 1994, 1 juv. (MNHN).

Caroline Is. Palau I., Mutremdiv Pt., Jun 1981, coll. W.B. Saunders, ♂ 37.7 mm (USNM 354775).

Japan. Shikoku I., Mimase, Tosa Bay, 250 m, Apr 1968: ♂ 33.7 mm (SMF 15104, ex. coll. T. Sakai). Tosa Bay, 4 ♀ 33.9–34.3 mm (SMF 22555, ex. coll. T. Sakai). Tosa Bay, 34.2 mm (SMF, ex. coll. T. Sakai); Tosa Bay, ♂ 34.0 mm, ♀ 35.0 mm (NHM 1961.6.5.38/39, ex. coll. T. Sakai).

Taiwan. Tashi fishing port, 22 Mar 1986, coll. T.Y. Chan, ♀ ovig. 34.8 mm (NTOU).

Indonesia. Kai Is., KARUBAR, Stn DW 3, 5°48′S, 132°13′E, 301–278 m, 22 Oct 1991, ♂ 39.6 mm (MNHN).

Philippines. Mindanao, Iligan Bay, R/V *Albatross* Stn 5508, 8°17.24′N, 124°11.42′E, 494 m, 5 Aug 1909, ♂ 34.4 mm (USNM). Btw Negros, Siquijor, R/V *Albatross* Stn 5538, 9°08.15′N, 123°23.20′E, 468 m, 19 Aug 1909, ♂ 35.8 mm (USNM). MUSORSTOM, Stn 43, 13°50.5′N, 120°28.0′E, 484–448 m, 24 Mar 1976, 2 ♂ 23.8, 23.0 mm, ♀ 24.4 mm, 1 juv. (MNHN B18055). Stn 44, 13°46.9′N, 120°29.5′E, 610–592 m, 24 Mar 1976, ♂ broken, ♀ 15.1 mm (MNHN B18057). MUSORSTOM 3, Stn CP97, 14°00′N, 120°18′E, 189–194 m, 1 Jun 1985, 1 juv. (MNHN B17999). Stn CP122, 12°20′N, 121°42′E, 673–675 m, 4 Jun 1985, ♂ 18.1 mm (MNHN B18000). Stn CP128, 11°50′N, 121°42′E, 815–821 m, 5 Jun 1985, ♀ ovig. 35.3, ♀ parasitized 22.5 mm (MNHN B18001).

Laccadive Sea. 8°37′N, 75°37.30′E, ♀ parasitized 26.2 mm (NHM 1899.8.26.4, ex. Indian Museum). 9°34.57′N, 75°36.30′E, ♀ 12.6 mm, (NHM 1896.9.8.10, ex. Indian Museum).

Seychelles. 4°34.2′S, 56°26.6′E, 650–630 m, 22 Oct 1987, ♂ 31.3 mm (MNHN B19100). 9°34.57′N, 75°36.30′E: ♀ 12.6 mm (NHM 1896.9.8.10, ex. Indian Museum).

Réunion. 350–500 m, 2 Feb 1974, coll. P. Guézé, ♀ 31.8 mm (MNHN B19135). R/V *Marion Dufresne,* Stn CP 122, 20°57,9′S, 55°14.5′E, 450–580 m, 1 Sept 1982, ♀ 31.7 mm (MNHN B 19134).

Geyser Reef. Stn 114, 12°22.3′S, 46°28.2′E, 300–600 m, 11 Apr 1977, coll. M. Faubert, ♀ 24.1 mm (MNHN B19044).

Comoro Is., Stn 61, 12°46.0′S, 44°58′E, 475–510 m, 29 Mar 1977, coll. M. Faubert, 1 juv. (MNHN B19045).

Madagascar. 12°43.5′S, 48°14.5′E, 370 m, 14 Apr 1971, coll. A. Crosnier, ♀ ovig. 30.9 mm (MNHN B18583). Stn CH 24, 22°30.5′S, 43°07′E, 430–460 m, 13 Jan

1986, ♀ ovig. 34.7 mm (MNHN B18585). Stn CH 27, 22°21′S, 43°05.5′E, 450 m, 15 Jan 1986, coll. R. von Cosel, ♀ 32.6 mm dry (MNHN B18582). Stn CH 32, 22°25.8′S, 43°04.3′E, 450–475 m, 19 Jan 1986, coll. R. Cleva, ♀ ovig. 32.7 mm (MNHN B19726). Stn CH 37, 22°18.2′S, 43°04.8′E, 450–475 m, 21 Jan 1986, coll. R. von Cosel, ♀ ovig. 31.6 mm (MNHN B18587). Stn CH 38, 22°23.7′S, 43°05.5′E, 400–500 m, 21.01.1986, coll. R. von Cosel, ♀ ovig. 33.5 mm (MNHN B18581). Stn CH 58, 23°36.2′S, 43°30.5′E, 510 m, 27 Feb 1973, coll. R. von Cosel, ♀ ovig. 33.2 mm (MNHN B18588). Stn CH 59, 23°36.0′S, 43°29.6′E, 600–610 m, 27 Feb 1973, ♂ 30.3 mm, (MNHN B18586). Stn CH 60, 22°25.6′S, 43°06.2′E, 475 m, 18.10.1986, coll. R. von Cosel, ♀ ovig. 33.3 mm (MNHN B19038). Stn CH 61, 23°36.1′S, 43°31.0′E, 445–455 m, 27 Feb 1973, ♂ 31.3 mm, (MNHN B19736). Same data, ♀ 32.5 mm, ♀ ovig. 31.7 mm (MNHN B18584). Stn CH 81, 22°22.8′S, 43°03.3′E, 525, 25 Oct 1986, coll. R. von Cosel, ♀ 31.9 mm (MNHN B19039). Stn CH 122, 22°16.8′S, 43°02.7′E, 600 m, 30 Nov 1986, ♂ 33.0 mm, ♀ 22.7 mm (MNHN B19041). Stn CH 127, 22°S, 43°E, 610 m, 1 Dec 1986, coll. R. von Cosel, ♀ 22.3 mm (MNHN B19040).

Redescription.—Dorsal surface of carapace unevenly granulate, obtuse granulate tubercles laterally on branchial region. Frontal lobes triangular, closely granulate. Third maxilliped minutely granulose. Subhepatic margins of carapace inflated, median subhepatic tubercle followed, in young specimens, by smaller tubercle. Anterolateral margin posteriorly set with 3 granulate tubercles, posteriormost largest. Posterolateral margin bituberculate, posterior tubercle larger. Posterior margin bearing 2 dorsoventrally flattened denticles laterally. Branchial, intestinal regions demarcated by deep grooves; intestinal region swollen, bearing prominent tubercle anteriorly, long, upcurved spur posteriorly (Fig. 1D).

Cheliped, pereiopods granulate throughout. Cheliped merus in adult male nearly as long as carapace, in female 0.85 carapace length; fingers as long as upper margin of palm.

Male thoracic sternites minutely granulate; margin of abdominal sulcus raised, granulate. Telson slender, third as long as fused abdominal segments. Male first pleopod with digitate process preapically (Figs. 3G, H).

Color.—"(after three weeks in alcohol) . . . dorsal surface of the carapace . . . pinkish-orange, with the tubercles . . . red; ventral surfaces . . . pale pinkish-white" (Yaldwyn & Dawson 1976:95). Color photo: Ikeda, 1998:82, pl. 19, fig. 1a–d.

Distribution.—Indo-Pacific Ocean: Fiji, New Caledonia, New Zealand, Caroline Is., Japan, Taiwan, Indonesia, Philippines, Andaman Sea, Laccadive Sea, Seychelles, Agalega Is., Comoro Is., Geyser Reef, Madagascar, Réunion, Mozambique channel, East Africa; 85–977 m.

Remarks.—The description and drawings of *Randallia vitjazi* (Zarenkov 1994:104, pl. 5, pl. 8Б) are clearly that of *T. pustulosus,* including the filiform preapical process of the first male pleopod. Sakai (1976: 99, pl. 14, fig. 6) believed that Doflein's specimen (*R. pustulosa*) from the Nicobars was "a different species, which seems to be related to *R. pustuloides* Sakai", whereas Chen (1989:217) declared it simply "Non *Randallia pustulosa*" [Wood-Mason]; the specimen was not available to me at the time of writing.

Key to Species of *Tanaoa,* new genus

1. Anterolateral margins of carapace bearing low granulate tubercles; intestinal region bearing low tubercle posteriorly . . . . *T. distinctus,* new combination
– Anterolateral margins of carapace bearing prominent granulate tubercles; intestinal region bearing prominent tubercle anteriorly, upcurved spur posteriorly . . 2
2. Carapace length of adult >30 mm; preapical process of male first pleopod filiform . . . *T. pustulosus,* new combination

– Carapace length of adult >12 mm; preapical process of male first pleopod lamellate .... *T. nanus,* new species

Tokoyo, new genus

Diagnosis.—Carapace circular, globose, regions indistinct. Front narrow, bilobed. Eyes small, retractible. Outer orbital margin trisutured, V-shaped gap proximally on ventral margin. Antennules obliquely folded, basal antennular segment squat, operculiform, sealing lower antennular aperture. Antennae small, slender, basal antennal segment inserted in orbital hiatus. Postorbital region concave. Lateral margins rounded, bearing median tubercle. Posterior margin of carapace narrow, tridentate.

Third maxilliped exopod sealing efferent branchial channel, slightly shorter than endopod; merus of endopod subtriangular, shorter than subrectangular ischium; endopod of adult female with vertical line of setae medially. Anterior margin of efferent branchial channel produced, deeply cleft, separated by narrow groove from lower orbital margin.

Chelipeds long, slender, subequal. Cheliped merus and palm subcylindrical; fingers shorter than upper margin of palm, inner margins denticulate.

Pereiopods slender, short; dactyls nearly as long as propodi; upper surface of dactyls distally setose, tips corneous.

Male abdominal sulcus deep, nearly reaching buccal cavity; lateral walls of abdominal sulcus with elongate cavities anteriorly. Male abdomen narrow, twice as long as wide at base. Abdominal segments 3–6 fused, basio-lateral regions of fused segments slightly inflated, bearing denticle preapically; lateral margin carinate, carina fitting into groove between thoracic segments 4 and 5. Telson triangular, fifth as long as fused segments. Abdominal segments 4–6 of female fused, swollen, shield-like; telson lingulate, posterior margin arched. Margin of abdominal fossa in female prominent, anteriorly thickened.

Male first pleopod elongate, slightly sinuous, attenuate, distally sharply bent interiorly; second pleopod short, distally scoop-like.

Type species.—*Randallia eburnea* Alcock, 1896.

Species.—*Tokoyo cirrata,* new species, *Tokoyo eburnea* (Alcock, 1896).

Etymology.—Tokoyo, in Japanese mythology, was a girl who slew a sea-serpent that intimidated the fisherfolks. The name *Tokoyo* is to be considered as an arbitrary combination of letters, and heretofore takes the gender feminine.

Remarks.—*Tokoyo,* new genus, differs from *Randallia* s. s. in having the antennular operculum sealing only the bottom half of the antennular aperture, a bilobate anterior margin of efferent branchial channel, and fused segments 3–6 of the male abdomen. *Tokoyo* differs from the other three new genera described herein in its tridentate posterior margin of the carapace, the preapically positioned denticle on the fused segment of male abdomen, and the lingulate telson in the female.

Tokoyo cirrata, new species
Figs. 1E, 4A–C

Type material.—Holotype: Vanuatu. MUSORSTOM 8, Stn CP 1086, 15°36.58′S, 167°16.32′E, 182–215 m, 5 Oct 1994, coll. B. Richer de Forges, 1 ♂ 13.0 mm (MNHN B.28511). Paratypes: Same data, 12 ♂ 9.7–13.0 mm, 6 ♀ 11.7–12.2 mm, 4 ♀ ovig. 11.7–13.2 mm, 7 juv. (MNHN B.28512).

Material examined.—Vanuatu. MUSORSTOM 8, Stn CP 976, 19°25.22′S, 169°26.73′E, 160–182 m, 22 Sep 1994, coll. B. Richer de Forges, ♂ broken, ♀ ovig. 12.3 mm, 1 juv. (MNHN). Stn CP 1070, 15°36.59′S, 167°16.42′E, 184–190 m, 4 Oct 1994, coll. B. Richer de Forges, ♂ 9.1 mm, ♀ ovig. 13.7 mm, 1 juv. (MNHN).

Australia. Queensland, Moreton Bay, 36 m, Sep 1966, 2 ♂ 23.4, 24.3 mm (AMS P15383). East of Swains Reef, 22°26.75′S, 153°09.17′E, 139 m, 8 Sep 1995, ♂ 23.9 mm (AMS P56719).

Description.—Dorsal surface of carapace minutely and evenly granulate. Frontal lobes squat, minutely granulate. Subhepatic margin of carapace somewhat swollen, with row of granules, separated from anterolateral margin by shallow concavity. Lateral margin bearing medially small tubercle. Intestinal region weakly swollen, demarcated laterally by indistinct grooves. Posterior margin bearing 3 rounded, dorso-ventrally flattened denticles, median denticle smallest (Fig. 1E).

Third maxillipeds bearing conical granules, setae anteriorly, low granulation posteriorly. Thoracic sternites indistinctly granulate; anterior sternite with diagonal granulate ridge laterally.

Cheliped with well-spaced minute granules. Cheliped merus in adult male 1.60–1.80 as long as carapace; palm thicker distally; dactyl two-thirds as long as upper margin of palm, gap proximally between dactyl, pollex. Cheliped merus in female one-third longer than carapace, palm cylindrical. Pereiopods punctate.

Fused abdominal segments of male bearing flattened triangular denticle. Telson one-fifth as long as fused abdominal segments.

Tip of first male pleopod vermiculate, coiled, curled anteriorly (Figs. 4A–C).

Etymology.—From the Latin, *cirratus,* curly, and refers to the shape of first pleopod.

Color.—Dorsal surface of carapace orange, margins paler; posterior denticles white. Chelipeds pale orange, distal margins of merus, carpus, propodus stained with darker orange.

Distribution.—Southwestern Pacific: Vanuatu and Australia; 36–215 m.

Remarks.—*Tokoyo cirrata,* new species, differs from *T. eburnea* Alcock, 1896, in having an anteriorly coiled tip of the first male pleopod, and color pattern of the carapace.

Tokoyo eburnea (Alcock, 1896), new combination
Figs. 1F, 4D–F

Randallia eburnea Alcock, 1896:197.—Alcock & Anderson, 1897: pl. 30, fig. 4.—Ihle, 1918:246.—Sakai, 1934:289, pl. 18, fig. 4; 1935:54, pl. 9, fig. 3; 1937:132, fig. 22; 1965:42, pl. 17, fig. 1; 1976:98, pl. 29, fig. 1.—Uchida, 1949:720, fig. 2082.—Serène, 1954:491, 1968:45.—Utinomi, 1956:72, pl. 36, fig. 8.—Tyndale-Biscoe & George, 1962:87, fig. 7.7.—Chang, 1963:7, fig. 1.—Zarenkov, 1969:24, fig. 7.3.—Takeda & Miyake, 1970:225.—Campbell, 1971:41.—Takeda, 1973:32, fig. 3e, f; 1975:143; 1997: 238; 2001:230.—Serène & Soh, 1976:12, pl. 3, fig. c.—Yaldwyn & Dawson, 1976: 96.—Serène & Vadon, 1981:118, 124.—Richer de Forges, 1983:634.—Chen, 1989:212, figs 12, 13.—Huang, 1989: 309, 1994:579.—Ng et al., 2001:10.—Chen & Sun, 2002:338, fig. 149.—Davie, 2002:275.

Randallia japonica Yokoya, 1933:130, text-fig. 46.

Material examined.—Japan: Shikoku I., Tosa Bay, Nov 1958, colls T. & K. Sakai, 2 ♀ ovig. 18.6, 17.3 mm (USNM 120708). Tosa Bay, 110 m, 10 May 1990, ♂ 14.8 mm (SMF 22577). Tosa Bay, ♀ 19.1 mm (SMF, ex. coll. Sakai). Off Ashizuri-Misaki, 366 m, 24 Nov 1958, ♀ 17.3 mm (SMF, ex. coll. Sakai). Honshu I., SW Seno Umi, R/V *Albatross* Stn 3703, 57 m, 7 May 1900, 1 juv. (USNM 134214).

China. Off Dougliai, 28 Jun 1976, ♂ 12.3 mm, ♀ 13.2 mm (SMF13206).

Taiwan. Tashi, 24 Jan 1997, coll. T.Y. Chan, 2 ♀ ovig. 20.1, 19.1 mm (NTOU). Tashi, Dec 1997, coll. T.Y. Chan, 2 ♂ 17.8, 17.3 mm (NTOU).

Indonesia. Off Borneo, 5°57′N, 109°34′E, 150 m, 1963, ♀ ovig. 24.4 mm (NHM 1964. 9.9.3). Btw Wowoni, Buton Is., 4°20′S, 122°58′E, 75–94 m, 'Siboga' Stn 204, 20 Sep 1899, ♀ 19.7 mm, 3 juvs. (ZMA 242361).

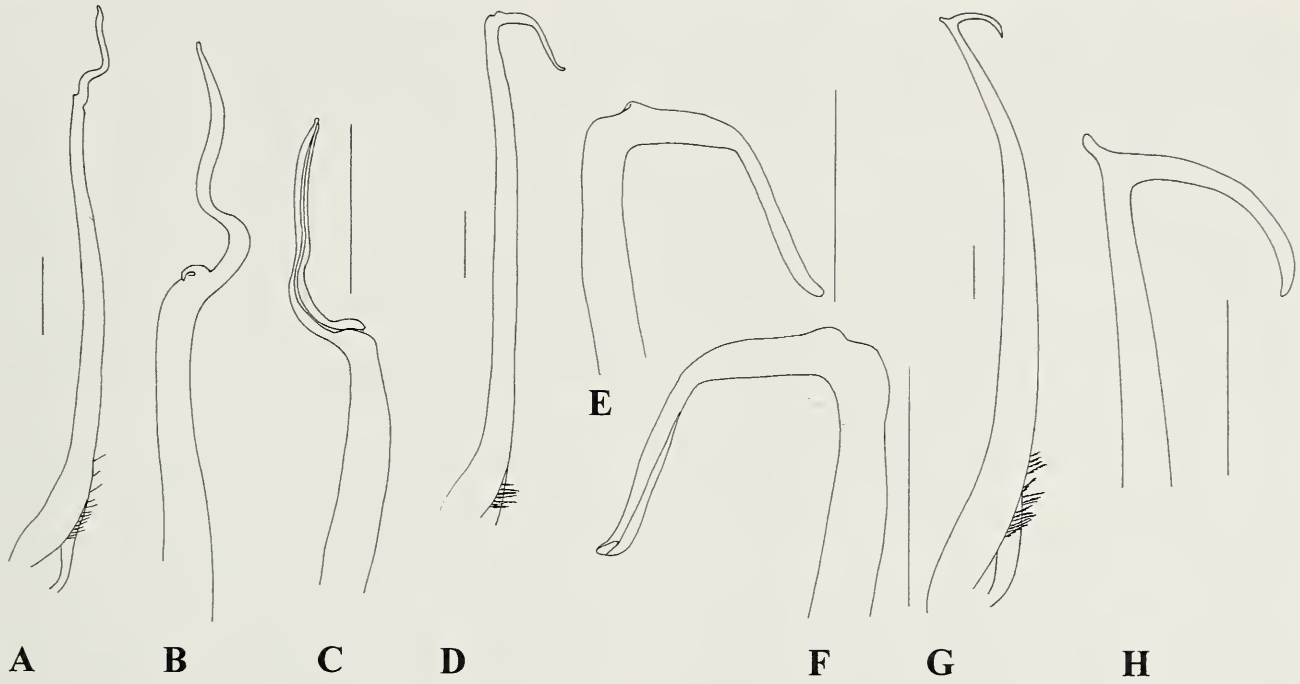

Fig. 4. A, B, C, *Tokoyo cirrata,* new species, holotype. ♂ cl 13.0 mm, Vanuatu, MUSORSTOM 8, Stn CP 1086 (MNHN): A, first pleopod; B, apex of first pleopod; C, apex of first pleopod, dorsal view. D, E, F, *Tokoyo eburnea* (Alcock, 1896), ♂ cl 14.8 mm, Japan, Tosa Bay (SMF 22577): D, first pleopod; E, apex of first pleopod; F, apex of first pleopod, dorsal view. G, H, *Toru granuloides* (Sakai, 1961), ♂ cl 25.8 mm, Loyalty Is., MUSORSTOM 6, Stn DW 487 (MNHN): G, first pleopod; H, apex of first pleopod. Scales = 1 mm.

Philippines. MUSORSTOM 1, Stn 16, 13°59′N, 120°12.3′E, 164–150 m, 20 Mar 1976, det. H. Chen, ♂ 27.4 mm, ♀ 26.9 mm (USNM 237656 ex. Paris Museum). Stn CP 34, 14°01′N, 120°15.8′E, 191–188 m, 23 Mar 1976, ♀ 32.1 mm (MNHN B 18975). Stn CP 58, 13°58.0′N, 120°13.7′E, 143–178 m, 26 Mar 1976, 9 ♂ 23.4–35.0 mm, 2 ♀ 19.4, 28.3 mm, 9 ♀ ovig. 26.1–29.0 mm, 4 juvs. (MNHN B 18058). MUSORSTOM 3, Stn CP 88, 14°01′N, 120°17′E, 183–187 m, 31 May 1985, 8 ♂ 12.0–23.5 mm, 12 ♀ 10.5–26.0 mm (MNHN B 17989). Stn CP 96, 14°00′N, 120°18′E, 190–194 m, 1 Jun 1985, 10 ♂ 11.1–23.8 mm, 5 ♀ 14.5–21.4 mm (MNHN B 17988).

Andaman Sea. Thailand. Similan I., R/V *Te Vega,* 08°46′N, 97°46′E, 75–81 m, 4 Nov 1963, 4 ♂ 11.4–15.5 mm, 3 ♀ 6.4–12.9 mm (USNM 273786).

Laccadive Sea. 11°05.45′N, 75°04.08′E: ♂ 9.6 mm (NHM 1896.9.8.20, ex. Indian Museum).

Redescription.—Dorsal surface of carapace minutely and evenly granulate. Frontal lobes squat, minutely granulate. Subhepatic margin of carapace somewhat swollen, with row of granules, separated from anterolateral margin by shallow concavity. Lateral margin bearing medially small tubercle. Intestinal region slightly swollen, demarcated laterally by indistinct grooves. Posterior margin bearing 3 rounded, dorsoventrally flattened denticles, median denticle smallest (Fig. 1F).

Third maxillipeds bearing conical granules, setae anteriorly, low granulation posteriorly. Thoracic sternites indistinctly granulate; anterior sternite with diagonal granulate ridge laterally.

Cheliped with well-spaced minute granules. Cheliped merus in adult male almost twice as long as carapace; palm thicker distally; dactyl half as long as upper margin of palm, gap proximally between dactyl, pollex. Cheliped merus in female one-third longer than carapace, palm cylindrical, dactyl two thirds as long as upper margin of palm. Pereiopods punctate.

Fused abdominal segments of male bearing flattened triangular denticle. Telson one-fifth as long as fused abdominal segments.

First male pleopod distally deflexed interiorly (Figs. 4D–F).

Color.—"Yellowish-pink, with deeper pink on anterior margins of merus and hand of chelipeds; anterior portion of carapace and distal joint of merus of walking legs yellow. Fingers white" (Tyndale-Biscoe & George 1962:87). "[B]right brick red above and white below" (Chang 1963:7).

Distribution.—Indo-Pacific Ocean: Australia, Japan, China, Taiwan, Vietnam, Indonesia, Philippines, Andaman Sea, Laccadive Sea; 35–366 m.

Remarks.—Alcock (1896:198) erroneously described the male abdominal segments 3–5 as fused, when in fact segments 3–6 are fused, as remarked by Ihle (1918: 246). Chen (1989, fig. 13b) erroneously depicted the sixth male abdominal segment as articulate. Examination of immature specimens showed that the pleopod drawn by Zarenkov (1969, fig. 7.3) is of a young male. The specimens from Borneo and the Philippines are much larger than the others examined, but no morphological differences were detected.

Key to Species of *Tokoyo,* new genus

1. First male pleopod with anteriorly coiled apical process .... *T. cirrata,* new species
– First male pleopod with interiorly deflexed apical process ....
.... *T. eburnea,* new combination

Toru, new genus

Diagnosis.—Carapace subcircular, globose. Front narrow, uptilted, bilobed. Eyes small, retractible. Outer orbital margin trisutured, V-shaped gap proximally on ventral margin. Antennules obliquely folded, basal antennular segment squat, operculiform, sealing lower antennular aperture. Antennae small, slender, basal antennal segment inserted in orbital hiatus. Postorbital region concave. Intestinal region swollen, demarcated by grooves, 2 pairs of pits along cardiobranchial grooves. Posterior margin of carapace narrow, bilobate.

Third maxilliped exopod slightly shorter than endopod, not quite sealing efferent branchial channel; endopod of adult female medially with vertical line of setae; merus of endopod subtriangular, shorter than subrectangular ischium. Anterior margin of efferent branchial channel produced, bilobed, separated by narrow groove from lower orbital margin.

Chelipeds long, slender, equal. Cheliped merus, palm subcylindrical; fingers as long as upper margin of palm, inner margins denticulate. Pereiopods slender, short; dactyls shorter than propodi; upper surface of pereiopodal dactyls setose, tips corneous.

Fourth thoracic sternite not swollen laterally. Abdominal sulcus of male deep, elongate, nearly reaching buccal cavity, anterior margin raised; lateral walls of abdominal sulcus with elongate cavities anteriorly. Abdominal segments 3–6 of male fused, basio-lateral regions inflated, fused segment narrowing distally, bearing denticle at distal margin; lateral margin carinate, carina fitting into groove at suture between sternites 4 and 5. Telson lingulate, two-fifths as long as fused segment, not reaching tip of abdominal sulcus. Abdominal segments 4–6 of female fused, shield-like; margin of abdominal cavity prominent, rampart-like. Telson ogival, basal margin sinuous.

Male first pleopod elongate, attenuate, bearing long apical process; second pleopod short, distally scoop-like.

Type species.—*Randallia granuloides* Sakai, 1961.

Species.—*Toru granuloides* (Sakai, 1961), *T. mesjatzevi* (Zarenkov, 1990), *Toru pilus* (Tan, 1996), *Toru septimus,* new species.

Etymology.—Toru is the Polynesian god of the chasms of the deep. The name *Toru* is to be considered as an arbitrary combination of letters and heretofore takes the gender masculine.

Remarks.—*Toru,* new genus, is differentiated from *Tanaoa,* new genus, in having a lingulate telson in the male, the lateral walls of male abdominal sulcus are excavate anteriorly, the male first pleopod bearing a long apical process, the margins of the female abdominal cavity prominent, rampart-like, and the fourth thoracic sternite even; whereas in *Tanaoa* the male telson tapers narrowly, the lateral walls of the male abdominal sulcus are entire, the preapical margin of the male first pleopod bear a minute process perpendicular with tip, the margins of the female abdominal cavity do not form a rampart-like edge, and the fourth thoracic sternite is greatly swollen laterally.

Toru granuloides (Sakai, 1961), new combination

Figs. 2A, 4G, H

Randallia granuloides Sakai, 1961:136, pl. 3, fig. 3; 1976:96, text-fig. 52.—Serène, 1968:45.—Yaldwyn & Dawson, 1976: 96.—Richer de Forges, 1983:634.

Material examined.—Wallis I. MUSORSTOM 7, Stn DW 583, 13°11′S, 176°14′W, 330–365 m, 22 May 1992, ♀ 18.5 mm (MNHN). Stn DW 584, 13°11′S, 176°14′W, 360–400 m, 22 May 1992, 1 juv. (MNHN). Stn DW 605, 13°21′S, 176°08′W, 335–340 m, 26 May 1992, ♂ 16.6 mm (MNHN).

Fiji. MUSORSTOM 10, Stn CP 1386, 18°18.5′S, 178°05.1′E, 230–344 m, 19 Aug 1998, ♀ ovig. 20.1 mm (MNHN). BORDAU 1, Stn CP 1434, 17°11′S, 178°41′W, 400–401 m, 2 Mar 1999, ♂ 17.8 mm (MNHN).

Loyalty Is. MUSORSTOM 6, Stn DW 416, 20°42.15′S, 166°59.60′E, 343 m, 16 Feb 1989, ♂ 27.3 mm (MNHN). Stn DW 428, 20°23.54′S, 166°12.57′E, 420 m, 17 Feb 1989, ♂ 18.9 mm, ♀ 9.5 mm (MNHN). Stn DW 456, 21°00.71′S, 167°26.35′E, 240 m, 20 Feb 1989, ♂ 23.0 mm (MNHN). Stn DW 487, 21°23.30S, 167°46.40′E, 500 m, 23 Feb 1989, ♂ 25.8 mm, ♀ 13.8 mm (MNHN). BATHUS 2, Stn CP 737, 23°03.42′S, 166°59.97′E, 350–400 m, 13 May 1993, ♂ 23.2 mm (MNHN).

New Caledonia. MUSORSTOM 4, Stn 194, 18°52.8′S, 163°21.7′E, 545 m, 19 Sep 1985, ♂ 25.8 mm (MNHN B18411). Stn 236, 22°11′S, 167°15′E, 495–550 m, 2 Oct 1985, 2 juv. (MNHN B21245).

Japan. ♂ 19.3 mm, ♀ ovig. 21.5 mm (SMF, ex. coll. Sakai). 2 ♂ 18.8, 19.0 mm (SMF, ex. coll. Sakai).

Redescription.—Dorsal surface of carapace granulate, granules closer set posteriorly. Frontal lobes rounded, minutely and closely granulate. Subhepatic margins of carapace very slightly swollen, Lateral margin medially set with small tubercle. Posterior margin bearing 2 lamellate, granulate, triangular tubercles laterally. Intestinal region swollen, topped by low tubercle, demarcated by deep grooves (Fig. 2A). Third maxilliped granulose.

Cheliped and pereiopods closely granulate throughout. Cheliped merus in adult male as long as carapace; fingers as long as upper margin of palm. Pereiopodal dactyls anteriorly tomentose.

Thoracic sternites and abdomen minutely granulate. Preapical denticle on fused abdominal segment in male triangular.

Shaft of first male pleopod slightly curved, with sickle-shaped apical process (Figs. 4G, H).

Distribution.—Western Pacific: Fiji, Wallis I., Vanuatu, Loyalty Is., New Caledonia, Japan; 50–550 m.

Remarks.—Sakai (1961:136) believed "The nearest relative of this new species [*Randallia granuloides*] is *R. granulata* Miers (1886)". Yaldwyn & Dawson (1976: 96), as well as Richer de Forges (1983: 634), relegated *R. granuloides* and *R. granulata* to the same "species-group". However, despite superficial similarity owing to the granulate carapace and elongate chelipeds they belong in different genera: *Toru granuloides,* new combination, differs from *R. granulata* in the form of the male telson, ogival rather than rounded as in *R. granulata*; and in the form of the first male pleopod, bent distad in *R. granulata.*

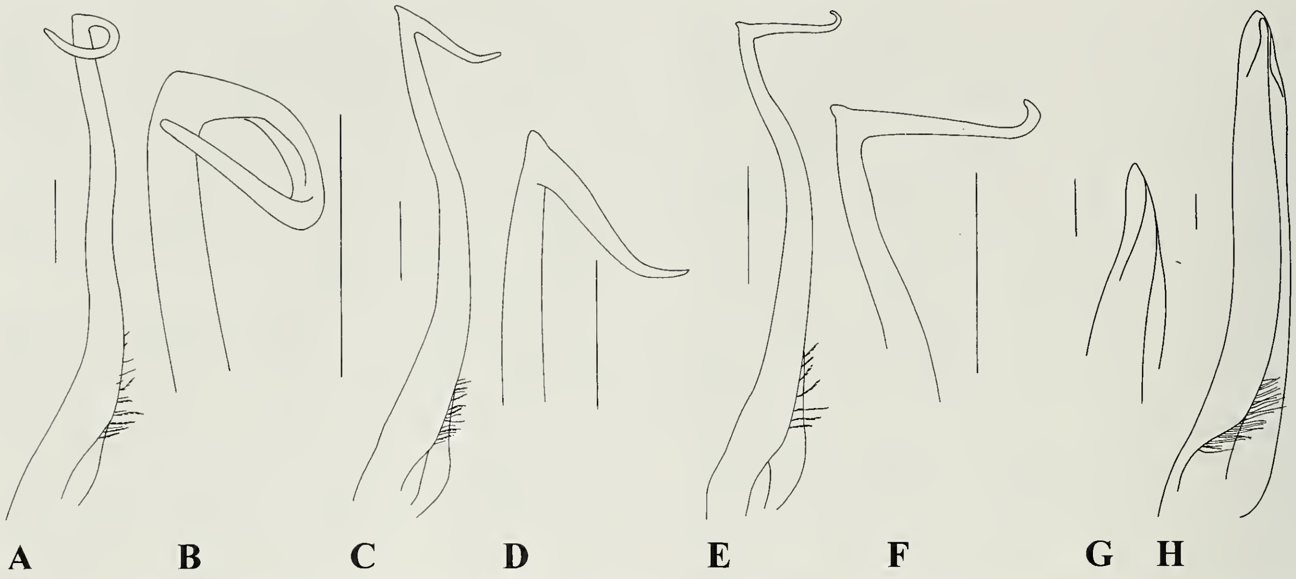

Fig. 5. A, B, *Toru pilus* (Tan, 1996), ♂ cl 11.5 mm, New Caledonia, BATHUS 4, Stn CP 946, (MNHN): A, first pleopod; B, apex of first pleopod. C, D, *Toru septimus,* new species, holotype. ♂ cl 13.1 mm, Loyalty Is., Stn DW 421 (MNHN): C, first pleopod; D, apex of first pleopod. E, F, *Toru trituberculatus* (Sakai, 1961), ♂ cl 8.6 mm, Indonesia, Tanimbar I., KARUBAR, Stn CP 67 (MNHN): E, first pleopod; F, apex of first pleopod. G, H, *Urashima pustuloides* (Sakai, 1961): paratype, ♂ cl 34.3 mm, Japan, Shikoku I., Mimase, Tosa Bay (NHM 1961.6.5.46–48): G, first pleopod; H, apex of first pleopod. Scales = 1 mm.

Toru mesjatzevi (Zarenkov, 1990), new combination

Randallia mesjatzevi Zarenkov, 1990:67, pl. 7.

Redescription.—Dorsal surface of carapace granulate, granules conical anteriorly. Frontal lobes rounded, minutely and closely granulate. Subhepatic margins of carapace very slightly swollen, Lateral margin uniformly rounded. Posterior margin bearing 2 lamellate, granulate, triangular tubercles laterally. Intestinal region somewhat swollen, demarcated by shallow grooves. Third maxilliped granulose, endopod medially with vertical ridge of conical granules.

Cheliped and pereiopods closely granulate throughout. Cheliped merus in adult male as long as carapace; fingers as long as upper margin of palm. Anterior margin of pereiopodal meri, carpi and propodi prominently spinose. Pereiopodal dactyls anteriorly tomentose.

Thoracic sternites and abdomen minutely granulate. Preapical denticle on fused abdominal segment in male triangular.

Shaft of first male pleopod slightly sinuous, with sickle-shaped apical process.

Distribution.—Off Kenya; 130–150 m.

Remarks.—Zarenkov's (1990, pl. 7, fig. 13) illustration of the first male pleopod of *Toru mesjatzevi,* with its sickle-shaped apical process, clearly places the species within the genus *Toru.* The species is larger than its cogeners (CL 36.0, 33.0 mm), and is notable for its prominently spinose pereiopods. The specimens were not available to me at the time of writing.

Toru pilus (Tan, 1996), new combination
Figs. 2B, 5A, B

Randallia pila Tan, 1996:1051, fig 7l–n, 8a, c–f, 4G, H.

Type Material.—Holotype: Philippines. R/V *Albatross* Stn 5454, 13°12′N, 123°50.30′E, 300 m, 7 Jun 1909: ♂ 13.0 mm (USNM). Paratype: Luzon, San Bernardino Straits, R/V *Albatross* Stn 5453, 13°12′N, 123°48.18′E, 271 m, 7 Jun 1909, ♀ ovig. 10.0 mm (USNM).

Material examined.—Fiji. MUSORSTOM 10, Stn CP 1325, 17°16.4′S, 177°49.8′E, 282–322 m, 7 Aug 1998, 12 ♂ 9.5–11.4 mm, ♀ 10.4 mm, 6 ♀ ovig. 9.1–11.0 mm (MNHN). Stn CP 1327, 17°13.3′S, 177°51.6′E, 370–389 m, 7 Aug 1998, 6 ♂ 7.5–10.4 mm, ♀ 9.0 mm, 4 ♀ ovig. 9.5–10.6 mm, 1 juv. (MNHN). Stn CP 1348, 17°30.3′S, 178°39.6′E, 353–390 m, 11 Aug 1998, ♂ 10.5 mm, ♀ ovig. 10.9 mm (MNHN). Stn CP 1349, 17°31.1′S, 178°38.8′E, 244–252 m, 11 Aug 1998, ♀ 10.0 mm (MNHN). Stn CP 1390, 18°18.6′S, 178°05.1′E, 234–361 m, 19 Aug 1998, ♀ 11.9 mm (MNHN). BORDAU 1, Stn CP 1406, 16°39′S, 179°37′E, 360–380 m, 25 Feb 1999, 2 ♂ 10.8, 10.0 mm (MNHN). Stn CP 1448, 16°45′S, 179°59′E, 410–500 m, 4 Mar 1999, ♂ 10.0 mm (MNHN).

Vanuatu. MUSORSTOM 8, Stn CP 964, 20°19.60′S, 169°49.00′E, 360–408 m, 21 Sep 1994, coll. B. Richer de Forges, ♀ ovig. 13.0 mm, 2 juv. (MNHN). Stn CP 1047, 16°53.62′S, 168°10.49′E, 486–494 m, 30 Sep 1994, coll. B. Richer de Forges, 3 ♂ 10.1–10.8 mm, ♀ 10.4 mm, 1 juv. (MNHN). Stn CP 1088, 15°09.23′S, 167°15.13′E, 425–455 m, 6 Oct 1994, coll. B. Richer de Forges, ♂ 11.6 mm, ♀ 11.3 mm (MNHN). Stn CP 1106, 15°05.27′S, 167°11.88′E, 305–314 m, 7 Oct 1994, coll. B. Richer de Forges, ♂ 9.3 mm (parasitized), 2 ♀ ovig. 13.2, 12.7 mm, ♀ broken (MNHN). Stn CP 1137, 15°41.52′S, 167°02.67′E, 360–371 m, 11 Oct 1994, coll. B. Richer de Forges, ♂ 11.0 mm, ♀ broken (MNHN).

New Caledonia. BATHUS 1, Stn CP 695, 20°34.59′S, 164°57.88′E, 410–430 m, 17 Mar 1993, ♂ 8.6 mm (MNHN). BATHUS 4, Stn CP 946, 20°33.8′S, 161°58.35′E, 386–430 m, 10 Aug 1994, ♂ 11.5 mm (MNHN).

Redescription.—Dorsal surface of carapace boldly granulate. Front prominently produced, frontal lobes anteriorly rounded, minutely granulate, pilose. Postorbital region depressed, concave. Rounded ridge extending from outer orbital margin across hepatic region. Subhepatic margin of carapace mammiform, separated by shallow arc from trituberculate anterolateral margin. Intestinal region swollen, demarcated by indistinct grooves, bearing conical tubercle posterioly. Posterior margin bearing laterally 2 lamellar denticles (Fig. 2B). Third maxillipeds bearing conicalal granules anteriorly. Thoracic sternites granulate.

Cheliped and pereiopods closely granulate throughout. Cheliped merus in adult male 0.85 as long as carapace; fingers nearly as long as upper margin of palm.

Male abdomen minutely granulate, preapical denticle narrowly triangular. Shaft of first male pleopod nearly straight, apical process incurved, looped (Figs. 5A, B).

Distribution.—Western Pacific: Fiji, Vanuatu, New Caledonia, Philippines; 234–500 m.

Remarks.—*Toru pilus* differs from the other species described herein of *Toru,* in having a prominently produced front, pronounced postorbital concavity, ridged hepatic region, and distally looped first male pleopod.

The male holotype of *T. pilus* is badly broken; the detached chelipeds (Tan 1996, fig. 4H, 8b) do not belong with the carapace; the distal segment of the first male pleopod is looped, not as depicted by Tan (1996, fig. 8a, f). The female paratype is entire.

Toru septimus, new species

Figs. 2C, 5C, D

Type Material.—Holotype: Loyalty Is., Stn DW 421, 20°26.27′S, 166°40.17′E, 245 m, 16 Feb 1989, 1 ♂ 13.1 mm (MNHN B.28513). Paratypes: Idem, 1 ♂ 12.2, mm, 2 ♀ 13.4, 13.3 mm (MNHN B.28514).

Material examined.—Fiji. MUSORSTOM 10, Stn CP 1386, 18°18.5′S, 178°05.1′E, 230–344 m, 19 Aug 1998, 1 juv. (MNHN).

Vanuatu. MUSORSTOM 8, Stn CP 963, 20°20.10′S, 169°49.08′E, 400–440 m, 21 Sep 1994, coll. B. Richer de Forges, 4 ♂ 10.1–14.8 mm, 6 ♀ 10.5–13.9 mm, 1 juv. (MNHN). Stn CP 986, 19°20.57′S, 169°31.48′E, 602–648 m, 23 Sep 1994, coll. B. Richer de Forges, ♀ 12.8 mm

(MNHN). Stn CP 1006, 18°50.24′S, 168°56.87′E, 574–611 m, 25 Sep 1994, coll. B. Richer de Forges, 1 juv. (MNHN). Stn CP 1017, 17°52.80′S, 168°26.20′E, 294–295 m, 27 Sep 1994, coll. B. Richer de Forges, ♂ 12.3 mm, ♀ 12.1 mm (MNHN). Stn CP 1018, 17°52.88′S, 168°25.08′E, 300–301 m, 27 Sep 1994, coll. B. Richer de Forges, ♂ 11.7 mm, ♀ broken (MNHN). Stn CP 1092, 15°10.80′S, 167°12.33′E, 314–321 m, 6 Oct 1994, coll. B. Richer de Forges, 3 juvs. (MNHN). Stn CP 1094, 15°08.02′S, 167°11.99′E, 312–314 m, 6 Oct 1994, coll. B. Richer de Forges, 1 juv. (MNHN).

Loyalty Is. MUSORSTOM 6, Stn DW 417, 20°41.80′S, 167°03.65′E, 283 m, 16 Feb 1989, ♂ 12.7 mm (MNHN). Stn DW 423, 20°25.85′S, 166°40.50′E, 280 m, 16 Feb 1989, 1 juv. (MNHN). Stn DW 440, 20°48.80′S, 167°17.25′E, 288 m, 19 Feb 1989, ♀ 12.6 mm (MNHN). Stn DW 451, 20°59′S, 167°24.50′E, 330 m, 20 Feb 1989, ♀ 7.3 mm (MNHN). Stn DW 457, 21°00.42′S, 167°28.71′E, 353 m, 20 Feb 1989, 2 juvs. (MNHN). Stn DW 479, 21°09.13′S, 167°54.95′E, 310 m, 22 Feb 1989, ♂ 13.0 mm, 1 juv. (MNHN). Stn DW 481, 21°21.85′S, 167°50.30′E, 300 m, 23 Feb 1989, ♀ 12.0 mm (MNHN). BATHUS 1, Stn CP 707, 21°42.72′S, 166°35.75′E, 347–375 m, 19 Mar 1993, 2 ♂ 9.9, 12.6 mm, 1 juv. (MNHN). BATHUS 2, Stn CP 742, 22°33.45′S, 166°25.86′E, 340–470 m, 14 May 1993, ♀ ovig. 13.6 mm (MNHN).

New Caledonia. Lagoon, 22°33.41′S, 166°25.74′E, 300 m, 12 Sep 1994, ♀ 9.5 m (MNHN). BIOCAL, Stn CP 105, 21°31′S, 166°22′E, 330–335 m, 8 Sep 1985, 2 ♂ 9.0, 12.5 mm, ♀ 9.0 (MNHN B18412). Stn CP 108, 22°03′S, 167°06′E, 335 m, 9 Sep 1985, ♂ 10.5 mm, ♀ ovig. 13.5 mm (MNHN B19177).

Chesterfield Is., MUSORSTOM 5, Stn 258, 25°32.8′S, 159°46.10′E, 300 m, 8 Oct 1986, ♂ 12.5 mm (MNHN B21212). Stn 261, 25°26.58′S, 159°45.88′E, 300 m, 8 Oct 1986, ♂ 13.7 mm (MNHN B18372). Stn 268, 24°44,70′S, 159°39.20′E, 280 m, 9 Oct 1986, ♂ 13.9 mm (MNHN B21211). Stn 268, 24°44,70′S, 159°39.20′E, 280 m, 9 Oct 1986, 3 ♂ 9.1–13.0 mm (MNHN B18378). Stn 275, 24°46.60′S, 159°40.30′E, 285 m 9 Oct 1986, ♂ 10.8 mm, 2 ♀ 13.1, 14.1 mm, 1 juv. (MNHN B18376). Stn 276, 24°48.90′S, 159°40.90′E, 269–258 m, 9 Oct 1986, 4 ♂ 10.7–13.1 mm, ♀ 7.8 mm, ♀ ovig. 11.8 mm (MNHN B18493). Stn 277, 24°10.60′S, 159°34.90′E, 270 m, 10 Oct 1986, 2 ♂ 10.4, 13.5 mm, 2 juv. (MNHN B18368). Stn 280, 24°09.99′S, 159°35.75′E, 270 m, 10 Oct 1986, 4 ♂ 10.3–10.5 mm, 2 ♀ 10.3, 10.0 mm, 3 juvs. (MNHN B18377). Stn 281, 24°10.54′S, 159°34.32′E, 272 m, 10.10.1986, ♀ ovig. 11.1 mm (MNHN B18484). Stn 284, 24°09.96′S, 159°33.49′E, 10 Oct 1986, ♀ ovig. 13.5 mm (MNHN B 18374). Stn 285, 24°09.35′S, 159°34.04′E, 245–255 m, 10 Oct 1986, ♂ 11.8 mm (MNHN B18495). Stn 287, 24°05.40′S, 159°36.30′E, 270 m, 10 Oct 1986, ♀ ovig. 11.2 mm (MNHN B18490). Stn 288, 24°04.80′S, 159°36.80′E, 270 m, 10 Oct 1986, ♂ 12.6 mm, 3 juv. (MNHN B18488). Stn 289, 24°01.50′S, 159°38.40′E, 273 m, 10 Oct 1986, 8 ♂ 10.3–12.4 mm, 9 ♀ 9.2–13.0 mm, 1 juv. (MNHN B18454). Stn 291, 23°07.70′S, 159°28.40′E, 300 m, 11 Oct 1986, ♂ 11.2 mm, ♀ damaged (MNHN B18485). Stn 307, 22°11.07′S, 159°24.07′E, 350–345 m, 12 Oct 1986, ♂ 10.4 mm, ♀ ovig. 13.7 mm (MNHN B18489). Stn 309, 22°10.20′S, 159°22.80′E, 340 m, 12 Oct 1986, ♂ 10.6 mm (MNHN B18492). Stn 319, 22°24′S, 159°16.50′E, 320–325 m, 13 Oct 1986, ♂ 9.7 mm (MNHN B21321). 22°40′S, 167°10′E, 200–350 m, 10 Oct 1986, ♂ 9.2 mm (MNHN B19163). BATHUS 4, Stn DW 902, 19°00.84′S, 163°14.83′E, 341–351 m, 4 Aug 1994, ♂ 14.3 mm, 1 juv. (MNHN). Stn CP 905, 19°02.45′S, 163°15.65′E, 294–296 m, 4 Aug 1994, ♂ 13.8 mm (MNHN).

Description.—Carapace with dorsal surface evenly, minutely granulate. Frontal lobes squat, rounded, pilose. Subhepatic margin of carapace mammiform, separated by shallow arc from trituberculate anterolateral margin. Intestinal region swollen, demarcated by indistinct grooves, bearing conical tubercle posterioly. Posterior margin bearing laterally 2 lamellar, rounded denticles. Third maxilliped pilose, bearing conicalal granules anteriorly (Fig. 2C). Thoracic sternites granulate.

Cheliped and pereiopods closely granulate throughout. Cheliped merus in adult male nearly as long as carapace; fingers as long as upper margin of palm.

Male abdomen minutely granulate proximally, preapical denticle triangular. Shaft of first male pleopod sinuous, apical process bent at right angle, sigmoid (Figs. 5C, D).

Etymology.—From Latin, *septem,* seven, for the shape of the apical process of the first male pleopod.

Remarks.—*Toru septimus,* new species, differs from the closely allied *T. trituberculatus* in its finer granulation on carapace and chelipeds, the rounded, rather than subquade, frontal lobes, and in the sigmoid shape of the apical process of the first male pleopod.

Distribution.—Western Pacific: Fiji, New Caledonia, Loyalty Is., Vanuatu; 200–648 m.

Toru trituberculatus (Sakai, 1961), new combination

Figs. 2D, 5E, F

Randallia trituberculata Sakai, 1961:134, pl. 3, fig. 2; 1965:42, pl. 17, fig. 2; 1976: 98, pl. 29, fig. 1, text-fig. 53.—Serène, 1968:45.—Serène & Vadon, 1981:119, 124.—Richer de Forges, 1983:634.—Chen, 1989:215, fig. 14, pl. 3, fig. 2.—Takeda, 2001:230.—Chen & Sun, 2002: 340, fig. 150, pl. 14.3.

Material examined.—Japan. Shikoku I., Tosa Bay, 19 Nov 1958, coll. T. & K. Sakai, ♂ 12.7 mm, ♀ 11.4 mm (USNM 120707). Tosa Bay, 3 ♂ 11.8–13.0 mm (SMF, ex. coll. Sakai). ♂ 13.2 mm (SMF, ex. coll. Sakai). Mimase, Dec 1961, ♂ 13.5 mm (SMF, ex. coll. Sakai). Mimase, Mar 1963, ♂ 13.0 mm (SMF, ex. coll. Sakai).

Indonesia. Tanimbar I., KARUBAR, Stn CP 67, 8°58′S, 132°06′E, 233–146 m, 1 Nov 1991, ♂ 8.6 mm (MNHN). Stn CP 86, 9°26′S, 131°13′E, 225–223 m, 4 Nov 1991, 5 ♂ 8.6–11.1 mm, 6 ♀ 9.0–11.9 mm (MNHN).

Philippines. MUSORSTOM 1, Stn 27, 13°59.8′N, 120°18.6′E, 192–188 m, 22 Mar 1976, ♀ 11.2 (MNHN B18084). Stn 30, 14°01.3′N, 120°18.7′E, 186–177 m, 22 Mar 1976, ♂ 7.1 mm (MNHN B18086). Stn 34, 14°01.0′N, 120°15.8′E, 191–188 m, 23 Mar 1976, ♀ 10.6 mm (MNHN B18083). Stn 51, 13°49.4′N, 120°04.2′E, 200–170 m, 25 Mar 1976, ♂ damaged, ♀ ovig. 11.3 mm (MNHN B18085). Stn 64, 14°00.5′N, 120°16.3′E, 194–195 m, 27 Mar 1976, ♀ 8.3 mm (MNHN B18082). MUSORSTOM 3, Stn 88, 14°01′N, 120°17′E, 183–187 m, 31 May 1985, ♀ ovig. 10.7 mm (MNHN B17982). Stn CP 100, 14°00′N, 120°18′E, 189–199 m 1 Jun 1985, ♂ 11.0 mm (MNHN B17983). Stn CP 108, 14°01′N, 120°18′E, 188–195 m, 2 Jun 1985, ♂ 9.9 mm, ♀ ovig. 11.1 mm (MNHN B17984). Stn CP 120, 12°06′N, 121°16′E, 219–220 m, 3 Jun 1985, 2 ♀ 7.9, 8.8 mm (MNHN B17986). Stn CP 139, 11°53′N, 122°14′E, 240–267 m, 6 Jun 1985, 10 ♂ 10.1–11.8 mm, 6 ♀ 7.6–11.3 mm (MNHN B17985).

Redescription.—Carapace with dorsal surface granulate, granules more prominent anteriorly. Frontal lobes squat, subquadrate, minutely granulate, pilose. Subhepatic margin of carapace prominently granulate, mammiform; separated by shallow arc from trituberculate anterolateral margin. Intestinal region swollen, demarcated by distinct grooves, bearing conicalal tubercle posterioly. Posterior margin bearing laterally 2 lamellar, rounded denticles (Fig. 2D).

Third maxillipeds pilose, bearing conical granules anteriorly. Thoracic sternites granulate.

Cheliped, pereiopods closely granulate throughout. Cheliped merus in adult male

0.85 as long as carapace; fingers as long as upper margin of palm.

Male abdomen minutely granulate proximally, preapical denticle triangular. Shaft of first male pleopod sinuous, apical process bent at right angle, tip upcurved (Figs. 5E, F).

Color.—"[T]he carapace . . . is yellowish-red, but the surface near the postero-lateral and posterior margins is pale whitish" (Sakai 1965:42).

Distribution.—Pacific Ocean: Japan, Indonesia, Philippines; 35–267 m.

Remarks.—*Toru trituberculatus* is not "most closely related to *R. distincta* Rathbun (1906)" as claimed by Sakai (1961: 135), it belongs in a different genus. *Toru trituberculatus* differs from *Tanaoa distinctus* in having a lingulate telson in the male, anteriorly excavate lateral walls of the male abdominal sulcus, prominent margins to the female abdominal cavity, and bearing a digitate apical process on the male first pleopod.

Key to Species of *Toru*, new genus

1. Anterolateral margin of carapace lacking tubercules 2
– Anterolateral margin of carapace trituberculate 3
2. Lateral margin medially set with small tubercle; pereiopods closely granulate . . . . *T. granuloides,* new combination
– Lateral margin uniformly rounded; anterior margin of pereiopodal meri, carpi and propodi prominently spinose . . . . *T. mesjatzevi,* new combination
3. Front prominently produced, postorbital region concave; hepatic region ridged; first male pleopod distally looped . . . . *T. pilus,* new combination
– Frontal lobes squat, postorbital region not concave; hepatic region lacking ridge; first male pleopod distally bent at right angle 4
4. Carapace and chelipeds finely granulate; apical process of first male pleopod sigmoid, tip not upcurved . . . . *T. septimus,* new species
– Carapace and chelipeds prominently granulate; apical process of first male pleopod not sigmoid, tip upcurved . . . . *T. trituberculatus,* new combination

Urashima, new genus

Diagnosis.—Carapace subrhomboidal, globose. Front narrow, bilobed. Eyes small, retractible. Outer orbital margin trisutured, V-shaped gap proximally on ventral margin. Antennules obliquely folded, basal antennular segment squat, operculiform, sealing bottom half of antennular aperture. Antennae small, slender, basal antennal segment inserted in orbital hiatus. Postorbital region concave. Hepatic, branchial regions demarcated by grooves, 2 pairs of pits along cardiobranchial grooves. Intestinal region swollen, demarcated by grooves. Posterior margin of carapace narrow, bilobate.

Third maxilliped exopod slightly shorter than endopod, not quite sealing efferent branchial channel; endopod of adult female medially with vertical line of setae; merus of endopod subtriangular, shorter than subrectangular ischium. Anterior margin of efferent branchial channel produced, bilobed, separated by narrow groove from lower orbital margin.

Chelipeds subequal. Cheliped merus subcylindrical; fingers laterally compressed, as long as upper margin of palm, inner margins denticulate. Pereiopods slender, prominently granulate, short; all but last dactyl as long as propodi; upper surface setose, tips corneous.

Fourth thoracic sternite swollen laterally. Abdominal sulcus of male deep, elongate, nearly reaching buccal cavity, anterior margin raised. Abdominal segments 3–6 of male fused, basio-lateral regions inflated, fused segment narrowing distally, bearing denticle at distal margin; lateral margin carinate, carina fitting into groove at suture between sternites 4 and 5. Telson slender, nearly half as long as fused segment, not reaching tip of abdominal sulcus. Abdominal segments 4–6 of female fused, shield-like; margin of abdominal cavity prominent, rampart-like. Telson ogival, basal margin sinuous.

Male first pleopod elongate, stocky, distally flattened; second pleopod short, recurved, distally attenuate.

Type species.—*Randallia pustuloides* Sakai, 1961.

Species.—*Urashima lamellidentatus* (Wood-Mason, 1892), *Urashima pustuloides* (Sakai, 1961).

Etymology.—Urashima, according to Japanese legend, was a handsome fisherman who married a mermaid and dwelt with her undersea. The name *Urashima* is to be considered as an arbitrary combination of letters, and heretofore takes the gender masculine.

Remarks.—*Urashima,* new genus, differs from the other genera discussed herein in the laterally compressed cheliped fingers, the granulate pereiopodal carpi and propodi, and the oar-shaped first male pleopod.

Urashima lamellidentatus (Wood-Mason, 1892), new combination
Fig. 2E

Randallia lamellidentata Wood-Mason, 1892: pl. 5, figs 5, 5a, 5b.—Alcock, 1894:404; 1896:195; 1899:26.—Kemp & Sewell, 1912:29.—Ihle, 1918:312.—Serène, 1954:491; 1968:45.—Yaldwyn & Dawson, 1976:96.—Richer de Forges, 1983:634.

Type Material.—Holotype: Andaman Is. 11°3.40′N, 92°46.40′E, ♂ juv. cl 11.9 mm (NHM 1896.9.8.7 ex. Indian Museum).

Redescription.—Dorsal surface of carapace unevenly tuberculate, tubercles more pronounced laterally, posteriorly. Frontal lobes squat, rounded, minutely granulate. Anterior margin of efferent branchial channel deeply sutured (Fig. 2E). Third maxilliped unevenly granulate, endopod merus with median rise proximally.

Subhepatic margin of carapace with lamellate crest, followed by pearliform granule. Branchial margin of carapace with 2 lamellate crests separated by granulate denticle. Posterolateral margin set with pearliform granules. Posterior margin laterally with lamellate rounded denticles. Intestinal region inflated, bearing posteriorly small, upcurved conical tubercle.

Cheliped stout, prominently granulate; merus two-thirds as long as carapace, granules larger, pearliform distally. Upper margin of palm prominently crested, fingers laterally compressed; upper, lower margins carinate. Pereiopodal carpi and propodi bearing rows of conical granules on upper margin, as well as merus of last pereiopods.

Thoracic sternites granulate. Fused abdominal segments in male lacking horizontal ridge, distal tubercle spur-like, prominent. Margins of abdominal sulcus in female lamellate, prominent. First male pleopod stout, sinuous, distally flattened, oar-like.

Color.—"[W]hite, with a pinkish blush" (Alcock 1894:404).

Distribution.—Indian Ocean: Andamans, Maldives; 340–640 m.

Remarks.—*Urashima lamellidentatus* differs from *U. pustuloides* in bearing lamellate crests on the anterolateral margins of the carapace, and lamellate rounded denticles laterally on the posterior margin of the carapace.

Urashima pustuloides (Sakai, 1961), new combination
Figs. 2F, 5G, H

Randallia pustuloides Sakai, 1961:135, pl. 3, fig. 4; 1976:99, 100, pl. 30, fig. 1, text-fig. 54.—Yaldwyn & Dawson, 1976: 96.—Richer de Forges, 1983:634 (tab.).—Chen, 1989:219, fig. 16.—Tan, 1996:1054.—Takeda, 1997:238.—Ikeda, 1998:83, pl. 20, figs 1a, b, 2, 3a–b.—Ng et al., 2001:10.

Type Material.—Paratypes: Japan. Shikoku I., Mimase, Tosa Bay, coll. K. Sakai, ♂ 34.3 mm, 2 ovig. ♀ 38.0, 38.9 mm (NHM 1961.6.5.46–48).

Material examined.—Japan. Shikoku I., Mimase, Tosa Bay, coll. K. Sakai, ♀ 37.6

mm (SMF). ♂ 35.3 mm (SMF). ♂ 35.6 mm, ♀ 38.4 mm (SMF). ♂ 36.7 mm (SMF). ♂ 37.2 mm, ♀ 37.6 mm (SMF 7700). Dec 1961:2 ♂ 26.7, 36.3 mm (SMF). 250 m, Apr 1968, ♂ 37.1 mm, ovig. ♀ 38.6 mm (SMF 15103). Off Ashizuri, 366 m, 24 Nov 1958, 2 ♀ 36.7, 37.7 mm, ♀ broken (SMF).

Taiwan. I-Lan county, 1998, coll. T.Y. Chan, ♂ 32.8 mm (MNHN B26326). Tongkuang, 25 Feb 1995, 300 m, coll. T.Y. Chan, 2 ♂ 33.3, 33.6 mm, 2 ♀ 26.0, 25.9 mm (NTOU). Tashi, 5 Mar 1997, 200 m, coll. T.Y. Chan, ♀ 18.3 mm (NTOU).

Philippines. Btw Negros, Siquijor, R/V *Albatross* Stn 5538, 9°08.15′N, 123°23.20′E, 468 m, 19 Aug 1909, id. C.G.S. Tan, ♀ 38.3 mm (USNM). MUSORSTOM 2, Stn CP 20, 14°00′N, 120°18′E, 185–192 m, ♂ 25.9 mm (MNHN B18081).

Indonesia. KARUBAR, Tanimbar I., Stn CP69, 356–368 m, 8°42′S, 131°53′E, 2 Nov 1991, 2 ♂ 37.4, 38.2 mm, 3 ♀ 25.0–31.6 mm (MNHN). Stn CP 77, 352–346 m, 8°57′S, 131°27′E, 3 Nov 1991, 3 ♂ 25.3–27.2 mm, ♀ 38.9 mm (MNHN).

Australia. 18°05′S, 118°08′E, 440–442 m, 22 Aug 1983, ♀ 37.9 mm (WAM c14731). 14°51′S, 121°35′E, 300 m, 3 Aug 1989, ♂ 37.0 mm (WAM 577-92).

Redescription.—Dorsal surface of carapace unevenly tuberculate, larger, pustule-like tubercles on branchial region. Frontal lobes squat, rounded, minutely granulate. Anterior margin of efferent branchial channel deeply sutured (Fig. 2F). Third maxilliped unevenly granulate, merus with median ridge proximally.

Subhepatic margin of carapace inflated, median tubercle followed by 1 or 2 smaller, pearliform granules. Lateral margin of carapace medially with 3 flattened, triangular, upcurved denticles, decreasing in size posteriorly. Posterolateral margin set with pearliform tubercles. Posterior margin with lateral triangular denticles, closely set with pearliform tubercles. Intestinal region inflated, bearing posteriorly small, upcurved conical tubercle.

Cheliped prominently granulate; granules larger, pearliform distally; merus three-quarters as long as carapace. Fingers laterally compressed; upper, lower margins carinate. Pereiopodal meri distally granulate on upper margin, fifth merus bearing conical granules on posterior surface.

Thoracic sternites with low granulation. Fused abdominal segment in male lacking horizontal ridge, distal tubercle spur-like, prominent. Margins of abdominal sulcus in female lamellate, prominent. First male pleopod stout, sinuous, distally oar-shaped (Figs. 5G, H).

Distribution.—Pacific Ocean: Japan, Taiwan, Philippines, Indonesia, Australia; 85–468 m.

Remarks.—Sakai (1961), and Chen (1989) considered *Urashima pustuloides* related to *Tanaoa pustulosus.* However, *U. pustuloides* in addition to the characters cited by Chen (1989), and Takeda (1997), is easily distinguished from *T. pustulosus* in having laterally compressed, rather than rounded, cheliped fingers; granulate, rather than smooth pereiopodal carpi and propodi; and oar-shaped, rather than bearing preapical process on the first male pleopod.

Key to Species of *Urashima,* new genus

1. Anterolateral margins of carapace bearing lamellate crests; posterior margin of carapace with lamellate denticles; upper margin of cheliped palm prominently crested .... *U. lamellidentata,* new combination
– Anterolateral margins of carapace lacking lamellate crests; posterior margin of carapace with triangular denticles; cheliped palm subcylindrical .... *U. pustuloides,* new combination

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Literature Cited

Alcock, A. 1894. XLIV.—Natural history notes from H. M. Indian Marine Survey Steamer 'Investigator', Commander R. F. Hoskyn, R.N., late commanding. Series II., No. 1. On the results of the deep-sea dredging during the season 1890–91 (concluded).—The Annals and Magazine of Natural History 13:400–411.

———. 1896. Materials for Carcinological Fauna of India. N. 2. The Brachyura Oxystomata.—Journal of the Asiatic Society of Bengal 65(2):134–296.

———. 1899. An Account of the Deep-Sea Brachyura collected by the Royal Indian Marine Survey Ship "Investigator". Calcutta, 85 pp.

———, & A. R. J. Anderson. 1894. Natural history notes from H. M. Indian Marine Survey Steamer 'Investigator', Commander C. F. Oldham, R.N., commanding. Series II., No. 14. An account of a recent collection of deep-sea Crustacea from the Bay of Bengal and Laccadive Sea.—Journal of the Asiatic Society of Bengal 63(2):141–185.

———, & ———. 1897. Crustacea, part V. Illustrations of the Zoology of the Royal marine surveying Steamer investigator, Calcutta pl. 28–32.

Austin, W. C. 1985. An annotated checklist of marine invertebrates in the cold temperate Northeast Pacific. 3:1–682. Khoyatan Marine Laboratory.

Baker, C. F. 1912. Notes on the crustacea of Laguna Beach.—First annual Report of the Laguna Marine Laboratory at Laguna Beach, Orange County, California 1912:100–117.

Bonfil, R., & A. Carvacho. 1989. The crabs of Bahía de Todos Santos, Baja California, part I. Dromiidae, Leucosiidae, Majidae and Parthenopidae (Crustacea: Decapoda: Brachyura).—Ciencias Marinas 2:79–109.

Boone, L. 1930. Crustacea: Stomatopoda and Brachyura. Scientific Results of the cruises of the Yachts "Eagle" and "Ara", 1921–1928, William K. Vanderbilt, Commanding. Crustacea: Stomatopoda and Brachyura.—Bulletin of the Vanderbilt Marine Museum 2:1–228, 74 pls.

Borradaile, L. A. 1916. Crustacea, I. Decapoda. British Antarctic ("Terra Nova") Expedition, 1910. Natural History Report, Zoology 3(2):75–110.

Campbell, B. M. 1971. New records and new species of crabs (Crustacea: Brachyura) trawled off southern Queensland: Dromiacea, Homolidea, Gymnopleura, Corystoidea, and Oxystomata.—Memoires of the Queensland Museum 16(1): 27–48.

Chang, C. 1963. A check-list of Taiwan crabs with descriptions of 19 new records.—Biological Bulletin, Tunghai University 14:1–23, 2 pls.

Chen, H. 1989. Leucosiidae (Crustacea, Brachyura). *In* J. Forest, ed., Résultats des Campagnes MUSORSTOM, vol. 5.—Mémoires du Muséum national d'Histoire naturelle (A) 144:181–263.

Chen, H., & H. Sun. 2002. Brachyura: marine primitive crabs. *In* Fauna Sinica Invertebrata: Arthropoda: Crustacea, 30: xiii + 597, figs 1–237, pls 1–6. Science Press, Beijing.

Davie, P. J. F. 2002. Crustacea: Malacostraca: Eucarida (part 2): Decapoda—Anomura, Brachyura. *In* A. Wells & W. W. K. Houston, eds., Zoological Catalogue of Australia. Vol. 19.3B. CSIRO Publishing, Melbourne, 641 pp.

Doflein, F. 1904. Brachyura. *In* Wissenschaftliche Ergebnisse der Deutschen tiefsee-Expedition Auf dem Dampfer "Valdivia", 1898–1899, Jena, 6: i–xiv, 1–314, 58 pl.

Galil, B. S. 2001. A new genus of leucosiid crabs (Crustacea, Brachyura).—Zoosystema 23(1): 65–75.

Garth, J. S. 1940. Some new species of brachyuran crabs from Mexico and the Central and South American mainland.—Allan Hancock Pacific Expedition 5(3):53–96, pl. 11–26.

———. 1960. Distribution and affinities of the brachyuran Crustacea. *In* The biogeography of Baja California and adjacent seas, part II. Marine Biotas.—Systematic Zoology 9(3):105–123.

———. 1966. Eastern Pacific Expeditions of the New York Zoological Society. Oxystomatous and allied crabs from the west coast of tropical America.—Zoologica 51:1–16.

Gibbes, L. R. 1850. On the carcinological collections of the United States, and on enumeration of species contained in them, with notes on the most remarkable, and descriptions of new species.—Proceedings of the American Association for the Advancement of Science 3:167–201.

Hendrickx, M. E. 1990. The stomatopod and decapod crustaceans collected during the GUAYTEC II cruise in the central Gulf of California, Mexico, with the description of a new species of *Plesionika* Bate (Caridea: Pandalidae).—Revista de Biología Tropical 38(1):35–53.

———. 1992. Distribution and zoogeographic affinities of decapod crustaceans of the Gulf of California, Mexico.—Proceedings of the San Diego Society of Natural History 20:1–11.

———. 1995. Checklist of brachyuran crabs (Decapoda: Brachyura) from the eastern tropical Pacific.—Bulletin de l'Institute Royal des Sciences Naturelles de Belgique 65:125–150.

———. 1997. Los Cangrejos Braquiuros (Crustacea: Brachyura: Dromiidae, hasta Leucosiidae) del Pacífico Mexicano. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, 178 pp.

Holmes, S. J. 1900. Synopsis of California stalk-eyed Crustacea.—Occasional Papers of the California Academy of Sciences 7:1–256, 4 pls.

Huang, Z. 1989. Brachyura (Dromiacea, Gymnopleura, Oxystomata, Oxyrhyncha, Corystoidea). *In* Wei Ch., ed., Fauna of Zhejiang. Crustacea. Zhejiang Science & Technology Publishing House, pp. 280–387.

———. 1994. Marine species and their distributions in China's seas. China Ocean Press, Beijing, 764 pp + 134 index.

Ihle, J. E. W. 1918. Die Decapoda Brachyura der Siboga-Expedition. III. Oxystomata: Calappidae, Leucosiidae, Raninidae. Siboga Expeditie 39b2: 1–322.

Ikeda, H. 1998. The deep-sea crabs of Sagami Bay. Hayama Shiosai Museum, Inamoto Printing, Kanagawa, 180 pp., 73 pls.

Kemp, S., & R. B. Sewell. 1912. Notes on the Decapoda in the Indian Museum. III. The species obtained by R.I.M.S. S. 'Investigator' during the season 1910–11. R.B.—Records of the Indian Museum Calcutta 7:15–32.

McLay, C. L. 1988. Crabs of New Zealand.—Leigh Laboratory Bulletin 22:1–463, 85 figs.

Miers, E. J. 1886. Report on the Brachyura collected by H.M.S. Challenger during the years 1873–1876.—Report on the Scientific Results of the Voyage of H.M.S. Challenger during the years 1873–76, (Zool) 17:1–362.

Ng, P. K. L., C. H. Wang, P. O. Ho, & H. T. Shih. 2001. An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). National Taiwan Museum Special Publication Series 11:1–86.

Ovaere, A. A. 1989. *Ihleus* gen. nov., a new leucosiid genus (Crustacea, Brachyura).—Bulletin de l'Institut Royal des Sciences Naturalles de Belgique, Biologie 59:95–100.

Poupin, J., & B. Richer de Forges. 1991. New or rare crustaceans from French Polynesia (Crustacea: Decapoda).—Memoirs of the Queensland Museum 31:211.

Randall, J. W. 1839. Catalogue of the Crustacea brought by Thomas Nuttal and J.K. Townsend, from the west coast of North America and the Sandwich Islands, with descriptions of such species as are apparently new, among wich are included several species of different localities, previously existing in the collection of the Academy.—Journal of the Academy of Natural Sciences of Philadelphia 8:106–147.

Rathbun, M. J. 1893. Scientific results of explorations by the U.S. Fish Commission Steamer Albatross. XXIV. Descriptions of new genera and species of crabs from the west coast of North America and the Sandwich Islands.—Proceedings of the United States National Museum 16: 223–260.

———. 1898. The Brachyura collected by the U.S. fish Commission Steamer Albatross on the voyage from Norfolk, Virginia, to San Francisco, California, 1887–1888.—Proceedings of the United States National Museum 21:567–616.

———. 1904. Decapod crustaceans of the northwest coast of North America.—Harriman Alaska Expedition 10:1–211, 10 pls.

———. 1906. The Brachyura and Macrura of the Hawaiian Islands.—Bulletin of the United States Fish Commission 23(3):829–930.

———. 1922. New species of crabs from Curaçao.—Proceedings of the Biological Society of Washington 35:103–104.

———. 1935. Preliminary descriptions of seven new species of oxystomatous and allied crabs.—Proceedings of the Biological Society of Washington 48:1–4.

———. 1937. The Oxystomatous and allied crabs of America.—Bulletin of the United States National Museum 166:1–278.

Richer de Forges, B. 1983. *Randallia serenei* (Crustacea, Decapoda, Brachyura), espèce nouvelle de Leucosiidae du Pacifique.—Bulletin du Muséum national d'Histoire naturelle, Paris 5(2): 633–640.

Rodríguez de la Cruz, M. C. 1987. Crustáceos decápodos del Golfo de California. Sría. Pesca (ed.). Mexico, D.F. 306 pp.

Sakai, T. 1934. Brachyura from the coast of Kyusyu, Japan.—Science Reports of the Tokyo Bunrika Daigaku B 1(25):281–330.

———. 1935. Crabs of Japan. 66 plates in life colours with descriptions.—Tokyo, Sanseido Co.

———. 1937. Studies on the crabs of Japan. II. Oxystomata.—Science Reports of the Tokyo Bunrika Daigaku, 3, suppl. 2:67–192.

———. 1961. New species of Japanese crabs from the collection of His Majesty the Emperor of Japan.—Crustaceana 3(2):131–150.

———. 1965. The crabs of Sagami Bay collected by His Majesty the Emperor of Japan. Tokyo, Maruzen Co, I–xvi, 1–206 [English]; 1–92 [Japanese], pl. 1–100, 1 map.

———. 1976. Crabs of Japan and the adjacent seas (Tokyo: Kodansha). [In three volumes: 1. English text, xxxix+773 pp., figs. 1–379; 2. Plates volume, 16 pp., 1–251; 3. Japanese text, 461 pp. Figs 1–2.].

Schmitt, W. L. 1921. The marine decapod Crustacea of California with special reference to the decapod Crustacea collected by the United States Bureau of Fisheries Steamer *Albatross* in connection with the biological survey of San Francisco Bay during the years 1912–1913.—University of California Publications in Zoology 23:188, fig. 116.

Serène, R. 1954. Sur quelques espèces rares de brachyures (Leucosidae) de l'Indo-Pacifique.—Treubia 22(3):453–500, pls 7–10.

———. 1968. Prodromus for a check list of the non-planctonic marine fauna of South ast Asia.—Singapore National Academy of Science. Special Publication no. 1. 122 pp.

———, & C. L. Soh. 1976. Brachyura collected during the Thai-Danish Expedition (1966).—Phuket Marine Biological Center Research Bulletin 12:1–37, figs 1–28, 8 pls.

———, & C. Vadon. 1981. Crustacés Décapodes: Brachyures. Liste préliminaire, description de formes nouvelles et remarques taxonomiques. *In* Résultats des Campagnes MUSORSTOM, vol. 1. Philippines. Mémoires ORSTOM 91: 117–140, pl. 1–4.

Stimpson, W. 1857a. Notices of new species of Crustacea from western North America, being an abstract from a paper to be published in the Journal of the society.—Proceedings of the Boston Society of Natural History 6:84–89.

———. 1857b. On the Crustacea and Echinodermata of the Pacific Shores of North America, part I. Crustacea.—Boston Journal of Natural History 6:444–532.

———. 1860. XI. Notes on North American Crustacea. I.—Annals of the Lyceum of Natural History in New York 7:49–93.

Takeda, M. 1973. Report on the crabs from the sea around the Tsushima Islands collected by the Research Vessel "Genaki" for the Trustees of the National Science Museum, Tokyo.—Bulletin of the Liberal Arts & Science College, Nihon University 1:17–68.

———. 1975. Crabs from the East China Sea, VI. A collection from off the Danjo Islands made by the R/V Hakuhô Maru Cruise KH-73-3.—Bulletin of the National Science Museum, Zoology 1(3):137–156.

———. 1997. Deep-sea decapod crustacean fauna of Suruga Bay, Central Japan.—National Science Museum Monographs 12:229–255, pls 1–5.

———. 2001. Annotated list of crabs from Tosa Bay, Southwest Japan, collected by the R/V *Kotaka Maru* during the years 1997–2000.—National Science Museum Monographs 20:217–262.

———, & S. Miyake. 1970. Crabs from the East China Sea. IV. Gymnopleura, Dromiacea and Oxystomata.—Journal of the Faculty of Agriculture, Kyushu University 16(3):193–235, pl.1.

Tan, C. G. S. 1996. Leucosiidae of the *Albatross* expedition to the Philippines, 1907–1910 (Crustacea: Brachyura: Decapoda).—Journal of Natural History 30:1021–1058.

Tyndale-Biscoe, M., & R. W. George. 1962. The Oxystomata and Gymnopleura (Crustacea, Brachyura) of Western Australia with descriptions of two new species from Western Australia and one from India.—Journal of the Royal Society of Western Australia 45(3):65–96, pl. 1–3.

Uchida, S. 1949. Illustrated Encyclopedia of the Fauna of Japan (Exclusive of Insects). Hokuryukan, Tokyo, 1898 pp.

Utinomi, H. 1956. Coloured illustrations of sea shore animals of Japan. Hoikusha, Osaka, 167 pp., 64 color pls.

Weymouth, F. W. 1910. Synopsis of the true crabs (Brachyura) of Monterey Bay, California.—Leland Stanford Junior University Publications University Series 4:1–64, 14 pls.

Wood-Mason, J. 1892. Crustaceans, part 1. Illustrations of the zoology of H. M. Indian Marine Surveying Steamer Investigator, pl. 1–5.

Wood-Mason, J., & A. Alcock. 1891. XXVII. Natural history notes from H.M. Indian Marine Survey Steamer "Investigator", Commander R.F. Hoskyn, R.N., commanding. No. 21. Note on the results of the last seasons's Deep-sea Dredging.—The Annals and Magazine of Natural History 7:258–272. (Crustacea attributed to Wood-Mason).

Yaldwyn, J. C., & E. W. Dawson. 1976. First records of the crab genera *Homola, Randallia,* and *Rochinia* from New Zealand (Crustacea: Decapoda: Brachyura).—Records of the National Museum of New Zealand 1(6):91–103.

Yokoya, Y. 1933. On the distribution of decapod crustaceans inhabiting the continental shelf around Japan, chiefly based upon materials collected by s. s. Soyo-Maru during the years 1923–1930.—Journal of the College of Agriculture, Tokyo Imperial University 12(1):1–226, 71 figs.

Zarenkov, N. A. 1969. Crabs of the family Leucosiidae (subfamilies Ebaliinae and Iliinae) collected in tropical waters of Indian and Pacific oceans.—Nauchnye Doklady Vysshei Shkoly, biologicheskie Nauki, SSSR 12(10):16–26 [in Russian].

———. 1990. Plankton and benthos from the Nazca and Sala-y-Gomez ridges.—Transactions of the P. P. Shirshov Institute of Oceanology, Academy of Sciences of the USSR, Nauka, Moscow 124: 218–244 [in Russian].

———. 1994. Crabs from seamounts of the western part of the Indian Ocean. *In* A. P. Kuznetsov & A. N. Mironov, eds., Bottom fauna of Seamounts.—Transactions of the P. P. Shirshov Institute of Oceanology, Russian Academy of Sciences, Nauka, Moscow 129:97–151 [in Russian].

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Type catalogue of the Crustacea Decapoda in the collections of the Museu de Zoologia da Universidade de São Paulo, Brazil

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Abstract.—Data and pertinent information on the type specimens of eighty-four species of Crustacea Decapoda held in the Museu de Zoologia da Universidade de São Paulo, Brazil, are provided. The taxa are arranged in alphabetic order. Included are references where all taxa were described, collection data, and changes in nomenclature.

Resumo.—São apresentados dados e informações referentes aos espécimes-tipo de oitenta e quatro espécies de Crustacea Decapoda, depositados na coleção carcinológica do Museu de Zoologia da Universidade de São Paulo, Brasil. O tratamento das espécies é feito em ordem alfabética dentro das famílias, e uma lista de referências inclui todos os trabalhos nos quais as espécies foram descritas.

Brief History of Museu de Zoologia da Universidade de São Paulo

The origin of Museu de Zoologia da Universidade de São Paulo can be traced back to 1886, the year of foundation of the Comissão Geográfica e Geológica (Geographical and Geological Commission, CGG) of the Province of São Paulo. The aim of the Commission was to improve scientific knowledge of the province.

In the last decade of the XIX century, Francisco de Paula Mairynk acquired private collections belonging to Colonel Joaquim Sertório and offered them to the provincial government in order to create a State Museum. After several years, these collections were incorporated into collections already held by the Comissão Geográfica e Geológica. This acquisition created the nucleus of a museum of natural history.

By the end of 1893, the State Museum received the name Museu Paulista. In 1895, as a commemoration of Brazilian independence, the present building of the Museu Paulista was inaugurated. This building is located near the streamlet where Emperor Dom Pedro I proclaimed independence for Brazil.

The Section of Zoology of the Museu Paulista was established in 1925. In 1939 the Section was transferred to the Department of Zoology of the Secretariat of Agriculture, Industry, and Commerce of the state of São Paulo. A new building was then constructed in order to accommodate the collections.

In 1969, The University of São Paulo incorporated the Department of Zoology into its bureaucratic structure. At that time the Department received its present name of Museu de Zoologia (MZUSP).

The Crustacea Collection

The carcinological collection of the MZUSP was established on 19 March 1962, with 76 dried specimens found in the basement of the museum. Through 1966, the collection was augmented by collections from rivers, mangrove swamps, and beaches. The acquisition in 1967 of the Oceanographic Vessel *Prof. W. Besnard* by the Oceanographic Institute of the University of São Paulo (IOUSP) then enabled significant quantitative and qualitative improvements in the collection. The partnership between MZUSP and IOUSP in projects Ilha Grande (1966–1969) and GEDIP (Grupo Executivo do Desenvolvimento da Indústria da Pesca) I (1968–1969) and II (1972), in addition to other, less extensive surveys, was crucial in bringing the collection to its present state.

The collection was originally intended to lodge only species of the order Decapoda, because of space limitations. Nevertheless, other excellent collections were eventually added, for instance that of Cirripedia, donated by Dr. Paulo S. Young of the Museu Nacional do Rio de Janeiro, and a collection of Isopoda assembled by the late Dr. Plínio Soares Moreira of IOUSP. Presently, the collection includes approximately 15,000 lots, and about 230,000 specimens of Decapoda, which are chronologically registered and sequentially numbered. There are about 6000 uncatalogued lots. This collection is considered one of the best in Latin America.

Organization of Catalogue

The catalogue presented herein includes all type specimens of Decapoda presently held in the MZUSP collection. Data and information on 84 species of Crustacea Decapoda are presented, including Brachyura (46), Anomura (17), Caridea (10), and Thalassinidea (11). All specimens are preserved in 70% ethanol.

The highest hierarchical levels (superfamilies and families) are ordered according to Martin & Davis (2001). The genera and species are arranged alphabetically within each family.

Species are listed by the scientific name under which each was originally described. Information regarding any subsequent name changes is provided in the Remarks with a reference to the source of the change. Inconsistencies between the original description and the type specimen, register number, label or any additional comment are also noted. Instances of type specimens which have been donated to or lodged in other museums are also noted in the Remarks.

Only types as recognized by the International Code of Zoological Nomenclature (1999), hereafter referred to as the ICZN, are included in this list.

The collection includes some specimens considered "possible-types". This material, being potentially useful for future research on the group, is included in this paper, and pertinent details explained in the Remarks.

Other abbreviations used: coll (collector); DOUFPE (Departamento de Oceanografia da Universidade Federal de Pernambuco); EPA (Expedição Permanente do Amazonas); INPA (Instituto Nacional de Pesquisas da Amazônia); ITA (Instituto das Tecnologias Ambientais); juv (juvenile or juveniles); ovig. (ovigerous); Proj (Project); RD (Project Rio Doce); sta (station); TAAF MD 55 (Terres Australes et Antarctiques Françaises); UFRGS (Universidade Federal do Rio Grande do Sul).

Suborder Pleocyemata Burkenroad, 1963
Infraorder Caridea Dana, 1852
Superfamily Palaemonoidea Rafinesque, 1815
Family Palaemonidae Rafinesque, 1815
Macrobrachium birai, Lobão, Melo, & Fernandes, 1986:50

Holotype.—♂, Rio Branco, tributary of Rio Itapitangui, Cananéia, State of São Paulo, 24°54′44″S, 47°58′30″W, coll. V. L. Lobão and W. M. Fernandes, Dec 1984, MZUSP 8027.

Paratypes.—All same data as holotype: 1 ♂, MZUSP 8028; 1 ♂, MZUSP 8029; 1 ♂, MZUSP 8030; 1 ♂, MZUSP 8031; 1 ♂, MZUSP 8032; 1 ♀, MZUSP 8033.

Remarks.—This species was redescribed in a later paper by Melo et al. (1988:89).

Macrobrachium holthuisi Genofre & Lobão, 1978:273, fig. 1

Holotype.—♂, Rio Guaecá, São Sebastião, State of São Paulo, coll. V. Lobão, 21 Sep 1978, MZUSP 5283.
Paratypes.—4 ♀, same data as holotype, MZUSP 4830.

Macrobrachium inpa Kensley & Walker, 1982:6, figs. 7–9, 12c

Paratype.—1 ♂, Igarapé in the forest reserve of INPA, Campina, km 60 BR-174, State of Amazonas, 21 Jan 1981, MZUSP 7014.

Macrobrachium petronioi Melo, Lobão, & Fernandes, 1986:51

Holotype.—♂, Rio Branco, tributary of Rio Itapitangui, Cananéia, State of São Paulo, 24°54′44″S, 47°58′30″W, coll. V. L. Lobão and W. M. Fernandes, Dec 1984, MZUSP 8034.
Paratypes.—All same data as holotype: 1 ♂, MZUSP 8035; 1 ♂, MZUSP 8036; 1 ♀, MZUSP 8037; 1 ♀, MZUSP 8038.
Remarks.—This species was redescribed in a later paper by Melo et al. (1988:92).

Pseudopalaemon gouldingi Kensley & Walker, 1982:18, figs. 20, 21

Paratypes.—118 juv, near the mouth of Rio Urubaxi, State of Amazonas, coll. M. Golding, 11 Feb 1980, MZUSP 7013.

Superfamily Alpheoidea Rafinesque, 1815
Family Alpheidae Rafinesque, 1815
Alpheus chacei Carvacho, 1979:455, figs. 4–6

Holotype.—♀ ovig, Balneário Atalaia, State of Sergipe, coll. M. A. Santos, 12 Jul 1972, MZUSP 4545.

Alpheus estuariensis Christoffersen, 1984:191, figs. 1, 2

Holotype.—♂, Estuary of Rio Potengi, Natal, State of Rio Grande do Norte, in nursery of shrimps, mud, coll. S. L. S. Bueno, 26 Jan 1979, MZUSP 4544.

Alpheus pouang Christoffersen, 1979:324

Holotype.—♂, Proj Sol, sta 1019, 23°39′S, 43°37′W, 27 May 1970, MZUSP 4543.

Lepthalpheus axianassae Dworschak & Coelho, 1999:477, figs. 1–30

Paratypes.—1 ♀, 1 ♂, Praia do Araçá, São Sebastião, State of São Paulo, coll. V. R. Coelho and S. de A. Rodrigues, 9 Aug 1998, MZUSP 13010.

Superfamily Processoidea Ortmann, 1890
Family Processidae Ortmann, 1890
Processa brasiliensis Christoffersen, 1979:364

Paratypes.—2 ♂, R/V *Calypso,* sta 77, 18°00′S, 38°18′W, 48 m, 28 Nov 1961, MZUSP 4554.

Infraorder Thalassinidea Latreille, 1831
Superfamily Callianassoidea Dana, 1852
Family Callianassidae Dana, 1852
Biffarius delicatulus Rodrigues & Manning, 1992a:324, figs. 1a–w

Holotype.—♂, Praia do Araçá, São Sebastião, State of São Paulo, near mangrove, coll. S. de A. Rodrigues, 18 May 1985, MZUSP 10582.

Callianassa guara Rodrigues, 1971:210, figs. 61–76

Holotype.—♂, Guarujá, State of São Paulo, coll. T. K. S. Björnberg, Oct 1961, MZUSP 2729.
Remarks.—Transferred to *Sergio* Manning & Lemaitre, 1994 by Manning & Lemaitre (1994:39).

Callianassa guassutinga Rodrigues, 1971:204, figs. 41–60

Holotype.—♂, Praia do Araçá, São Sebastião, State of São Paulo, coll. S. de A. Rodrigues, Sep 1965, MZUSP 2728.

Remarks.—Transferred to *Sergio* Manning & Lemaitre, 1994 by Manning & Lemaitre (1994:39).

Callianassa mirim Rodrigues, 1971:214, figs. 77–98

Holotype.—♂, Baia de Santos, State of São Paulo, coll. S. de A. Rodrigues, Mar 1966, MZUSP 2730.

Remarks.—Transferred to *Sergio* Manning & Lemaitre, 1994, by Manning & Lemaitre (1994:39).

Eucalliax cearensis Rodrigues & Manning, 1992a:327, figs. 2a–v

Holotype.—♂, Barra do Rio Ceará, Fortaleza, State of Ceará, coll. S. de A. Rodrigues, 21 Feb 1984, MZUSP 10583.

Lepidophthalmus sinuensis Lemaitre & Rodrigues, 1991:625, figs. 1–4

Paratypes.—5 ♀, Fazenda Agrosoledad, Córdoba, Colombia, nursery of Penaeidae, coll. S. de A. Rodrigues & R. Lemaitre, 20 Jul 1990, MZUSP 10751.

Lepidophthalmus siriboia Felder & Rodrigues, 1993:367, figs. 2e–h, 4a–f, 5a–g, 6a–l

Holotype.—♂, Rio Anil, São Luiz, State of Maranhão, coll. D. Felder and S. de A. Rodrigues, 18 Feb 1984, MZUSP 11083.

Paratypes.—8 ♀, same data as holotype, MZUSP 11084.

Poti gaucho Rodrigues & Manning, 1992b:10, figs. 1a–v

Holotype.—♀, State of Rio Grande do Sul, 33°43′S, 51°13′W, coll. S. de A. Rodrigues, MZUSP 10581.

Family Laomediidae Borradaile, 1903

Axianassa australis Rodrigues & Shimizu, 1992:317, figs. 1–20

Holotype.—♂, Fazenda Maricultura, Valença, State of Bahia, near mangrove swamp, coll. S. L. S. Bueno, Mar 1983, MZUSP 10584.

Superfamily Axioidea Huxley, 1879

Family Axiidae Huxley, 1879

Eutrichocheles pindatyba Rodrigues & Kensley, 1991:556, figs. 1–16

Holotype.—♂, Santa Cruz, State of Espírito Santo, 19°57′S, 40°08′W, coll. M. L. Christoffersen, Mar 1979, MZUSP 10580.

Remarks.—Transferred to *Paraxiopsis* De Man, 1905 by Kensley (1996:709).

Family Micheleidae Sakai, 1992

Meticonaxius capricorni Coelho, 1987:64, figs. 1a–d, 2a, b, 3

Holotype.—♀, R/V *Alm. Saldanha,* Proj Sul II, sta 10, 23°52′S, 43°11′W, 27 Mar 1972, MZUSP 7113.

Paratype.—1 ♂, R/V *Alm. Saldanha,* Cabo São Tomé, State of Rio de Janeiro, sta 9, 11 Feb 1969, MZUSP 7114.

Infraorder Anomura MacLeay, 1838

Superfamily Galatheoidea Samouelle, 1819

Family Aeglidae Dana, 1852

Aegla franca Schmitt, 1942:476, fig. 51, pl. 26d

Paratypes.—3 ♂, Franca, State of São Paulo, coll. E. Garbe, Oct 1910, MZUSP 622.

Aegla inermis Bond-Buckup & Buckup, 1994:221, figs. 35a–e, 76a

Paratype.— 1 ♀, Arrôio Kilômetro, tributary of Arrôio Cará, Osório-Borussia, State of Rio Grande do Sul, coll. A. Rossi, 23 Jan 1979, MZUSP 11278 (Formerly UFRGS 345P).

Aegla itacolomiensis Bond-Buckup & Buckup, 1994:212, figs. 31a–e, 75d

Paratype.—1 ♀, Arrôio Demétrio, Fazenda Fialho, Taquara, State of Rio Grande do Sul, coll. G. Bond-Buckup, Mar 1989, MZUSP 11280 (Formerly UFRGS 881P).

Aegla jarai Bond-Buckup & Buckup, 1994:229, figs. 40a–e, 72c

Paratypes.— 2 ♂, Arroio Bandeirinha, Lages, State of Santa Catarina, coll. A. Rossi, 22 Apr 1978, MZUSP 11279 (Formerly UFRGS 249P).

Aegla ligulata Bond-Buckup & Buckup, 1994:216, figs. 33a–e, 74a

Paratype.— 1 ♀, Arrôio Carvalho, Terra de Areia, State of Rio Grande do Sul, coll. L. Buckup, 9 Nov 1977, MZUSP 11273 (Formerly UFRGS 252P).

Aegla microphthalma Bond-Buckup & Buckup, 1994:262, figs. 61a–e, 70c

Holotype.—♀, Caverna Santana, Iporanga, State of São Paulo, coll. E. Trajano, MZUSP 7405.

Paratypes.—1 ♀, same data as holotype, MZUSP 7408; 2 ♂, 2 ♀, same data as holotype, MZUSP 11274.

Aegla perobae Hebling & Rodrigues, 1977:290, figs. 1a–e

Holotype.—♂, Caverna Peroba, São Pedro, State of São Paulo, 18 Jan 1973, MZUSP 4005.

Paratypes.—12 ♂, 4 ♀, same data as holotype, MZUSP 4006.

Aegla rosanae Campos Jr., 1998:137, figs. 1–4

Holotype.—♂, head-water of córrego Benfica, Bacia do Rio Paraíba, Piquete, State of São Paulo, coll. R.S. Lima, O. Takeshi and O. Campos Jr., 26 Jun 1992, MZUSP 11162.

Remarks.—Considered a junior synonym of *Aegla paulensis* Schmitt, 1942:490 by Bond-Buckup & Buckup (2000:385).

Aegla rossiana Bond-Buckup & Buckup, 1994:208, figs. 29a–e, 73a

Paratypes.— 1 ♀, 2 ♂, Rio Jordão, Criciúma, State of Santa Catarina, coll. L. Buckup, 17 Sep 1977, MZUSP 11274 (Formerly UFRGS 230P).

Aegla spinosa Bond-Buckup & Buckup, 1994:224, figs. 37a–e, 72d

Paratypes.— 1 ♂, 1 ♀, Rio São João, Campos Novos, km 310, State of Santa Catarina, coll. A. Rossi, 22 Apr 1978, MZUSP 11276 (Formerly UFRGS 246P).

Aegla violacea Bond-Buckup & Buckup, 1994:210, figs. 30a–e, 76b

Paratypes.— 1 ♂, 1 ♀, Arroio do Cerro Negro, Guaiba, Mariana Pimentel, State of Rio Grande do Sul, coll. L. Buckup, D. Schossler and N. Fontana, 10 May 1988, MZUSP 11281 (Formerly UFRGS 1123P).

Family Galatheidae Samouelle, 1819

Munida atlantica Melo Filho & Melo, 1994:50, figs. 1–7

Holotype.—♀, Aracati, State of Ceará, R/V *Canopus,* sta 45, 04°14′S, 37°22′W, 58 m, Aug 1965, MZUSP 11387.

Munida brasiliae Coelho, 1973f:344

Paratypes.—5 ♂, 3 ♀, R/V *Alm. Saldanha,* sta 1708, 02°44′S, 39°01′W, 66 m, 22 Oct 1967, MZUSP 6611.

Remarks.—Considered a synonym of *Munida angulata* Benedict, 1902 by Melo-Filho & Melo (2001:1143).

Munida heblingi Melo-Filho & Melo, 1994:53, figs. 8–14

Holotype.—♂, R/V *Alm. Saldanha,* Proj Leste I, sta 1953A, State of Espírito Santo, MZUSP 11388.

Munida petronioi Melo Filho & Melo, 1994:55, figs. 15–21

Holotype.—♂, R/V *Alm. Saldanha,* Proj Norte-Nordeste I, sta 1684B, 03°59′S, 35°53′W, 75 m, 18 Oct 1967, MZUSP 11389.

Munida victoria Melo-Filho, 1996:272, figs. 1–7

Holotype.—♂, R/V *Marion Dufrèsne,* Proj TAAF-55 BR, sta 55, 19°40′S, 38°43′W, 900 m, 30 May 1987, MZUSP 12256.

Family Porcellanidae Haworth, 1825
Porcellana paivacarvalhoi Rodrigues da Costa, 1968c:405r

Paratype.—1 ♂, Bairro São Francisco, São Sebastião, State of São Paulo, MZUSP 8951.

Remarks.—Considered a synonym of *Porcellana platycheles* Pennant, 1777 by Veloso & Melo (1993:171).

Infraorder Brachyura Latreille, 1802
Section Dromiacea De Haan, 1833
Superfamily Dromioidea De Haan, 1833
Family Dromiidae De Haan, 1833
Dromia gouveai Melo & Campos Jr., 1999:281, figs. 3a, b

Holotype.—♂, Salvador, Geribotuba, State of Bahia, MZUSP 10222.

Paratype.—1 ♂, Saco de Mamanguá, Santos, State of São Paulo, MZUSP 5526.

Superfamily Homoloidea De Haan, 1839
Family Latreilliidae Stimpson, 1858
Latreillia williamsi Melo, 1990b:28, figs. 1, 2

Holotype.—♂, R/V *Prof. W. Besnard,* Proj GEDIP, State of Rio Grande do Sul, sta 396, 34°26′S, 51°47′W, 155 m, sand and gravel, 27 Aug 1968, MZUSP 3295.

Paratypes.—All same data as holotype: 1 ♀, MZUSP 5492; 1 ♀, MZUSP 5493; 1 ♂, MZUSP 5494.

Section Eubrachyura de Saint Laurent, 1980
Subsection Raninoida De Haan, 1839
Superfamily Raninoidea De Haan, 1839
Family Raninidae De Haan, 1839
Ranilia guinotae Melo & Campos Jr., 1994:69, figs. 16–22

Holotype.—♂, Santos, State of São Paulo, stomach content of the fish *Diplectrum formosum* Linnaeus, MZUSP 10932.

Paratype.—1 ♂, same data as holotype, MZUSP 11106.

Ranilia saldanhai Rodrigues da Costa, 1970:33, fig. 1

Holotype.—♂, R/V *Alm. Saldanha,* dredging, 26–60 m, 07°55′S, 34°48′W, MZUSP 8223.

Remarks.—Considered a synonym of *Ranilia muricata* H. Milne Edwards, 1837 by Melo & Campos Jr. (1994:69). The holotype is a male and not a female as listed by Rodrigues da Costa (1970:33).

Superfamily Cyclodorippoidea Ortmann, 1892
Family Cyclodorippidae Ortmann, 1892
Clythrocerus analogus Coelho, 1973d:343

Paratype.—1 ♀, R/V *Alm. Saldanha,* Proj Norte-Nordeste, sta 1743A, 75 m, 00°51′S, 43°41′24″W, MZUSP 4828.

Remarks.—Transferred to *Deilocerus* Tavares, 1996 by Tavares (1996:275).

Clythrocerus bidentatus Campos Jr. & Melo, 1999:7, figs. 1, 2

Holotype.—♀, R/V *Prof. W. Besnard,* Proj Monitoramento, sta 28, 22°24′S, 40°42′W, 60 m, 09 Aug 1991, MZUSP 11077.

Clythrocerus carinatus Coelho, 1973c:343

Paratypes.—1 ♂, 1 ♀, R/V *Alm. Saldanha,* Proj Norte-Nordeste, sta 1804B, 27 m, sand, 25 Nov 1967, MZUSP 4827; 1 ♀, R/V *Alm. Saldanha,* Proj Geomar, sta 27, 00°02′30″S, 46°15′00″W, 5 Jun 1968, MZUSP 4825; 1 ♀, R/V *Alm. Saldanha,* Proj Norte-Nordeste, sta 1763, 00°25′S, 47°17′W, MZUSP 12044.

Cyclodorippe angulata Tavares, 1991:633, figs. 6b, 8c, 11a–c

Holotype.—♀, R/V *Marion Dufrèsne,* Proj TAAF MD55-BR, sta 16, 310–360 m, 20°26′S, 36°41′W, 2 Jun 1987, MZUSP 10266.

Cyclodorippe longifrons Campos Jr. & Melo, 1999:38, figs. 1, 2

Holotype.—♂, Proj Monitoramento, sta 05, 21°20′S, 40°16′W, 115 m, 18 Jul 1991, MZUSP 12055.
Paratypes.—All same data as holotype: 1 ♀, MZUSP 12056; 1 ♀, MZUSP 12057.

Deilocerus coelhoi Campos Jr. & Melo, 1998:130, figs. 1, 2

Holotype.—♂, Proj Monitoramento, sta 57, 23°36′S, 41°56′W, 170 m, 20 Aug 1991, MZUSP 11523.
Paratypes.—All same data as holotype: 1 ♀, MZUSP 11524; 1 ♀, MZUSP 11522.

Family Cymonomidae Bouvier, 1897
Cymonomus guillei Tavares, 1991:639, figs. 7b, 8d, 9b, 11d

Holotype.—♀, R/V *Marion Dufrèsne,* Proj TAAF MD55-BR, sta 54, 19°36′S, 38°53′W, 640 m, 30 May 1987, MZUSP 10268.

Cymonomus guinotae Tavares, 1991:640, figs. 7c, 8b, 9c, 10a–c

Holotype.—♀, R/V *Marion Dufrèsne,* Proj TAAF MD55-BR, sta 64, 23°46′S, 42°10′W, 610 m, 2 Jun 1987, MZUSP 10269.
Remarks.—Transferred to *Cymonomoides* Tavares, 1993 by Tavares (1993:141).

Cymonomus magnirostris Tavares, 1991:635, figs. 7a, 8e, 9a, 10d–f

Holotype.—♀, R/V *Marion Dufrèsne,* Proj TAAF MD55-BR, sta 64, 23°46′S, 42°10′W, 610 m, 2 Jun 1987, MZUSP 10267.

Cymonomus meloi Campos Jr., 1997:129, fig. 1

Holotype.—♂, Proj Integrado, Ubatuba, State of São Paulo, MZUSP 10771.

Cymonomus oyakawai Campos Jr., 1997:131, fig. 2

Holotype.—♂, R/V *Prof. W. Besnard,* Proj GEDIP, State of Rio Grande do Sul, sta 1646, 34°25′S, 51°49′W, 166 m, 18 Jan 1972, MZUSP 6161.

Cymonomus tavaresi Campos Jr., 1997:132, fig. 3

Holotype.—♀, R/V *Emília,* Proj Ilha Grande, State of Rio de Janeiro, sta C. (288), 2 m, 30 Jul 1966, MZUSP 9193.

Subsection Heterotremata Guinot, 1977
Superfamily Leucosioidea Samouelle, 1819
Family Leucosiidae Samouelle, 1819
Ebalia conica Coelho, 1973a:342

Holotype.—♂, R/V *Alm. Saldanha,* sta 1784, off Cabo Norte, State of Amapá, 03°08′S, 49°07′W, 85 m, 16 Nov 1967, MZUSP 6603.
Paratypes.—1 ♂, 1 ♀, R/V *Alm. Saldanha,* sta 1677, 04°41′S, 35°24′W, 65 m, 17 Oct 1967, MZUSP 6551; 1 ♂, R/V *Alm. Saldanha,* sta 1676A, 04°46′S, 35°24′W, 39 m, 16 Oct 1967, MZUSP 6561.
Remarks.—Transferred to *Lithadia* Bell, 1855 by Coelho & Ramos-Porto (1986:67).

Ebalia obliqua Coelho, 1973b:342

Holotype.—♂, North of State of Pernambuco, Proj ITA, 37 m, 17 Jan 1969, MZUSP 6544.
Paratypes.—1 ♂, 2 carapaces, R/V *Alm. Saldanha,* Proj Geomar, sta 34, 00°21′S, 46°58′W, 30 m, 7 Jun 1968, MZUSP 6554; 1 ♂ juv, Proj Pernambuco, sta 27, 03 Feb 1969, MZUSP 6558; 1 ♂, Proj Pernambuco, sta 35B, 07 Feb 1969, MZUSP 6556.
Remarks.—Transferred to *Lithadia* Bell, 1855 by Coelho & Ramos-Porto (1986:67).

Ebalia vertiginosa Coelho, 1973e:343

Holotype.—♂, R/V *Canopus,* sta 14, 01°30′S, 38°43′W, 47 m, 12 Jul 1965, MZUSP 6559.

Paratypes.—1 ♀, R/V *Akaroa,* sta 37, 09°27′50″S, 35°17′45″W, 32 m, 6 Sep 1965, MZUSP 6549; 1 ♂, R/V *Canopus,* sta 61, 02°51′S, 38°51′W, 60 m, 25 Aug 1965, MZUSP 6552; 1 ♀, R/V *Akaroa,* sta 59, 09°46′10″S, 35°34′40″W, 31 m, 7 Sep 1965, MZUSP 6555.

Remarks.—Transferred to *Lithadia* Bell, 1855 by Coelho & Ramos-Porto (1986:67).

Speloeophoroides capixaba Melo & Torres, 1998b:130, figs. 1–6

Holotype.—♂, State of Espírito Santo, Proj Rio Doce, sta RD-54, 18°54′08″S, 39°15′04″W, 41 m, 1973, MZUSP 9149.

Speloeophorus brasiliensis Melo & Torres, 1998a:126, figs. 7–10

Holotype.—1 ♂, Praia do Francês, Marechal Deodoro, State of Alagoas, MZUSP 12045.

Superfamily Majoidea Samouelle, 1819

Family Inachidae MacLeay, 1838

Podochela atlantica Coelho, 1997:223, figs. 1a–d

Holotype.—♂, R/V *Prof. W. Besnard,* Proj GEDIP, State of Rio Grande do Sul, sta 554, 32°12′S, 50°12′W, 149 m, 9 Mar 1969, MZUSP 3533.

Paratypes.—♀ ovig., R/V *Prof. W. Besnard,* Proj GEDIP, State of Rio Grande do Sul, sta 576, 34°28′S, 51°53′W, 155 m, 14 Mar 1969, MZUSP 3522; 1 ♀ ovig., R/V *Prof. W. Besnard,* Proj GEDIP, State of Rio Grande do Sul, sta 547, 30°48′S, 49°18′W, 160 m, Jul 1969, MZUSP 5975.

Podochela meloi Sankarankutty, Ferreira & Cunha, 2001:552, figs. 1, 2

Paratype.— 1 ♀, Estuary near Macau, State of Rio Grande do Norte, MZUSP 13192.

Podochela minuscula Coelho, 1972:119, figs. 1b, c

Paratype.—1 ♀ ovig., R/V *Alm. Saldanha,* Proj Norte-Nordeste I, sta 1722, 02°13.5′S, 40°43.5′W, 53 m, 29 Oct 1967, MZUSP 7213.

Family Mithracidae Balls, 1929

Mithrax (*Mithrax*) *besnardi* Melo, 1990a:20, figs. 1, 2

Holotype.—♀, R/V *Prof. W. Besnard,* Proj GEDIP, sta 1871, off Maldonado, Uruguay, 35°02′S, 52°42′W, 2100 m, 12 Aug 1972, MZUSP 4565.

Paratypes.—All same data as holotype: 1 ♂, MZUSP 6241; 1 ♀, MZUSP 6242; 1 ♂, MZUSP 7519.

Remarks.—The subgenus *Mithrax* was elevated to generic status in a revision of the genus *Mithrax* by Wagner (1990). However, it appears that Wagner was unable to consider *M.* (*M.*) *besnardi* as his revision, and Melo's (1990a) description, appeared in the same year.

Family Pisidae Dana, 1851

Libinia rostrata var. *bellicosa* Oliveira, 1944:87, figs. 1–3

Remarks.—A female specimen has been found from Ilha do Pinheiro, State of Rio de Janeiro, Brazil (MZUSP 8581), with similar information to that mentioned by Oliveira (1944) in his description of this taxon.

Superfamily Parthenopoidea MacLeay, 1838

Family Parthenopidae MacLeay, 1838

Heterocrypta aloysioi Rodrigues da Costa, 1968a:144, figs. 1, 2

Holotype.—♀, Praia do Araçá, São Sebastião, State of São Paulo, 3 Sep 1967, MZUSP 8224.

Paratype.—1 ♀, same data as holotype, MZUSP 8225.

Heterocrypta tommasii Rodrigues da Costa, 1959:595, fig. 1

Holotype.—♀ ovíg., Cananéia, State of São Paulo, 25°06′00″S, 47°51′05″W, 26 Jul 1959, MZUSP 8226.

Paratypes.—All same data as holotype: 1 ♂, 2 ♀, MZUSP 8227; 15 ♀, MZUSP 8580.

Remarks.—The holotype was originally deposited in IOUSP.

Lambrus aylthoni Righi, 1965:57, fig. 1

Holotype.—♂, Ilha Vitória, State of São Paulo, coll. A. Joly, Jul 1963, MZUSP 1820.

Paratypes.—1 ♂, Ilha Vitória, State of São Paulo, 5 Jul 1959, MZUSP 2048; 1 ♀, Ilha de Alcatrazes, State of São Paulo, coll. IOUSP, 5 Oct 1959, MZUSP 2049.

Remarks.—Transferred to *Parthenope* Weber, 1795 by Righi (1967:114).

Solenolambrus brasiliensis Rodrigues da Costa, 1961:1, figs. 1, 2

Holotype.—♂, State of São Paulo, 23°58′40″S, 46°80′30″W, MZUSP 8220.

Paratypes.—All same data as holotype: 1 ♀, MZUSP 8221; 1 ♀, MZUSP 8222.

Superfamily Cancroidea Latreille, 1802

Family Cancridae Latreille, 1802

Cancer luederwaldti Rathbun, 1930a:200, pls. 86–89

Holotype.—Sex undetermined, Santos, State of São Paulo, coll. H. Lüderwaldt, MZUSP 948.

Remarks.—Synonymized under *Cancer pagurus* Linnaeus, 1758 by Rathbun (1930b:528).

Superfamily Portunoidea Rafinesque, 1815

Family Trichodactylidae H. Milne Edwards, 1853

Goyazana rotundicauda Magalhães & Türkay, 1996:139, figs. 7, 10, 11

Holotype.—♂, Igarapé Manduaçu, Paraná Iupiá, Northwest of Fonte Boa, State of Amazonas, coll. EPA, 8–9 Oct 1968, MZUSP 7007.

Sylviocarcinus australis Magalhães & Türkay, 1996:113, figs. 36–38

Paratypes.—1 ♀, 2 ♂, Porto Espiridião, State of Mato Grosso, coll. P. E. Vanzolini, 25 Dec 1976, MZUSP 6301; 7 ♀, 10 ♂, São Luís de Cáceres, coll. E. Garbe, Nov 1917, MZUSP 2561; 1 ♀, 1 ♂, Estrada Transpantaneira, km 59, Poconé, State of Mato Grosso, coll. V. A. Araújo, 23 Jun 1985, MZUSP 9104; 2 ♂, Estrada Transpantaneira, km 59, Poconé, State of Mato Grosso, 27 Jun 1985, MZUSP 9505.

Superfamily Xanthoidea MacLeay, 1838

Family Goneplacidae MacLeay, 1838

Chasmocarcinus arcuatus Coelho Filho & Coelho, 1998:800, figs. 1–4

Paratypes.—2 ♂, R/V *Alm. Saldanha,* sta 7628, 01°19.5′N, 48°9.4′W, 45 m, 28 Jul 1987, MZUSP 13605. Formerly DOUFPE 536.

Chasmocarcinus hirsutipes Coelho Filho & Coelho, 1998:804, figs. 5–7

Paratypes.—2 ♂, Proj Geomar, sta 46, 01°05′N, 47°42.4′W, 63 m, 9 Jun 1970, MZUSP 13607. Formerly DOUFPE 514.

Chasmocarcinus meloi Coelho Filho & Coelho, 1998:809, figs. 8, 9

Paratypes.—2 ♀, R/V *Akaroa,* sta 181, 10°38.15′S, 36°17.2′W, 130 m, 4 Dec 1965, MZUSP 13606. Formerly DOUFPE 508.

Chasmocarcinus peresi Rodrigues da Costa, 1968b:335

Paralectotypes.—8 ♂, 8 ♀, R/V *Calypso,* sta 1816, Abrolhos, State of Bahia, 17°56′S, 38°40′W, 12 Feb 1962, MZUSP 8230; 5 ♀, 3 ♂, R/V *Calypso,* sta 1815, 21 m, Abrolhos, State of Bahia, 17°56′S, 38°40′W, 12 Feb 1962, MZUSP 8747.

Speocarcinus meloi D'Incao & Gomes da Silva, 1992:121, figs. 1–13

Holotype.—♂, R/V *Atlântico Sul,* Proj Crustáceo, 32°17′S, 50°48′W, 14 Dec 1984, MZUSP 9577.

Paratype.—1 ♀, same data as holotype, MZUSP 9578.

Family Panopeidae Ortmann, 1893

Hexanopanopeus heblingi Rodrigues & Loyola e Silva, 1998:263, figs. 1–20

Holotype.—♂, South of Ilha Anchieta, Ubatuba, State of São Paulo, 23°26′S, 43°05′W, coll. N. J. Hebling, 7 Jul 1983, MZUSP 12281.

Paratypes.—All same data as holotype: 4 ♂, 4 ♀, MZUSP 12282; 1 ♀, MZUSP 12283.

Superfamily Pseudothelphusoidea Ortmann, 1893

Family Pseudothelphusidae Ortmann, 1893

Brasiliothelphusa tapajoense Magalhães & Türkay, 1986:372, figs. 1, 2

Holotype.—♂, Rio Tapajós, Monte Cristo, State of Pará, coll. EPA, 20–28 Jul 1973, MZUSP 6550.

Paratypes.—2 ♂, 2 ♀, same data as holotype, MZUSP 6378.

Kingsleya ytupora Magalhães, 1986:617, figs. 11–13, 30, 31

Paratypes.—1 ♂, 2 ♀, Rio Trombetas, State of Pará, Cachoeira Porteira, under stones, shallow water, region of river-rapids, coll. C. Magalhães, 2 Oct 1985, MZUSP 7009; 7 ♂, Rio Curuá-Una, State of Pará, about 200 km upstream of the hydro-electric power station of Curuá-Una, under stones, river rapids, coll. R. Huet and A. G. dos Santos, Oct 1983, MZUSP 7010.

Subsection Thoracotremata Guinot, 1977

Superfamily Pinnotheroidea De Haan, 1833

Family Pinnotheridae De Haan, 1833

Alarconia guinotae Coelho, 1996:175, fig. 1

Holotype.—♂, State of Pará, R/V *Alm. Saldanha,* sta 1988, 00°26′S, 47°35′W, 25 m, 21 Nov 1968, MZUSP 12353.

Paratypes.—5 ♀, same data as holotype, MZUSP 12352.

Fabia insularis Melo, 1971:200, figs. 2, 3, pl. 2

Holotype.—♀, Proj Ilha Grande, State of Rio de Janeiro, R/V *Emilia,* sta 266, 20 Jul 1966, in the bivalve *Glycymeris (Glycymerella)* sp., MZUSP 3688.

Paratypes.—1 ♀, same data as holotype, MZUSP 3689; 1 ♀, Proj Ilha Grande, State of Rio de Janeiro, R/V *Emilia,* sta 268, 15 m, 17 Jul 1966, in the bivalve *Glycymeris longior* (Sowerby), MZUSP 36871; 1 ♀, Proj Ilha Grande, State of Rio de Janeiro, R/V *Emilia,* sta 251, 18 m, 17 Jul 1966, MZUSP 3690; 1 ♀, Proj Ilha Grande, State of Rio de Janeiro, R/V *Emilia,* sta 175, 26 m, 26 Jul 1966, MZUSP 3691; 1 ♀, Proj Ilha Grande, State of Rio de Janeiro, R/V *Emilia,* sta 174, 23 m, 22 Jul 1966, MZUSP 3692; 1 ♀, Proj Ilha Grande, State of Rio de Janeiro, R/V *Emilia,* sta 267, 10 m, 19 Jul 1966, MZUSP 3693.

Remarks.—Synonymized by Fennuci (1975:173) with *Fabia emiliai* (Melo, 1971), but subsequently reinstated by Martins & D'Incao (1996:6).

Pinnixa aidae Righi, 1967:107, figs. 21–26

Holotype.—♀ ovig., Enseada de Caraguatatuba, State of São Paulo, 23°38′S, 43°32′W, 5 km north of Rio Juqueriquerê, coll. J. Petersen, 5 Nov 1964, MZUSP 2231.

Allotype.—1 ♂, same data as holotype, MZUSP 2232.

Paratypes.—2 ♂, 6 ♀ (5 ovig.), same data as holotype, MZUSP 2233.

Remarks.—Transferred to *Austinixa* Heard & Manning, 1997 by Heard & Manning (1997:393).

Pinnixa angeloi Righi, 1967:110, figs. 27–32

Holotype.—♂, São Vicente, State of São Paulo, coll. W. Narchi, 17 Dec 1964, MZUSP 2136.

Allotype.—1 ♀, same data as holotype, MZUSP 2137.

Paratypes.—4 ♀, 1 ♀ juv, same data as holotype, MZUSP 2138; 1 ♀, Bertioga, State of São Paulo, coll. L. R. Tommasi, Jan 1964, MZUSP 2139; 1 ♀, 1 ♂, Enseada de Caraguatatuba, State of São Paulo, coll. J. A. Petersen, 5 Nov 1964, MZUSP 2140; 1 ♂, Ilha de Alcatrazes, State of São Paulo, coll. IOUSP, Jul 1965, MZUSP 2141; 1 ♂, Santos, State of São Paulo, coll. O. Schubart, Jun 1958, MZUSP 2142; 11 ♂, same data as holotype, MZUSP 2143; 2 ♂, 3 ♀ (2 ovig.), Praia Grande, State of São Paulo, 10 km north Itanhaém, coll. S. de A. Rodrigues, 15 Aug 1965, MZUSP 2144; 5 ♀, Mongaguá, State of São Paulo, coll. E. Schlenz, 9 Oct 1965, MZUSP 2145.

Remarks.—Synonymized under *Pinnixa patagoniensis* Rathbun, 1918 by Fenucci (1975:177), and subsequently transferred to *Austinixa* Heard & Manning, 1997 by Heard & Manning (1997:393).

Pinnotheres emiliai Melo, 1971:198, fig. 1, pl. 1

Holotype.—♂, Proj Ilha Grande, State of Rio de Janeiro, R/V *Emilia,* sta 102, 1 Jul 1966, in the bivalve *Anadara brasiliana* (Lamarck), MZUSP 3480.

Paratype.—1 ♂, Proj Ilha Grande, State of Rio de Janeiro, R/V *Emilia,* sta 266, 20 Jul 1966, in the bivalve *Glycymeris* (*Glycymerella*) sp., MZUSP 3481.

Remarks.—New combination proposed by Fennuci (1975:173) as *Fabia emiliai* (Melo, 1971), but subsequently reinstated by Martins & D'Incao (1996:11).

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Literature Cited

Balss, H. 1929. Oxyrhyncha und Schlussbetrachtungen, Decapoden des Roten Meeres 4: Expedition S.M. Schiff Pola in das Rote Meer, Nordliche und Sudliche Halfte 1895/96–1897/98. Zoologische Ergebnisse 36.—Denskschriffen der Akademie der Wissenschaften in Wien, Mathematisch, Naturwissenschafliche Klasse 102:1–30.

Bell, T. 1855. A monograph of the Leucosidae, with observations on the relations, structure, habits and distribution of the Family: a revision of the generic characters and descriptions of new genera and species, Hora Carcinologicae, or Notices of Crustacea.—Transactions of the Linnean Society 21:277–314, pls. 30–34.

Benedict, J. E. 1902. Description of a new genus and forty-six new species of crustaceans of the family Galatheidae, with a list of known marine species.—Proceedings of the United States National Museum 26(1311):243–334.

Bond-Buckup, G., & L. Buckup. 1994. A Família Aeglidae (Crustacea, Decapoda, Anomura).—Arquivos de Zoologia 32(4):159–346.

———, & ———. 2000. *Aegla rosanae* Campos Jr., um novo sinônimo de *Aegla paulensis* Schmitt (Crustacea, Aeglidae).—Revista Brasileira de Zoologia 17(1):385–386.

Borradaile, L. A. 1903. On the classification of the Thalassinidea.—Annals and Magazine of Natural History 12(7):534–551.

Bouvier, E. L. 1897. Sur la classification, les origines et la distribution des crabes de la famille des Dorippidés.—Bulletin de la Societè Philomathique de Paris (8)9, 1896(1897):54–70.

Campos, O. Jr. 1997. Três novas espécies brasileiras do gênero *Cymonomus* A. Milne-Edwards, 1880 (Crustacea, Brachyura, Podotremata).—Trabalhos Oceanográficos da Universidade Federal de Pernambuco 25:127–135.

———. 1998. Nova espécie do gênero *Aegla* da Bacia do Rio Paraiba, Brasil (Anomura: Aeglidae).—Iheringia, série Zoologia 85:137–140.

———, & G. A. S. Melo. 1998. Nova espécie brasileira do gênero *Deilocerus* (Brachyura, Podotremata, Cyclodorippidae).—Iheringia, série Zoologia 85:129–132.

———, & ———. 1999. Nova espécie brasileira do gênero *Clythrocerus* A. Milne-Edwards & Bouvier, 1899 (Crustacea, Brachyura, Podotremata).—Atlântica 21:5–10.

Carvacho, A. 1979. Les crevettes carides de la mangrove guadeloupéenne.—Bulletin du Muséum national d'Histoire Naturelle, Paris, Sèrie Zoologie, Biologie et Ecologie animale 2:445–470.

Christoffersen, M. L. 1979. Decapod Crustacea: Alpheoida. Campagne de la *Calypso* au large des côtes de l'Amérique du Sud (1961–1962). I. Resultats Scientifiques de la Campagne de la *Calypso.*—Annales de l'Institute Océanographique de Monaco 55:297–377.

———. 1984. The western atlantic snapping shrimps related of *Alpheus heterochaelis* Say (Crustacea, Caridea), with a description of a new species.—Papéis Avulsos de Zoologia 35(19):189–208.

Coelho, P. A. 1972. Descrição de três espécies novas de Majidae do Brasil (Decapoda: Brachyura).—Trabalhos Oceanográficos da Universidade Federal de Pernambuco 13:119–132.

———. 1973a. Descrição preliminar de *Ebalia conica* n. sp., do Norte e Nordeste do Brasil (Crustacea, Decapoda, Leucosiidae).—Ciência e Cultura 25(6):342.

———. 1973b. Descrição preliminar de *Ebalia obliqua* n. sp., do Norte e Nordeste do Brasil (Crustacea, Decapoda, Leucosiidae).—Ciência e Cultura 25(6):342.

———. 1973c. Descrição preliminar de *Clythrocerus carinatus,* n. sp., do Norte e Nordeste do Brasil (Crustacea, Decapoda, Dorippidae).—Ciência e Cultura 25(6):343.

———. 1973d. Descrição preliminar de *Clythrocerus analogus,* n. sp., do litoral brasileiro (Crustacea, Decapoda, Dorippidae).—Ciência e Cultura 25(6):343.

———. 1973e. Descrição preliminar de *Ebalia vertiginosa* n. sp., do Norte e Nordeste do Brasil (Crustacea, Decapoda, Leucosiidae).—Ciência e Cultura 25(6):343.

———. 1973f. Descrição preliminar de *Munida brasiliae,* n. sp., do Norte e Nordeste do Brasil (Crustacea, Decapoda, Galatheidae).—Ciência e Cultura 25(6):344.

———. 1987. Uma nova espécie de *Meticonaxius* do Brasil (Crustacea, Decapoda, Callianideidae).—Revista Brasileira de Zoologia 4(1):63–69.

———. 1996. Revisão do gênero *Alarconia* Glassell, 1938, no Brasil com a descrição de *Alarconia guinotae,* n. sp. (Crustacea, Decapoda, Pinnotheridae).—Trabalhos Oceanográficos da Universidade Federal de Pernambuco 24:173–178.

———. 1997. Description of *Podochela* (*Anisonotus*) *atlantica* n.sp., found in the Brazilian and Uruguayan coasts (Crustacea, Decapoda, Majidae).—Trabalhos Oceanográficos da Universidade Federal de Pernambuco 25:223–226.

———, & M. Ramos-Porto. 1986. Sinopse dos crustáceos decápodos brasileiros (Famílias Dorippidae e Leucosiidae).—Cadernos Ômega da Universidade Federal Rural de Pernambuco, série Ciências aquáticas, 2:67–77.

Coelho Filho, P. A., & P. A. Coelho. 1998. Descrição de três espécies novas de *Chasmocarcinus* Rathbun (Crustacea, Decapoda, Goneplacidae), do litoral brasileiro.—Revista Brasileira de Zoologia 15(3):799–814.

Dana, J. D. 1851. Conspectus crustaceorum quae in Orbis Terrarum circumnavegatione Carolo Wilkes e Classe Republicae Foederatae duce lexit et descripsit.—Proceedings of the Academy of Natural Sciences of Philadelphia 5:267–272.

———. 1852. Crustacea, Part 1 *in* United States Exploring during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. 13:1–685.

D'Incao, F., & B. M. Gomes da Silva. 1992. Description of *Speocarcinus meloi* sp. n. (Crustacea: Decapoda: Brachyura: Goneplacidae) of the Brazilian coast.—Iheringia, série Zoologia 71: 121–128.

Dworschak, P. C., & V. R. Coelho. 1999. On two alpheids from Araçá (São Paulo, Brazil) with a description of a new species of *Leptalpheus* (Decapoda, Caridea, Alpheidae).—Annalen des Naturhistorischen Museum in Wien 101B:475–488.

Felder, D. C., & S. A. Rodrigues. 1993. Reexamination of the ghost shrimp *Lepidophthalmus louisianensis* (Schmitt, 1935) from the northern Gulf of Mexico and comparison to *L. siriboia,* new species from Brazil (Decapoda, Thalassinidea, Callianassidae).—Journal of Crustacean Biology 13(2):357–376.

Fenucci, J. L. 1975. Los cangrejos de la Família Pinnotheridae del litoral Argentino (Crustacea, Decapoda, Brachyura).—Physis, seccion A, 34(88):165–184.

Genofre, G., & V. L. Lobão. 1978. *Macrobrachium holthuisi* sp. n., a new species of shrimp (Decapoda, Macrura).—Crustaceana 35(3):273–276.

De Haan, W. 1833 (1833–1850). Crustacea. *In* P. F. von Siebold, ed., Fauna Japonica sive descriptio animalium, quae in itinere per Japonium, Jussu et auspices superiorum, qui summum in India Batava imperium tenent, suscepto, annis 1823–1830 collegit, notis, observationibus et adumbrationibus illustravit. Lugduni- Batavorum, 243 pp.

Haig, J. 1956. The Galatheidae (Crustacea, Anomura) of the Allan Hancock Expedition with a review of the Porcellanidae of the western Atlantic.—Allan Hancock Atlantic Expedition Report 8:1–44.

———. 1968 *in* Rodrigues da Costa, H. 1968. Novas espécies de Porcellanidae brasileiros (Crustacea, Anomura).—Anais da Academia Brasileira de Ciências 40(3):405r–406r.

Haworth, A. H. 1825. A new binary arrangement of the macrurous crustacea.—Philosophical Magazine and Journal 65:183–184.

Heard, R. W., & R. B. Manning. 1997. *Austinixa,* a new genus of pinnotherid crab (Crustacea, Decapoda, Brachyura), with the description of *A. hardyi,* a new species from Tobago, West Indies.—Proceedings of the Biological Society of Washington 110(3):393–398.

Hebling, N. J., & M. D. Rodrigues. 1977. Sobre uma nova espécie brasileira do gênero *Aegla* Leach, 1820 (Decapoda, Anomura).—Papéis Avulsos de Zoologia 30(19):289–294.

Huxley, T. H. 1879. On the classification and the distribution of the crayfishes.—Proceedings of the Zoological Society of London 1878:752–788.

International Code of Zoological Nomenclature. 1999, fourth edition. The International Trust for Zoological Nomenclature, The Natural History Museum, London, 306 pp.

Kensley, B. 1996. The genus *Paraxiopsis* De Man, with descriptions of new species from the western Atlantic (Crustacea, Decapoda, Axiidae).—Bulletin of Marine Science 58(3):709–729.

———, & I. Walker. 1982. Palaemonid shrimps from the Amazon Basin, Brazil (Crustacea: Decapoda: Natantia).—Smithsonian Contributions to Zoology 362:1–28.

Latreille, P. A. 1802. Histoire naturelle générale et particulière des Crustacés et des Insectes 3:1–467.

Lemaitre, R., & S. A. Rodrigues. 1991. *Lepidophthalmus sinuensis*: a new species of ghost shrimp (Decapoda: Thalassinidea: Callianassidae) of importance to commercial culture of penaeid shrimps of the Caribbean coast of Colombia, with observations on its ecology.—Fishery Bulletin 89(4):623–630.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentii, synonymis, locis. Tenth edition, Laurentius Salvius, Stockholm 1:1–824.

Lobão, V. L., G. A. S. Melo, & W. M. Fernandes. 1986. Descrição de uma nova espécie do gênero *Macrobrachium* (Crustacea, Decapoda, Palaemonidae) da região sul de São Paulo.—XIII Congresso Brasileiro de Zoologia, Resumos: 50.

MacLeay, W. S. 1838. On the Brachyurous Decapod Crustacea brought from the Cape by Dr. Smith. *In* Illustrations of the Annulosa of South Africa, being a Portion of the Objects of Natural History chiefly collected during an Expedition into the interior of South Africa, under the Direction of Dr. Andrew Smith, in the years 1834, 1835 and 1836, fitted out by the Cape of Good Hope.—Association for Exploring Central Africa. London, p. 53–71, pls. 2, 3.

Magalhães, C. 1986. Revisão taxonômica dos caranguejos de água doce brasileiros da família Pseudothelphusidae (Crustacea, Decapoda).—Amazoniana 9(4):609–636.

———, & M. Türkay. 1986. *Brasiliothelphusa,* a new Brazilian freshwater crab genus (Crustacea, Decapoda, Pseudothelphusidae).—Senckenbergiana biologica 66(4–6):371–376.

———, & ———. 1996. Taxonomy of the neotropical freshwater crab family Trichodactylidae 3. The genera *Fredilocarcinus* and *Goyazana* (Crustacea, Decapoda, Brachyura).—Senckenbergiana biologica 75(1–2):131–142.

De Man, J. G. 1905. Diagnoses of new species of Macrurous Decapod Crustacea from the *Siboga* Expedition.—Tijdschrift der Nederlansche Dierkundige Vereeniging 9:587–614.

Manning, R. B., & R. Lemaitre. 1994. *Sergio,* a new genus of the ghost shrimp from the Americas.—Nauplius 1:39–43.

Martin, J. W., & G. E. Davis. 2001. An updated classification of the Recent Crustacea.—Natural History Museum of Los Angeles County, Science Series 39:1–124.

Martins, S. T. S., & F. D'Incao. 1996. Os Pinnotheridae de Santa Catarina e Rio Grande do Sul, Brasil (Decapoda: Brachyura).—Revista Brasileira de Zoologia 13(1):1–26.

Melo, G. A. S. 1971. Duas novas espécies de Pinnotheridae (Crustacea: Brachyura) do litoral brasileiro.—Papeis Avulsos de Zoologia 23(22): 197–203.

———. 1990a. Descrição de *Mithrax* (*Mithrax*) *besnardi* sp. n. espécie brasileira abissal bêntica de águas meridionais da América do Sul (Crustacea, Brachyura, Majidae).—Atlântica 12(1):19–26.

———. 1990b. Descrição de *Latreillia williamsi* sp. n. (Crustacea, Brachyura, Homoloidea), e a ocorrência da família Latreilliidae no litoral brasileiro.—Atlântica 12(1):27–34.

———, & O. Campos Jr. 1994. O gênero *Ranilia* A. Milne-Edwards, (Crustacea, Brachyura, Raninidae) no litoral brasileiro e descrição de uma nova espécie.—Iheringia, série Zoologia 77:63–75.

———, & ———. 1999. A família Dromiidae De Haan no litoral brasileiro, com descrição de uma nova espécie (Crustacea, Decapoda, Brachyura).—Revista Brasileira de Zoologia 16(2): 273–291.

———, V. L. Lobão, & W. M. Fernandes. 1986. *Macrobrachium petronioi* sp. n. (Crustacea, Decapoda, Palaemonidae), uma nova espécie de camarão de água doce da região de Cananéia, SP. XIII Congresso Brasileiro de Zoologia, Resumos: 51.

———, ———, & ———. 1988. Redescrição de *Macrobrachium birai* Lobão, Melo & Fernandes e de *Macrobrachium petronioi,* Melo, Lobão & Fernandes (Crustacea, Decapoda), palemonideos da região sul do Estado de São Paulo, Brasil.—Boletim do Instituto de Pesca 15(1): 89–97.

———, & F. A. Torres. 1998a. O gênero *Speloeophorus* (Decapoda, Brachyura, Leucosiidae) no litoral brasileiro, com descrição de uma nova espécie.—Iheringia, série Zoologia 84:121–128.

———, & ———. 1998b. Novo gênero e espécie de Leucosiidae (Decapoda, Brachyura) no litoral brasileiro.—Iheringia, série Zoologia 84:129–132.

Melo-Filho, G. A. S. 1996. Descrição de *Munida victoria* sp. n., e comparação com *M. microphthalma* A. Milne-Edwards, em sua primeira ocorrência na costa brasileira (Crustacea, Decapoda, Galatheidae).—Papéis Avulsos de Zoologia 39(14):271–280.

———, & G. A. S. Melo. 1994. Three new species of *Munida* (Crustacea: Anomura: Galatheidae) from the Brazilian coast.—Papéis Avulsos de Zoologia 39(5):49–60.

———, & ———. 2001. Espécies do gênero *Munida* Leach, 1820 (Crustacea: Decapoda: Galatheidae), distribuidas na costa do Brasil.—Revista Brasileira de Zoologia 18(4):1135–1176.

Milne Edwards, H. 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et, la classification de ces animaux. Paris, 532 pp.

———. 1853. Mémoire sur la famille des Ocypodiens.—Annales des Sciences Naturelles, series 3, Zoologie, Paris 20:163–228.

Oliveira, L. P. H. 1944. Sobre a existência na baía do Rio de Janeiro de uma Aranha do Mar originária do Oceano Pacífico: *Libinia rostrata* Bell, 1835; Majidae, Decapoda.—Memórias do Instituto Oswaldo Cruz 40(1):87–90.

Ortmann, A. 1890. Die Decapoden-Krebse des Strassburger Museums, mit besonderer Berücksichtigung der von Heern Dr. Döderlein bei Japan und bei den Lui-Kui Inseln gesammelten und zur. Zeit im Strassburger Museum aufbewahrten Formen.—Zoologische Jahrbücher Abtheilung für Systematik, Geographie und Biologie der Thiere 5:437–540.

———. 1892. Die Decapoden-Krebse des Strassburger Museums 5. Die Abtheilungen Hippidea, Dromiidea und Oxystomata.—Zoologische Jahrbücher Abtheilung für Systematik, Geographie und Biologie der Thiere 6:532–588.

———. 1893. Abtheilung: Brachyura (Brachyura genuine Boas), 2 Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Die Decapoden-Krebse des Strassburger Museums. 7. Theil.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 7:411–495.

Pennant, T. 1777. The British Zoology. 4. Crustacea, Mollusca, Testacea. London, 136 pp.

Rafinesque, C. S. 1815. Analyse de la nature au tableau de l'univers et des corps organices. Palermo, l'imprimerie de Jean Barravechia, 224 pp.

Rathbun, M. J. 1918. The Grapsoid crabs of America.—Bulletin of the United States National Museum 97:1–445.

———. 1925. The spider crabs of America.—Bulletin of the United States National Museum 129:1–613.

———. 1930a. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae and Xanthidae.—Bulletin of the United States National Museum 152:1–593.

———. 1930b. A correction. Science 72(1873):528.

Righi, G. 1965. Uma nova espécie de Parthenopidae (Crustacea: Brachyura).—Papéis Avulsos de Zoologia 18(7):57–60.

———. 1967. Sobre alguns Decapoda do Brasil (Crustacea: Brachyura).—Papéis Avulsos de Zoologia 20(10):99–116.

Rodrigues da Costa, H. 1959. *Heterocrypta tommasii,* nova espécie de Crustacea Brachyura.—Centro de Estudos Zoológicos 2:595–596.

———. 1961. Um novo caranguejo partenopídeo da costa brasileira. Descrição de *Solenolambrus brasiliensis,* n. sp. (Brachyura, Oxyrhyncha, Parthenopidae).—Centro de Estudos Zoológicos 9:1–6.

———. 1968a. As espécies de Parthenopidae que ocorrem nas costas do Brasil (Crustacea, Brachyura).—Atas da Sociedade de Biologia 12(3): 143–147.

———. 1968b. Crustacea Brachyura récoltés par les dragages de la *Calypso* sur les côtes brésiliennes (1962).—Recueil des Travaux de la Station Marine d'Endoume 43(59):333–342.

———. 1968c. Novas espécies de Porcellanidae brasileiros (Crustacea: Anomura).—Anais da Academia Brasileira de Ciências 40:465R–466R.

———. 1970. Ocorrência do gênero *Ranilia* Milne-Edwards no Brasil. Descrição de *Ranilia saldanhai* sp. n. (Brachyura: Gymnopleura).—Atas da Sociedade de Biologia 13(1–2):33–34.

Rodrigues, M. D., & J. Loyola e Silva. 1998. Descrição de *Hexanopanopeus heblingi* sp. n. (Crustacea, Decapoda, Brachyura, Xanthidae) do litoral brasileiro.—Revista Brasileira de Zoologia 15(1):261–271.

Rodrigues, S. A. 1971. Mud shrimps of the genus *Callianassa* Leach from the Brazilian coast (Crustacea: Decapoda).—Arquivos de Zoologia 20(3):191–223.

———, & B. Kensley. 1991. *Eutrichocheles pindatyba,* a new axiid shrimp (Crustacea, Decapoda, Thalassinidea) from Brazil.—Proceedings of the Biological Society of Washington 104(3): 556–560.

———, & R. B. Manning. 1992a. Two new callianassid shrimps from Brazil (Crustacea: Decapoda: Thalassinidea).—Proceedings of the Biological Society of Washington 105(2):323–330.

———, & ———. 1992b. *Poti gaucho,* a new genus and species of ghost shrimp from the southern Brazil (Crustacea: Decapoda: Callianassidae).—Bulletin of Marine Science 51(1):9–13.

———, & R. M. Shimizu. 1992. Description of a new *Axianassa* (Crustacea, Decapoda, Thalassinidea) from Brazil and its larval stages.—Proceedings of the Biological Society of Washington 105(2):317–323.

Sakai, K. 1992. The families Callianideidae and Thalassinidae, with the description of two new subfamilies, one new genus and two new species.—Naturalists 4:1–33.

Samouelle, G. 1819. The entomologist's useful compendium, or an introduction to the knowledge of British insects. London, 496 pp.

Sankarankutty, C., A. C. Ferreira, & I. M. C. da Cunha. 2001. On a new species of spider crab (Crustacea, Brachyura, Majidae) from the Northeast of Brazil.—Revista brasileira de Zoologia 18(2):551–556.

Schmitt, W. 1942. The species of *Aegla,* endemic South American fresh water crustaceans.—Proceedings of the United States National Museum 91:431–520.

Stimpson, W. 1858. Crustacea Anomoura. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit, Pars 7.—Proceedings of the Academy of Natural Sciences of Philadelphia 1858:225–252.

Tavares, M. S. 1991. Espèces nouvelles de Cyclodorippoidea Ortmann et remarques sur les genres *Tymolus* Stimpson et *Cyclodorippe* A. Milne-Edwards (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum national d'Histoire naturelle, Paris, 4° série, 12, Section A (3–4):623–648.

———. 1993. Description préliminaire de quatre nouveaux genres et trois nouvelles espèces de Cyclodorippoidea américains (Crustacea: Decapoda: Brachyura).—Vie et Milieu 43(2–3):137–144.

———. 1996. Révision systematique des Cyclodorippidae américains (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum National d'Histoire Naturelle, Paris, 4° sèrie, Section A 1–2:233–295.

Veloso, V. G., & G. A. S. Melo. 1993. Taxonomia e distribuição da família Porcellanidae (Crustacea, Decapoda, Anomura) no litoral brasileiro.—Iheringia, série Zoologia 75:171–186.

Weber, F. 1795. Nomenclator entomologicus secundum entomologiam systematicum 3. Fabricii, adjectis speciebus recens detectis et varietatibus. Chilonii, Kiel et Hamburgi, 171 pp.

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Establishment of a new genus for *Panopeus bermudensis* Benedict & Rathbun, 1891 and several other xanthoid crabs from the Atlantic and Pacific oceans (Crustacea: Decapoda: Xanthoidea)

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Abstract.—The new genus *Acantholobulus* is proposed to accommodate several brachyuran crab species formerly assigned to the genera *Panopeus* H. Milne Edwards, 1834 and *Hexapanopeus* Rathbun, 1898, with *Panopeus bermudensis* Benedict & Rathbun, 1898 as the type species. Characters of the carapace front, anterolateral dentition, male first pleopod, and larval stages define the new genus. Morphological findings are congruent with recently reported molecular evidence for distinction of this genus. The western Atlantic species *Hexapanopeus hemphillii* Benedict & Rathbun, 1891, *Panopeus gatunensis* Abele & Kim, 1989 and *Hexapanopeus heblingi* Rodrigues & de Loyola e Silva, 1998 are considered junior synonyms of *Acantholobulus bermudensis,* new combination. *Hexapanopeus schmitti* Rathbun, 1930 from the western Atlantic is assigned to the new genus, and *Panopeus margentus* Williams & Boschi, 1990 is concluded to be a junior synonym of *Acantholobulus schmitti,* new combination. *Panopeus mirafloresensis* Abele & Kim, 1989 from the eastern Pacific and *Panopeus pacificus* Edmondson, 1931 from Hawaii and Tahiti are also assigned to *Acantholobulus.* While provisionally retained among the Panopeidae Ortmann, 1893, genetic studies and larval morphology distance *Acantholobulus,* new genus, from typical panopeid crab genera examined to date.

The genus *Panopeus* H. Milne Edwards, 1834 includes a number of extremely common and abundant intertidal and upper subtidal marine and estuarine crab species, especially along warm-temperate to tropical coasts of the Americas. Taxonomic history of this group is confusing, and superficial similarities in morphology of the adults often make species identifications particularly difficult. This is especially true for juveniles of those species that attain large size as adults, since immature stages of these crabs superficially resemble adults of smaller panopeid species. However, the complex armature of male first pleopods (gonopods) in mature individuals of the small-sized species often facilitates ready distinction from the larger forms, the latter of which tend to share a very characteristic and conserved gonopod morphology (Williams 1984a, b). A unique gonopod morphology has been reported for *Panopeus bermudensis* Benedict & Rathbun, 1891 (Monod 1956), *P. pacificus* Edmondson, 1931 (Forest & Guinot 1961), *P. gatunensis* Abele & Kim, 1989 (Abele & Kim 1989), *P. mirafloresensis* Abele & Kim, 1989 (Abele & Kim 1989), and *P. margentus* Williams & Boschi, 1990 (Williams & Boschi 1990). In addition, differences in carapace granulation and dentition, together with the shape of the male abdomen, distinguish this group from most species of *Panopeus* and from other panopeid genera like *Hexapanopeus* Rathbun, 1898, *Rhithropanopeus* Rathbun, 1898, *Eurypanopeus* A. Milne-Edwards, 1881, and *Eurytium* Stimpson, 1859.

Earlier studies of larvae for American panopeid crabs, which included *P. bermudensis,* revealed unique characters in zoeal morphology for the latter species (Martin et al. 1984, 1985). More recently, one of us (DLF) has participated in comparative genetic studies that unambiguously position *P. bermudensis* apart from most panopeids for which mt16S DNA has been sequenced (Schubart et al. 2000). Finally, extensive collections from the Indian River lagoon, Florida, the Gulf of Mexico, and several Caribbean localities have facilitated studies of adult morphology that provided insight into variations in characters at both the specific and generic level. In view of our present evidence from adult morphology, larval characters, and molecular genetics, we herewith establish a new genus for this species and its closest relatives.

Materials examined include selected holdings from National Museum of Natural History Smithsonian Institution, Washington, D.C. (USNM), the Muséum national d'Histoire naturelle, Paris (MNHN), and the University of Louisiana, Lafayette Zoological Collections (ULLZ). Size is expressed as maximum carapace width (CW) measured in millimeters (mm) and includes the anterolateral teeth.

Acantholobulus, new genus

Type species.—*Panopeus bermudensis* Benedict & Rathbun, 1891.

Diagnosis of adult morphology.—Carapace (Fig. 1a) moderately convex, slightly elliptical in outline, regions well-defined by grooves, usually crossed by raised transverse lines of granules on anterior half. Frontal edge bilobed with distinct median fissure, thickened granulate margin usually with transverse concavity, sometimes defined as furrow between rows of granules above and below. Anterolateral teeth strongly developed, prominent, arrayed in distinct arc, third and fourth teeth with tips anteriorly directed, fifth tooth well defined, thick, acute. Abdomen of male with terminus rounded or weakly triangular, lateral extremities on third segment rounded, sixth segment slightly broader than long; lateral lobe of third segment not contacting coxa of fifth pereopod, seventh sternite distinctly exposed. Dactyl of major chela with strong basal tooth (Fig. 1b); color of immovable finger extended variably onto palm; carpus distally with distinct transverse groove. Fixed finger of major and minor chela in male deflected, less so in female. Male first pleopods (gonopods) terminally complex (Fig. 1c–f, 2a–l), subterminally with row of short denticles, field or row of a few strong setae, and strong subterminal tooth directed at right angle to shaft; terminal apex (accessory process) tapered, usually acute; soft, variously folded median lobe surrounding terminus of tract and bearing 1 to several strong, distally directed spines or setae.

Diagnosis of zoeal morphology.—Zoeal development (known for the former *Panopeus bermudensis* and *Hexapanopeus schmitti*) consisting of 4 stages; all stages lacking lateral carapace spines or with, at most, a small lateral protrusion of the carapace where such spines exist in other xanthoid larvae (Fig. 3a, b, e, h, i). Antennal protopod unarmed and slightly dilated at tip; antennal exopod absent or greatly reduced; antennal endopod absent or reduced (Fig. 3c, f, j). Arms of telson furca each with 1 dorsal spine located below (posterior to) insertion point of, and sometimes posterior to, furthest distal extent of telson marginal setae; other telson spines may be located anterior to this (e.g., Fig. 3g). Other characters as in the "Group I" xanthid zoeas (Rice 1980, Martin 1984, Martin et al. 1985).

Etymology.—Combines prefix "acantho-," meaning thorny as in a thorny plant, with "lobulus," meaning small lobe, in ref-

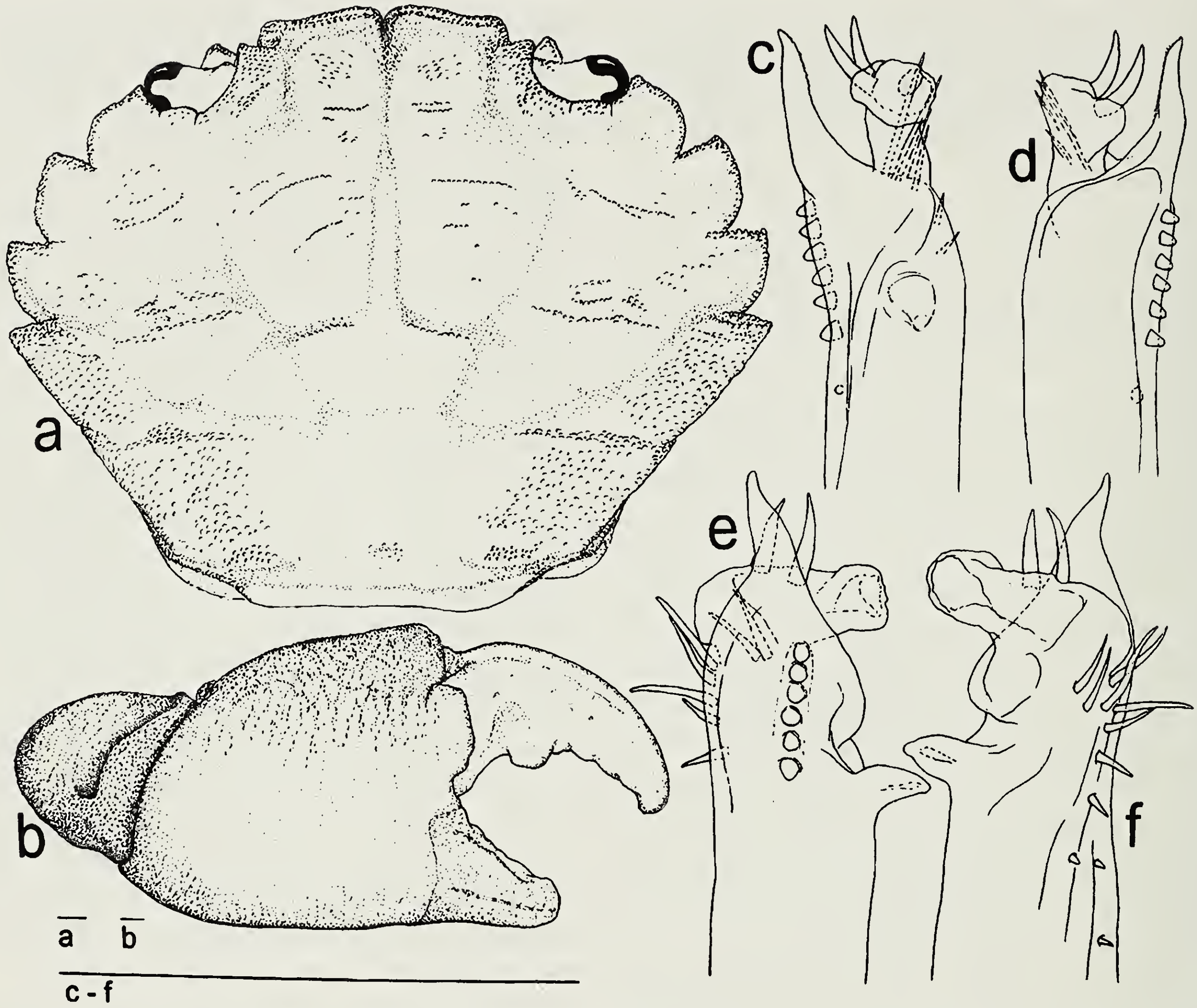

Fig. 1. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891), new combination, syntypic specimens from Bermuda, USNM 42804. Male, CW 12.5 mm: a, carapace and eyes, dorsal surface; b, major chela, external surface. Male, CW 7.6 mm: c–f, right gonopod mesial, lateral, abdominal and sternal surfaces, respectively. Scale lines indicate 0.5 mm.

erence to the median lobe of the male gonopod in this genus, which generally bears characteristic spiniform setae. The gender is masculine.

Assigned species.—Acantholobulus bermudensis (Benedict & Rathbun, 1891), new combination, formerly *Panopeus bermudensis,* senior synonym of *Hexapanopeus hemphillii* Benedict & Rathbun, 1891, *Panopeus gatunensis* Abele & Kim, 1989, and *Hexapanopeus heblingi* Rodrigues & de Loyola e Silva (1998), from throughout tropical to warm-temperate waters of the western Atlantic; *Acantholobulus miraflorensis* (Abele & Kim, 1989), new combination, formerly *Panopeus mirafloresensis,* including former eastern Pacific records of *P. bermudensis,* from throughout coastal waters of the tropical eastern Pacific region; *Acantholobulus pacificus* (Edmondson, 1931), new combination, formerly *Panopeus pacificus,* including "*Neopanope* sp. ?" of Edmondson, 1931), from Hawaii and Tahiti; and *Acantholobulus schmitti* (Rathbun, 1930), new combination, formerly *Hexapanopeus schmitti,* senior synonym of *Panopeus margentus* Williams & Boschi, 1990, from warm temperate Atlantic coastal waters of South America.

Acantholobulus bermudensis (Benedict & Rathbun, 1891), new combination
Figs. 1a–f, 2a–f, 3a–d

Panopeus herbstii var. *serratus* Miers, 1886:129.

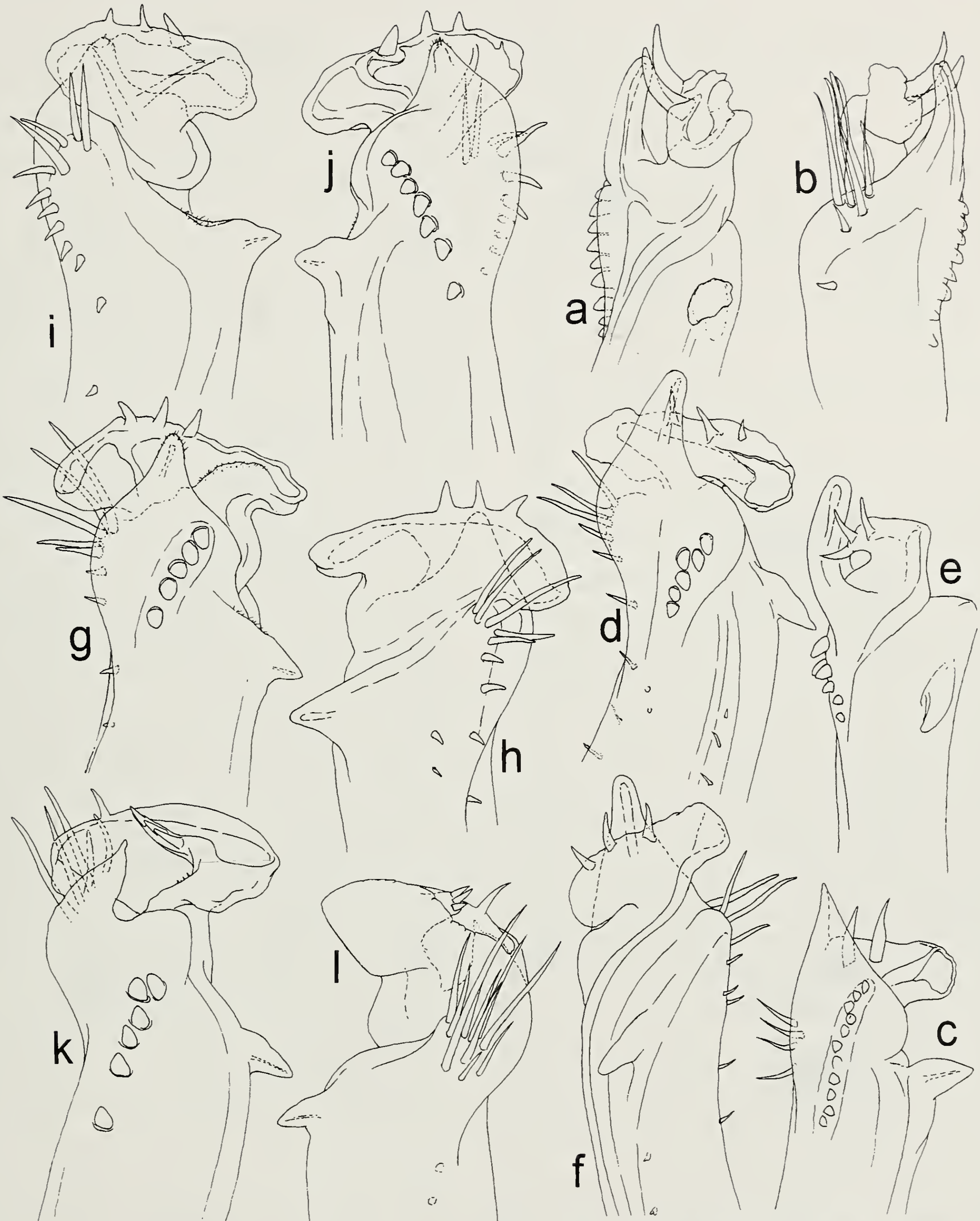

Fig. 2. *Acantholobulus bermudensis* (Benedict & Rathbun, 1891), new combination: a, b, syntypic male from Bermuda, USNM 42804, CW 12.5 mm, right gonopod mesial and lateral surfaces, respectively (subterminal tooth broken and missing from specimen, shown as dotted line); c, male from Macau, Rio Grande do Norte, Brazil, USNM 307299, (one of several specimens reported as "*Panopeus mirafloresensis*" by Ferreira & Sankarankutty 1997), CW 7.5 mm, right gonopod; d–f, male from Indian Key, Florida, USNM 15649 (holotype of *Hexapanopeus hemphillii* Benedict & Rathbun, 1891), CW 9.7 mm, right gonopod abdominal, mesial, and sternal surfaces, respectively. *Acantholobulus schmitti* (Rathbun, 1930), new combination: g, h, holotype male, Rio de Janeiro, Brazil, USNM 59831, CW 12.8 mm, right gonopod abdominal and sternal surfaces, respectively; i, j, male from Escollera Norte, Mar del Plata, Argentina, USNM 239191 (holotype of *Panopeus margentus* Williams & Boschi, 1990), CW 10.6 mm, left gonopod sternal and abdominal surfaces, respectively; k, l, male from Escollera Norte, Mar del Plata, Argentina, USNM 239195 (paratype of *Panopeus margentus* Williams & Boschi, 1990), CW 14.8 mm, right gonopod abdominal and sternal surfaces, respectively. Scale line indicates 0.5 mm.

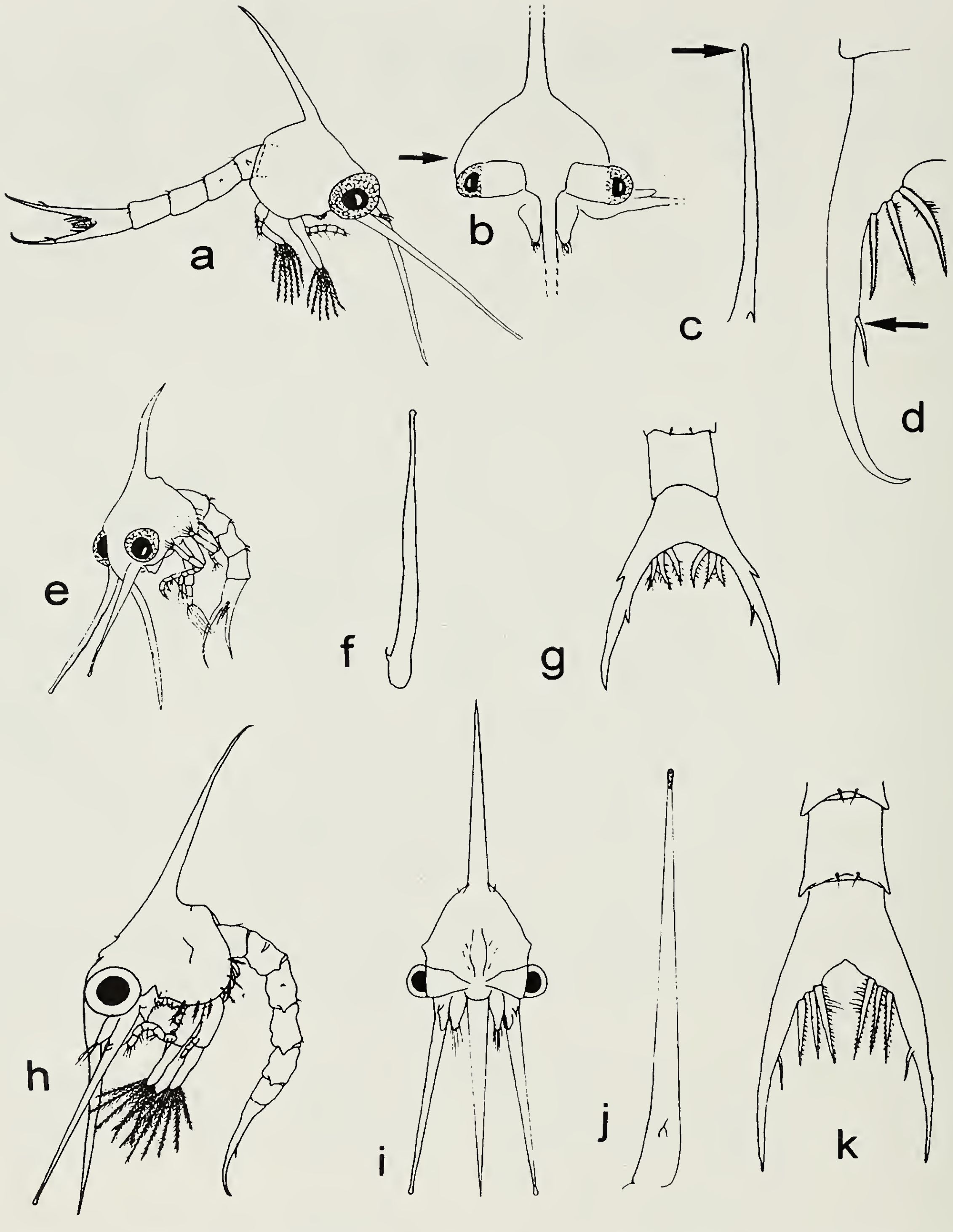

Fig. 3. Zoeal characters of *Acantholobulus*, new genus. a–d, *Acantholobulus bermudensis* (Benedict & Rathbun, 1891): a, second zoeal stage, lateral view; b, fourth zoeal stage, frontal view, arrow showing diagnostic lack of lateral carapace spine; c, second zoeal stage, antenna, arrow showing diagnostic dilated tip of protopod; d, left telsonal furca, dorsal view, arrow showing diagnostic posterior dorsal spine of furcal arm (from Martin et al., 1985, as *Panopeus bermudensis* Benedict & Rathbun, 1891). e–g, *Acantholobulus schmitti* (Rathbun, 1930), all figures of second zoeal stage: e, frontolateral view; b, antenna; c, telson, dorsal view (from Bakker et al., 1989, as *Hexapanopeus schmitti*). h–k, *Acantholobulus schmitti*: h, second zoeal stage, lateral view; i, third zoeal stage, frontal view showing lateral protrusions of carapace; j, second zoeal stage, antenna; k, second zoeal stage telson, dorsal view (from Rodríguez & Spivak 2001, as *Panopeus margentus* Williams & Boschi, 1990). Not drawn to scale.

Panopeus wurdemannii Benedict & Rathbun, 1891:357, 372, pl. 24, figs. 6, 7.

Panopeus bermudensis Benedict & Rathbun, 1891:357, 376, pl. 20, fig. 2, pl. 24, figs. 14, 15.—Rathbun 1930 (part): vii, 334 (key), 360–363, 365, 394, 583, fig. 56, pl. 165.—Rathbun 1933:60, 62.—Monod 1956:325, 336, figs. 439–440.—Felder 1973:5, 69, pl. 9, fig. 20.—Powers 1977:101.—Camp et al. 1977:35, 52, table 36.—Gore et al. 1978:221, 224, 228, 231–235, 237, 242–243, 248, table 2–4, figs. 8, 9, App. I.—Felder & Chaney 1979:15.—Martin 1984:227, 229, 230, 232, 233 (key to zoea), table 1.—Lemaitre 1981 (part, not Pacific range): 253–255, fig. 5a.—Markham & McDermott 1981:1273.—Martin et al. 1984:537–542, 544–549, 555–559, 563–564, 577–581, 589, 592–595, 597, 598, figs. 2–5, 10a, 11a, 12–13a, i, 17, 21–23a, i, 30–33a, i, 43–48, tables 4, 5.—Felder et al. 1985: 186, 208, fig. 14.—Martin et al. 1985: 84–103, figs. 1–7, tables 1, 2.—Abele & Kim 1986:xv, 59, 610 (key), 630, 631c.—Martin & Abele 1986:190, fig. 1K (not fig. 3C).—Martin 1988:76, 82, 89, 90, fig. 2f–h, j, k, 7, table 1.—Abele & Kim 1989:31, 36.—Williams & Boschi 1990:599.—Melo 1996 (part, not Pacific range):368 (key), 371, 598.—Camp et al. 1998:149, 212.—Schubart et al. 2000: 1168–1169, 1171, fig. 1, tables 1, 3.

Panopeus hemphillii Benedict & Rathbun, 1891:357, 374, pl. 24, figs. 12, 13.

Eupanopeus bermudensis.—Rathbun, 1898: 273.—Rathbun 1901:29.

Hexapanopeus hemphillii Rathbun, 1898: 273.—Rathbun 1901:31.—Rathbun 1930: 384 (key), 400–402, pl. 171, figs. 1, 2, 6.—Rathbun 1933:63.—Abele & Kim 1986:xiv, 57, 608 (key), 620, 621c–e.—Camp et al. 1998:148, 221.

Eupanopeus bermudensis var. *sculptus* Verrill, 1908:357.

Panopeus bermudensis? (juvenile).—Felder, 1973:62.

Panopeus species 2.—Martin & Abele, 1986:189, fig. 2B.

Panopeus gatunensis Abele & Kim, 1989: 3, 31, 32, 41, fig. 15a–h, table 3.

Panopeus permudensis (sic).—Sankarankutty & Manning, 1997:254.

Panopeus miraflorensensis.—Ferreira & Sankarankutty, 1997:153–155, fig. 1a–f (Brazilian specimens only; not *Panopeus miraflorensensis* Abele & Kim, 1989).

Hexapanopeus heblingi.—Rodrigues & de Loyola e Silva, 1998:263–270, figs. 1–20.

[not "*Panopeus bermudensis*" of Lebour, 1944:119, fig. 9a–d].

Material examined.—Type series, 16 specimens, of *Panopeus bermudensis* from Bermuda, USNM 42804; holotype male of *H. hemphillii* from Indian Key, Florida (USNM 15649); holotype male of *P. gatunensis* from Gatun Locks of Panama Canal, Caribbean side, Republic of Panama (USNM 237647); 2 males, 1 female reported as "*P. miraflorensensis*" by Ferreira & Sankarankutty (1997) from Macau, Rio Grande do Norte, Brazil (USNM 307299).

Diagnosis and common variations of adults.—Carapace (Fig. 1a) broadly oval; anterolateral teeth broadly developed, tending to lobiform, obtuse in small specimens, first and second broadly fused together with separation sometimes obscure; dorsal outline for each lobe of front arcuate near midline, becoming truncate or weakly concave laterally. Lines of granules on carapace usually including distinct short ridge (sometimes paired by short parallel ridge) on either half of epigastric region, composed of enlarged granules about same size as those of hepatic or branchial ridges. Color of movable finger (Fig. 1b) variably extended onto palm, varying from brown to tan, yellowish, or ivory; if dark, tips of fingers faded to near white. Palm usually with light, nearly white area distally near base of movable finger. Gonopod (Fig. 1c–f, 2a–f) with median lobe of terminus variously tubiform, slightly folded toward terminal apex (accessory process), not exceeding terminal apex distally, usually bearing 2–3 elongate,

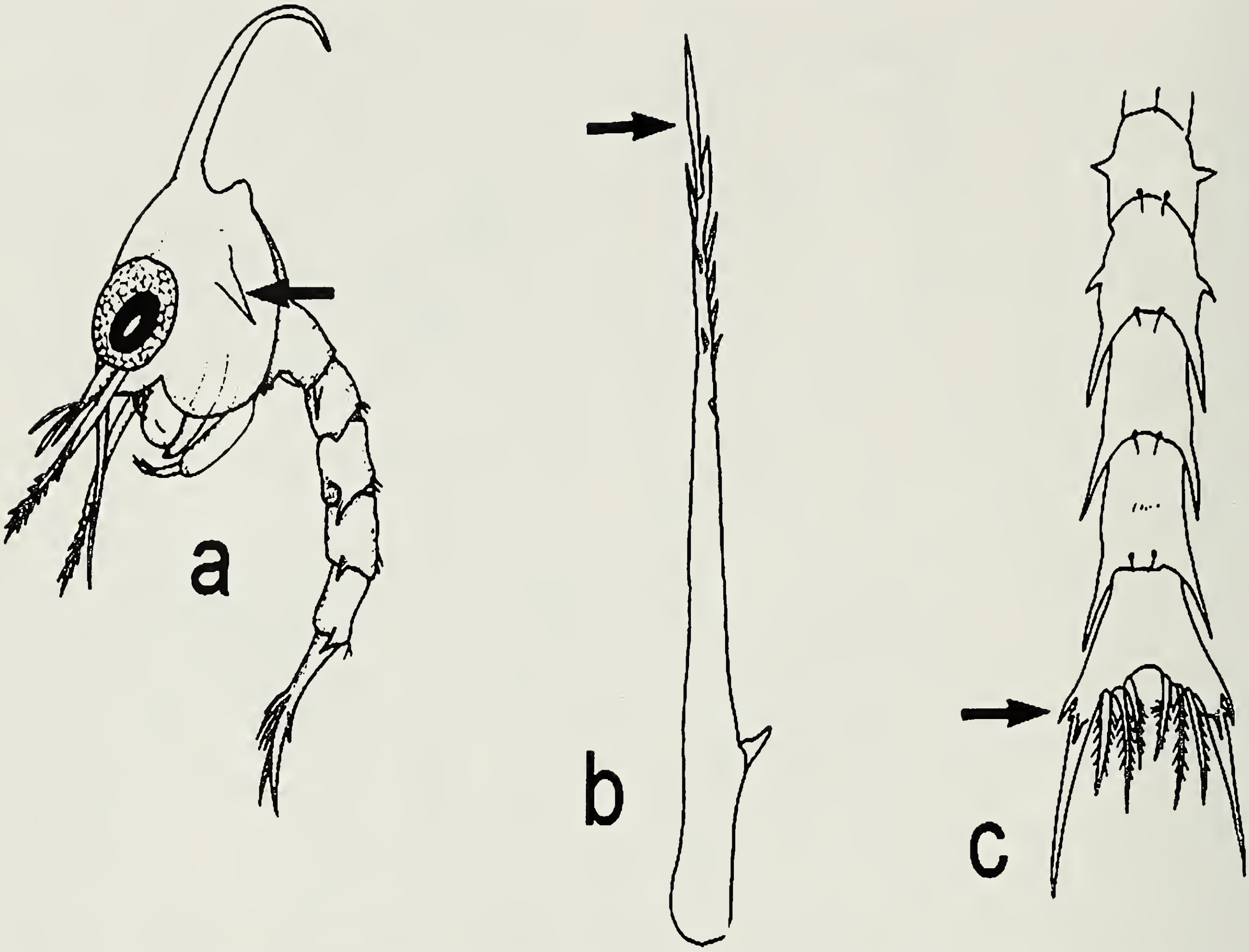

Fig. 4. Typical zoeal characters of the genus *Panopeus* H. Milne Edwards, 1834 and related genera in the family Panopeidae. a, second zoeal stage, lateral view, arrow showing well developed lateral carapace spine; b, second zoeal stage, antenna, arrow showing tapered distal extremity (note presence of spines and relative exopod/endopod sizes); c, third zoeal stage, telson in dorsal view, arrow showing placement of furcal spines (redrawn from Montú et al. 1998, as *Panopeus austrobesus* Williams 1984a).

curved spines. Zoeal stages (Fig. 3a–d) with arms of telsonal furca lacking lateral spination, each arm bearing single dorsointernal spine originating posterior to distal tips of internal marginal setae of furca. Occasional variants of adults include specimens having front a thickened lip, lacking transverse furrow on frontal lobes; bearing obscurely developed lines of granules dorsally on carapace; lacking dimorphism in chelae, with both being developed as enlarged minor chelae lacking basal tooth on movable finger; or bearing more or less than 2 or 3 spines on the median lobe of the gonopod terminus.

Distribution.—Warm-temperate and tropical shallow waters of the western Atlantic, from Bermuda and Florida, throughout the Gulf of Mexico and Caribbean Sea, the Antilles, and northern coastlines of South America to the state of Santa Catarina, Brazil.

Remarks.—No holotype was designated in the published original description of *Panopeus bermudensis* by Benedict & Rathbun (1891), though a "large male" was reported be 12 mm CW. Subsequently, Rathbun (1930) indicated that the type series consisted of 15 specimens "including holotype" and indicated that the "type male" as 14.4 mm CW. We presently find no specimen larger than a male of 12.5 mm CW in the type series of 16 specimens that comprise USNM 42804. We must surmise that the presumed holotype is either missing or that the size of the largest specimen and presumed holotype was in error as reported by Rathbun (1930). While 16 specimens remain in this lot, which exceeded the number reported by Rathbun, a small, possibly original tag with this lot does appear to indicate that the collection consists of "15+" specimens. In absence of any more definitive evidence that a designated holotype ever existed, we regard this series as syntypes.

Monod (1956:325) first noted the potential significance of the gonopod of *Panopeus bermudensis* as a generic-level character. Subsequent workers also called attention to the unique terminal gonopod morphology and its possible generic significance in both *P. bermudensis* and *Panopeus miraflorensis* (Martin & Abele 1986; Martin et al. 1984, 1985; Abele & Kim 1989). In addition, *Panopeus gatunensis,* herein recognized as a junior synonym of *Acantholobulus bermudensis,* was shown to have a gonopod similar to the aforementioned two species, differing primarily in having a supernumerary lateral spine. Without question, all three of these species share gonopod morphology diagnostic of *Acantholobulus.* However, we place no significance in the observation of a supernumerary lateral spine on the gonopod of *P. gatunensis* that was originally illustrated by Abele & Kim (1989: fig. 15f–h) especially since the holotype male (USNM 237647, the only known specimen) has only a single lateral spine on the opposite gonopod from that illustrated. Furthermore, supernumary lateral spines are occasionally seen among large series of specimens assignable to *A. bermudensis* from the Indian River region of Florida (ULLZ collections); when these occur, they are usually on only one side of the male. The holotype of *P. gatunensis* also appears to have a regenerated major chela, an atypically smooth carapace, and a very poorly defined transverse frontal furrow. These are, however, again features seen in a small percentage of specimens assignable to *A. bermudensis* from Florida, and none occur in such combination and consistency as to suggest that they are likely characters of a separate species.

Records of *Hexapanopeus hemphillii* are not to be found in the literature since Rathbun (1930), and our attempts to collect from habitats described in that work consistently yield only specimens assignable to *Acantholobulus bermudensis.* Examination of the male holotype of *H. hemphillii* (USNM 15649) revealed that it is clearly assignable to *Acantholobulus.* Its gonopod (Fig. 2d, e) differs from the typical form in *A. bermudensis* in that it bears three smaller, rather than two larger, spines on the medial lobe. This condition, however, is not uncommon among males in large samples of *A. bermudensis.* Also, white coloration on the fingers of the chelipeds, relative widths of the anterolateral teeth on the carapace, and the carapace shape, as used in the description and later diagnosis of *H. hemphillii* (see Benedict & Rathbun 1891, Rathbun 1930), all can be found among larger series of *A. bermudensis.* In the absence of dependable diagnostic characters for *H. hemphillii,* we must treat it as a junior synonym of *A. bermudensis.*

Likewise, no characters are offered in the description by Rodrigues & de Loyola e Silva (1998) that would differentiate *Hexapanopeus heblingi* from *A. bermudensis,* and interspecific comparisons they make are limited to western Atlantic species of *Hexapanopeus.* We have not been able to examine type materials of this species, but both the text and figures in the published description clearly detail features diagnostic of *Acantholobulus,* new genus, well within the range of variation that we have observed in *A. bermudensis.* At least for the present, we conclude that this species is also a junior synonym of *A. bermudensis,* a finding supported by the strong similarity of its larvae (Rodrigues 1997) to those of *A. bermudensis* (see Discussion below).

A report of *Panopeus miraforesensis* from Brazil (Ferreira & Sankarankutty 1997) is interpreted to also represent *Acantholobulus bermudensis* rather than the aforementioned species, which appears to be restricted to Pacific coastlines. Specimens upon which this Brazilian record was based were furnished to the late R. B. Manning prior to publication and (as noted by Ferreira & Sankarankutty 1997:157) he could not confirm that they represented *Panopeus mirafloresensis.* We have examined these specimens (USNM 307299), illustrated the male gonopod (Fig. 2c) and found them indistinguishable from *A. bermudensis.* We also observe, however, that the Pacific species *Acantholobulus mirafloresensis* (as herein assigned) is itself not readily distinguishable from *A. bermudensis* on the basis of characters reported to date, especially given the range of variation that we have observed in populations of the latter species. Records from the eastern Pacific region include mention of both *Panopeus bermudensis* (see Rathbun 1930, Garth 1961, Lemaitre 1981, Abele & Kim 1989, Lemaitre & Alvarez León 1992) and *P. mirafloresensis* (see Abele & Kim 1989: 36), and no attempt is herein made by us to resolve morphologically whether these eastern Pacific populations could represent more than one species. At least until further comparative study is undertaken and ongoing molecular analyses are completed, we recognize *A. mirafloresensis* as the eastern Pacific cognate of *A. bermudensis.* The natural range of latter species appears limited to warm-temperate and tropical shallow waters of the western Atlantic, as also concluded by Salgado Barragán & Hendrickx (1997).

Systematic review of congeners.—Recognition of *Panopeus margentus* as a junior synonym of *Acantholobulus schmitti* (Rathbun, 1930), new combination, was based upon examination of the holotype (USNM 239191) and paratypes (USNM 239195) of *Panopeus margentus,* all from Mar del Plata, Argentina. The description of *P. margentus* by Williams & Boschi (1990) included no comparisons to or mention of *Hexapanopeus schmitti,* even though the latter species has been documented to range into warm-temperate waters of southern Brazil and Uruguay. Instead, the authors did note its resemblance to *Panopeus bermudensis* and the Pacific *P. mirafloresensis,* both of which are in the present work established as congeners of *Acantholobulus schmitti.* We have found no consistent features of general carapace and cheliped morphology that would serve to distinguish *P. margentus* from larger specimens of *Acantholobulus schmitti.* Furthermore, the right gonopod as figured in the original description (Williams & Boschi 1990: fig. 1e, d) appears to be highly aberrant and perhaps damaged. Our own examination of the damaged holotype revealed the left gonopod of this specimen to be intact (Fig. 2i, j) and almost identical in terminal morphology to that herein figured for the holotype of *Acantholobulus schmitti* (Fig. 2g, h). However, as discussed below, the description of larval development for this species (*Panopeus margentus*) by Rodríguez & Spivak (2001) included some differences from that presented by Bakker et al. (1989) for *Hexapanopeus schmitti,* which should not be the case if these two names indeed refer to the same species (further addressed in Discussion below).

Materials of *Panopeus pacificus* from Hawaii and Tahiti, along with some questionably assigned to "*Neopanope* sp. ?" by Edmondson (1931), were reviewed by Forest & Guinot (1961) who provided detailed illustrations of gonopods, chelae, and carapace dentition for these specimens, all of which appear to be typical of *Acantholobulus.* Our direct examination of topotypic specimens of *P. pacificus* (four males, two females) collected by C. H. Edmondson from Pearl Harbor (USNM 96304) confirms this generic reassignment. We have also reexamined the two males of *P. pacificus* reported from Tahiti (MNHN B13963) by Forest & Guinot (1961) and found no characters to distinguish them from the Hawaiian materials. Edmondson (1931) preceded his original description of *P. pacificus* by noting the possibility of this species being "transported to Hawaii through shipments of oysters or on the bottoms of ships," especially since he found it only in association with "sponges, barnacles and tunicates attached to buoys and floats in Pearl Harbor, Oahu." This is typical habitat for most of the known *Acantholobulus* spp., and may indicate a high potential for their dispersal and introduction among fouling materials. At very least, it could account for wide distributions, such as that for *A. pacificus,* which appears to encompass both Hawaii and Tahiti. However, except for the apparent larger size evident in most specimens of *A. pacificus,* there are also no obvious morphological characters to distinguish it from *A. mirafloresensis.* More definitive conclusions about the relationship between these species and their relationships to others of the genus should be facilitated by molecular genetic studies that we have in progress.

While we have not re-examined materials of the "*Neopanope* sp.?" reported by Edmondson (1931:14), from Pearl Harbor, the chelae of one large male in the lot of *Panopeus pacificus* that we examined (USNM 96304) appears to match Edmondson's description of the chelae in his specimen of "*Neopanope* sp.?". In addition, the figure of the gonopod for "*Neopanope* sp.?" provided by Forest & Guinot (1961: fig. 106) is clearly typical of *Acantholobulus* and well within the range of variation to be expected in gonopod morphology for species in this genus. We thus conclude that the peculiar cheliped dentition reported for "*Neopanope* sp.?" by Edmondson (1931) is likely the result of cheliped regeneration and that these materials represent additional specimens of *A. pacificus,* new combination. Cheliped variations like those observed by Edmondson are not uncommon in populations of *A. bermudensis* that we have sampled in Florida (ULLZ collections). These have also been illustrated for variant specimens of both *A. bermudensis* (as *Panopeus gatunensis,* Abele & Kim, 1989: fig. 15) and *A. mirafloresensis,* (as *Panopeus mirafloresensis,* Abele & Kim, 1989: fig 18) from Panama.

Our proposed revisions are summarized as follow:

Former name	New name
Panopeus bermudensis	*Acantholobulus bermudensis,* new combination
Hexapanopeus schmitti	*Acantholobulus schmitti,* new combination
Panopeus mirafloresensis	*Acantholobulus mirafloresensis,* new combination
Panopeus margentus	junior synonym of *A. schmitti*
Panopeus gatunensis	junior synonym of *A. bermudensis*
Hexapanopeus hemphillii	junior synonym of *A. bermudensis*
Hexapanopeus heblingi	junior synonym of *A. bermudensis*

Discussion

The use of brachyuran larval morphology, especially characters of the first zoeal stage, in elucidating systematic and phylogenetic questions is now relatively well established (e.g., see references in Clark et al. 1998). Larval morphology has been of particular value for resolving relationships within the enormous superfamily Xanthoidea MacLeay, 1838 (e.g., Clark & Al-Aidaroos 1996, Clark & Galil 1998, Clark & Ng 1998, Fransozo et al. 2001, and papers cited therein). Several workers (Rice 1980; Martin 1984, 1988), have proposed recognizable groupings of xanthoid larvae in attempts to address systematic or phylogenetic questions. Within the xanthoid family Panopeidae Ortmann, 1893 sensu Guinot 1978 (see also Martin & Davis 2001), larval morphology is diverse. Prior to 1985, however, all known species of the Panopeidae save *Panopeus bermudensis* were thought to have lateral carapace spines, which is true of nearly all known xanthoid larvae. "Typical" zoeal larvae of panopeid crabs have well developed (although sometimes short) lateral carapace spines, a tapering antennal protopod that is often armed distally (and is never distally inflated), and two or three small spines on the telsonal furcae, all located at approximately the level of insertion of the three paired telsonal setae (Fig. 4). The larvae of *P. bermudensis* were described as differing from all other panopeid larvae in lacking these lateral carapace spines (Martin et al. 1985), having an antenna that is dilated at the tip and that lacks an exopod (actually present, but greatly reduced, see Discussion), and in bearing a single pair of telsonal spines located posterior to the distal tip of the interior telsonal setae. Remarkably, the zoeal stages of *Hexapanopeus schmitti* as described by Bakker et al. (1989) also lack a lateral carapace spine, have an antennal protopod that is dilated at the tip, have a reduced antennal exopod, and bear a pair of posterior spines on the telsonal furca (although, in addition, there is also a pair of more anterior furcal spines).

Our decision to group the former *Panopeus bermudensis* and *Hexapanopeus schmitti,* along with the former *Panopeus mirafloresensis* and *P. pacificus,* into *Acantholobulus,* new genus, on the basis of adult morphology is thus supported by larval morphology for at least the first two of these species. We expect that larval characters of the former *P. mirafloresensis* and *P. pacificus,* which remain undescribed, should resemble those of the two other species of *Acantholobulus.* Given the similarities in adult morphology herewith reported for proposed members of *Acantholobulus,* new genus, shared characters in larval morphology to the extent known within this group, and the established genetic distinction for at least one of its members (Schubart et al. 2000), the generic revision herein proposed is strongly supported.

Even so, some problems remain in our assignment of species to the new genus *Acantholobulus,* decision to synonymize *Panopeus margentus* with *Acantholobulus schmitti,* and conclusion that *Hexapanopeus hemphillii* and *H. heblingi* must be synonymized with *Acantholobulus bermudensis.* In the case of *Panopeus margentus,* our reasons for placing this species into synonymy with *Acantholobulus schmitti* on the basis of adult features have been given earlier. One would thus expect that reported larval descriptions would prove to be identical, and to large extent this is true; Rodríguez & Spivak (2001:818) state that "*Panopeus margentus* larvae are very similar to those of *H. schmitti.*" The larvae of *P. margentus* as described by Rodriguez & Spivak (2001) also lack lateral carapace spines, although a slight protrusion of the carapace can be seen (Fig. 1h, i), which may be a homologue of the lateral spine in typical panopeid zoeas. As described, however, the zoeal stages of *P. margentus* would appear to lack the second pair of telson furcal spines shown by Bakker et al. (1989) for *H. schmitti.*

In the course of our studies, we have reexamined the parental female (USNM 288046), as well as the larval stages of *P. margentus* (USNM 291175) described by Rodríguez & Spivak (2001). We cannot definitively separate the female from those of *A. schmitti,* though females of both of these species remain poorly described. Among the larvae, when mounted in glycerin and examined with differential interference contrast (DIC) optics, we do find zoeas at stages one through four in which a second, very small pair of telson furcal spines can be discerned at high magnifications (first called to our attention by J. Cuesta and B. Mahon). These, however, appear to be less conspicuous than those illustrated for zoeal stages of *A. schmitti* by Bakker et al. (1989), and it should be noted that they were not obvious on all specimens examined; in some cases, the small setal shaft appeared instead as a cluster of two or three miniscule setae or setal fragments and may have been worn or damaged.

For *Hexapanopeus heblingi* we examined

selected figures of the larvae illustrated by Rodrigues (1997, figs. 3–10). On the basis of these larval descriptions, zoeal stages of *H. heblingi* are essentially identical to those of *Panopeus bermudensis* described by Martin et al. (1984, 1985). The absence of a lateral carapace spine, the inflated tip of the antenna, the reduced antennal exopod, and other features are a nearly perfect match, supporting our synonymy of the two species under the name *Acantholobulus bermudensis.* Yet, descriptions of the megalopa appear to differ slightly. In the megalopa of *P. bermudensis,* described by Martin et al. (1984, 1985), the frontal region of the carapace bears anterolateral horns, and the cheliped bears a distinct recurved spine on the ischium. Neither of these characters is illustrated by Rodrigues (1997) for the species therein referred to as *H. heblingi.* Although frontal horns on the carapace are easily missed, especially if the carapace front is strongly deflected downward, the cheliped spine is a feature that rarely escapes notice.

We cannot further comment on this apparent discrepancy without directly re-examining the larvae referred to as *H. heblingi.* Minute structures are easily overlooked, and it is pertinent to note that Martin et al. (1985) also overlooked a diagnostic structure in the course of describing larvae that we now refer to *Acantholobulus bermudensis.* We have re-examined some of the actual larvae treated in that earlier study (ULLZ, uncatalogued slide mounts), and we must now report that the antenna does in fact possess a small exopod. It is entirely possible that other small features have also escaped the notice of previous workers, and a thorough reinvestigation of larval morphology in all of these xanthoid groups is warranted.

For the present, pending additional molecular studies to build on those of Schubart et al. (2000), we continue to treat species herewith assigned to *Acantholobulus,* new genus, as members of the Panopeidae. As noted above, however, both mtDNA sequences and larval morphology set this group apart from typical panopeid species, and definitive assignment must await improved understanding of familial separations among the Xanthoidea.

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Literature Cited

Abele, L. G., & W. Kim. 1986. An illustrated guide to the marine decapod crustaceans of Florida.—State of Florida Department of Environmental Regulation Technical Series, Vol. 8, no. 1 (in 2 parts). 760 p.

Abele, L. G., & W. Kim. 1989. The decapod crustaceans of the Panama Canal.—Smithsonian Contributions to Zoology 482:1–50.

Bakker, C. de, M. Montú, K. Anger, & L. L. Fernandes. 1989. Larval development of *Hexapanopeus schmitti* Rathbun, 1930 (Decapoda, Brachyura, Xanthidae) reared in the laboratory.—Nerítica 4:137–164.

Benedict, J. E., & M. J. Rathbun. 1891. The genus *Panopeus.*—Proceedings of the U.S. National Museum 14:355–385, plates 19–24.

Camp, D. K., N. H. Whiting, & R. E. Martin. 1977. Nearshore marine ecology at Hutchinson Island, Florida: 1971–1974. V. Arthropods.—Florida Marine Research Publications, Department of Natural Resources 25:i, 1–63.

Camp, D. K., W. G. Lyons, & T. H. Perkins. 1998. Checklists of selected shallow-water marine invertebrates of Florida.—Florida Marine Research Institute Technical Report TR-3, Florida

Department of Environmental Protection, 1998: i–xv, 1–238.

Clark, P. F., & A. M. Al-Aidaroos. 1996. The first zoeas of *Actaeodes hirsutissimus* (Rüppell, 1830) and *A. tomentosus* (H. Milne Edwards, 1834) (Crustacea: Decapoda: Brachyura: Xanthidae: Actaeinae).—Journal of King Abdulaziz University Marine Sciences 7, Special Issue: Symposium on the Red Sea Marine Environment: 207–214.

Clark, P. F., D. K. Calazans, & G. W. Pohle. 1998. Accuracy and standardization of brachyuran larval descriptions.—Invertebrate Reproduction and Development 33:127–144.

Clark, P. F., & B. S. Galil. 1998. The first stage zoea of *Pseudoliomera speciosa* (Dana, 1852) (Crustacea, Decapoda, Brachyura, Xanthidae).—Zoosystema 20:193–200.

Clark, P. F., & P. K. L. Ng. 1998. The larval development of the poisonous mosaic crab, *Lophozozymous pictor* (Fabricius, 1798) (Crustacea, Decapoda, Brachyura, Xanthidae, Zosiminae), with comments on familial characters for first stage zoeas.—Zoosystema 20:201–220.

Edmondson, C. H. 1931. New crustaceans from Kauai, Oahu, and Maui. Bernice P. Bishop Museum Occasional Papers 9(17):1–18.

Felder, D. L. 1973. An annotated key to crabs and lobsters (Decapoda, Reptantia) from coastal waters of the northwestern Gulf of Mexico.—Center for Wetland Resources, Louisiana State University, Baton Rouge, 103 p.

Felder, D. L., & A. H. Chaney. 1979. Decapod crustacean fauna of Seven and One-half Fathom Reef, Texas: species composition, abundance, and species diversity.—Contributions in Marine Science 22:1–29.

Felder, D. L., J. W. Martin, & J. W. Goy. 1985. Patterns in early postlarval development of decapods. *In* A. M. Wenner (ed.), Larval Growth, vol. 2 of F. Schram (ed.), *Crustacean Issues.* Pp. 163–225. Balkema Press, Rotterdam.

Ferreira, A. C., & C. Sankarankutty. 1997. Extension of the range of distribution of *Panopeus mirafloresensis* Abele & Kim (Crustacea: Decapoda: Xanthidae).—Nauplius 5:155–157.

Forest, J., & D. Guinot. 1961. Crustacés Décapodes Brachyoures de Tahiti et des Tuamotu. Expédition Française sur les récifs coralliens de la Nouvelle-Calédonie. Volume Préliminaire—Éditions de la Fondation Singer-Polignac, Paris: 1–195, 18 plates.

Fransozo, A. 1987. Desenvolvimento larval de *Eriphia gonagra* (Fabricius, 1781) (Decapoda, Xanthidae), em laboratório.—Revista Brasileira Zoologia 4:165–179.

Fransozo, A., M. L. Negreiros-Fransozo, J. W. Martin, & S. E. Trautwein. 2001. Morphology of the first zoeal stage of *Platypodiella spectabilis* (Herbst, 1794) (Decapoda, Brachyura, Xanthidae) obtained in the laboratory.—Gulf and Caribbean Research 13:79–85.

Fransozo, A., F. L. M. Mantelatto, & M. L. Negreiros-Fransozo. 1990. Larval development of *Hexapanopeus paulensis* Rathbun, 1930 (Crustacea, Brachyura, Xanthidae) under laboratory conditions.—Revista Brasileira Zoologia 7:31–45.

Garth, J. S. 1961. Part 2: Brachygnatha Brachyrhyncha. *In* Eastern Pacific expeditions of the New York Zoological Society, XLV: Non-intertidal brachygnathous crabs from the west Coast of Tropical America.—Zoologica (New York) 46: 133–159, 1 plate.

Garth, J. S. 1991. Taxonomy, distribution, and ecology of Galápagos Brachyura. Pp. 123–145 *in* M. J. James (ed.), Galápagos Marine Invertebrates.—Topics in Geobiology, vol. 8, Plenum Press, New York.

Gore, R. H., L. E. Scotto, & L. J. Becker. 1978. Community composition, stability, and trophic partitioning in decapod crustaceans inhabiting some subtropical sabellariid worm reefs.—Bulletin of Marine Science 28:221–248.

Gore, R. H., C. L. Van Dover, & K. A. Wilson. 1981. Studies on decapod Crustacea from the Indian River region of Florida. XX. *Micropanope barbadensis* (Rathbun, 1921): the complete larval development under laboratory conditions (Brachyura, Xanthidae).—Journal of Crustacean Biology 1:28–50.

Guinot, D. 1967. Recherches préliminaires sur les groupements naturels chez les Crustacés Décapodes Brachyoures III. A propos des affinités des genres *Dairoides* Stebbing et *Daira* de Haan.—Bulletin du Muséum national d'Histoire naturelle, 2e Série 39:540–563.

Guinot, D. 1978. Principes d'une classification évolutive des Crustacés Décapodes Brachyoures.—Bulletin Biologique de le France et de la Belgique (n. s.) 112:211–292.

Lebour, M. 1944. Larval crabs from Bermuda.—Zoologica (New York) 29:113–128.

Lemaitre, R. 1981. Shallow-water crabs (Decapoda, Brachyura) collected in the southern Caribbean near Cartagena, Colombia.—Bulletin of Marine Science 31:234–266.

Lemaitre, R., & R. Alvarez León. 1992. Crustáceos decápodos del Pacífico colombiano: Lista de especies y consideraciones zoogeograficas.—Anales del Instituto de Investigaciones Marinas, Punta Betín 21:33–76.

Markham, J. C., & J. J. McDermott. 1981. A tabulation of the Crustacea Decapoda of Bermuda. Proceedings of the Biological Society of Washington 83(4):1266–1276.

Martin, J. W. 1984. Notes and bibliography on the larvae of xanthid crabs, with a key to the known xanthid zoeas of the western Atlantic and Gulf of Mexico.—Bulletin of Marine Science 34: 220–239.

Martin, J. W. 1988. Phylogenetic significance of the brachyuran megalopa: evidence from the Xanthidae.—Symposia of the Zoological Society of London 59:69–102.

Martin, J. W., & L. G. Abele. 1986. Notes on the male pleopod morphology in the brachyuran crab family Panopeidae Ortmann, 1893, sensu Guinot (1978) (Decapoda).—Crustaceana 50:182–198.

Martin, J. W., & G. E. Davis. 2001. An updated classification of the Recent Crustacea.—Science Series 39, Natural History Museum of Los Angeles County.

Martin, J. W., D. L. Felder, & F. M. Truesdale. 1984. A comparative study of morphology and ontogeny in juvenile stages of four western Atlantic xanthoid crabs (Crustacea: Decapoda: Brachyura).—Philosophical Transactions of the Royal Society of London, series B, 303:537–604.

Martin, J. W., F. M. Truesdale, & D. L. Felder. 1985. Larval development of *Panopeus bermudensis* Benedict and Rathbun, 1891 (Brachyura, Xanthidae) with notes on zoeal characters in xanthid crabs.—Journal of Crustacean Biology 5:84–105.

McLeay, W. S. 1838. On the Bachyurous decapod Crustacea brought from the Cape by Dr. Smith [*included within* Illustrations of the Annulosa of South Africa]. Pp. 53–72, plate 3 *in* A. Smith, vol. V, Illustrations of the Zoology of South Africa, Invertebratae.

Melo, G. A. S. 1998. Malacostraca—Eucarida. Brachyura. Oxyrhyncha and Brachyrhyncha. Pp. 455–515 *in* Young, P. S. (ed.), Cataloge of Crustacea of Brazil. Museu Nacional (Serie Livros no. 6), Rio de Janeiro, Brazil.

Miers, E. J. 1886. Report on the Brachyura collected by H. M. S. Challenger during the years 1873–76.—Report on the scientific results of the voyage of H. M. S. Challenger, Zoology 17(49):1–362, plates 1–29.

Milne-Edwards, A. 1881. Description de quelques Crustacés Macroures provenant des grandes profondeurs de la mer des Antilles.—Annales Sciences Naturelles, series 6, Zoologie 11(4):1–16.

Milne Edwards, H. 1834. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et, la classification de ces animaux. Vol. 1, xxxv + 468 p., Paris.

Monod, Th. 1956. Hippidea et Brachyura ouest-africans. Mémoires de l'Institut Français d'Afrique Noire 45:1–674.

Montú, M., K. Anger, C. de Bakker, V. Anger, & L. Fernandes. 1988. Larval development of the Brazilian mud crab *Panopeus austrobesus* Williams, 1983 (Decapoda: Xanthidae) reared in the laboratory.—Journal of Crustacean Biology 8:594–613.

Ortmann, A. 1893. Abtheilung: Brachyura (Brachyura genuina Boas), II. Unterabtheilung: Cancroidea, 2. Section: Cancrinea, 1. Gruppe: Cyclometopa. Die Decapoden-Krebse des Sttrassburger Museums, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen, VII. Theil.—Zoologische Jarbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 7:411–495, plate 17.

Powers, L. 1977. A catalogue and bibliography to the crabs (Brachyura) of the Gulf of Mexico.—Contributions in Marine Science 20(supplement):1–190.

Rathbun, M. J. 1898. The Brachyura of the biological expedition to the Florida Keys and the Bahamas in 1893.—Bulletin from the Laboratories of Natural History of the State University of Iowa 4(3):250–294, plates 1–9.

Rathbun, M. J. 1901. The Brachyura and Macrura of Porto Rico.—Bulletin of the United States Fish Commission for 1900 20(2):1–137.

Rathbun, M. J. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae.—Bulletin of the U.S. National Museum 152:1–609.

Rathbun, M. J. 1933. Brachyuran crabs of Porto Rico and the Virgin Islands. *In* Scientific Survey of Porto Rico and the Virgin Islands.—New York Academy of Sciences 15(1):1–121.

Rice, A. L. 1980. Crab zoeal morphology and its bearing on the classification of the Brachyura.—Transactions of the Zoological Society of London 35:271–424.

Rodríguez, A., & E. D. Spivak. 2001. The larval development of *Panopeus margentus* (Decapoda: Brachyura: Panopeidae) reared in the laboratory.—Journal of Crustacean Biology 21:806–820.

Rodrigues, M. D. 1997. Desenvolvimento larval e juvenil de *Panopeus rugosus* A. Milne Edwards 1889 e de *Hexapanopeus heblingi* sp. n. e desenvolvimento juvenil de *Panopeus occidentalis* Saussure, 1857 (Crustacea, Decapoda, Xanthidae) em laboretório. Departamento de Zoologia, Universidade Federal do Paraná (Brasil), pp. 1–153.

Rodrigues, M. D., & J. de Loyola e Silva. 1998. Descrição de *Hexapanopeus heblingi* sp. n. (Crustacea, Decapoda, Brachyura, Xanthidae) do littoral Brasileiro.—Revista Brasileira Zoologia 15:261–271.

Salgado Barragán, J., & M. E. Hendrickx. 1997. Decapod crustaceans from the Pacific coast of Mexico, including new records and taxonomic remarks.—Revista de Biología Tropical 45:680–683.

Sankarankutty, C., & R. B. Manning. 1997. Observations on *Hexapanopeus schmitti* Rathbun from Brazil (Crustacea: Decapoda: Xanthidae).—Proceedings of the Biological Society of Washington 110:249–255.

Schubart, C. D., J. E. Neigel, & D. L. Felder. 2000. Molecular phylogeny of mud crabs (Brachyura: Panopeidae) from the northwestern Atlantic and the role of morphological stasis and convergence.—Marine Biology 137:11–18.

Stimpson, W. 1859. Notes on North American Crustacea, 1.—Annals of the Lyceum of Natural History of New York 7:49–93 [1–47], 1 plate.

Verrill, A. E. 1908. Decapoda Crustacea of Bermuda, part I. Brachyura and Anomura, their distribution, variations, and habits.—Transactions of the Connecticut Academy of Arts and Sciences 13:299–474, plates 9–28.

Williams, A. B. 1984a. The mud crab *Panopeus herbstii,* s.l. Partition into six species (Decapoda: Xanthidae).—Fishery Bulletin 81(4, for 1983): 863–882.

Williams, A. B. 1984b. Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., xvii + 550 pp.

Williams, A. B., & E. Boschi. 1990. *Panopeus margentus,* a new crab from the Argentine warm temperate subregion (Decapoda: Xanthidae).—Proceedings of the Biological Society of Washington 103(3):598–601.

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A new species of *Pseudopaguristes* McLaughlin, 2002 (Crustacea: Decapoda: Diogenidae) from Japan

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Abstract.—*Pseudopaguristes bollandi,* a new species of the recently established diogenid genus *Pseudopaguristes* McLaughlin, is described and illustrated from Okinawa, Japan. This is only the second species assigned to this genus.

A distinctive and unfamiliar hermit crab from Okinawa was recently send to the first author for identification. This specimen superficially looked very much like a species of the diogenid genus *Paguristes* Dana, 1851, particularly in having paired first and second pleopods modified as gonopods. However, the right cheliped was larger than the left, a character uncommon in species of that genus. Further examination revealed a gill formula aberrant for *Paguristes.*

McLaughlin (2002) recently established the new genus *Pseudopaguristes,* for *P. janetkae* McLaughlin, 2002, a brilliantly colored and strikingly sexually dimorphic species from Guam, Micronesia. Females of *Pseudopaguristes* could easily be assigned to the genus *Paguristes,* because the chelipeds are similar in size and armature, a character commonly seen in *Paguristes.* However, the males differ appreciably in having chelipeds quite dissimilar in armature, with the right largest. McLaughlin reported that males and females of *Pseudopaguristes* share with *Paguristes* the distinctive character of sexually modified pleopods. However, *Pseudopaguristes janetkae* has only eight functional pairs of gills, whereas *Paguristes* species have 13 pairs. In *Pseudopaguristes janetkae,* the paired arthrobranchs at the base of the third maxillipeds and chelipeds are rudimentary or vestigial, and there is no pleurobranch on the thoracic wall above the second pereopod. The specimen from Okinawa clearly belongs to *Pseudopaguristes* and represents a new species described herein. The holotype is deposited in the Natural History Museum and Institute, Chiba (CBM-ZC). Terminology used follows McLaughlin (1974) with the exception of the fourth pereopods as defined by McLaughlin (1997), and gill structure as defined by McLaughlin & de Saint Laurent (1998). Abbreviations used are; coll., collector; and SL, shield length, measured from the tip of the rostral lobe to the posterior margin of the shield.

Pseudopaguristes bollandi, new species
Figs. 1–8

Material examined.—Holotype: male, SL = 3.2 mm, 69 m, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow, 14 Aug 2000, coll. R. F. Bolland, CBM-ZC 6442.

Description.—Eight functional pairs of weakly quadriserial, phyllobranchiate gills (Fig. 1A, B). Shield (Fig. 1C) 1.2 times longer than broad; anterior margin between rostrum and lateral projections concave; lateral projections (Fig. 1D) triangular, right with small, submarginal, corneous spine, left unarmed; anterolateral angles (Fig. 1E) each with strong corneous spine (not visible

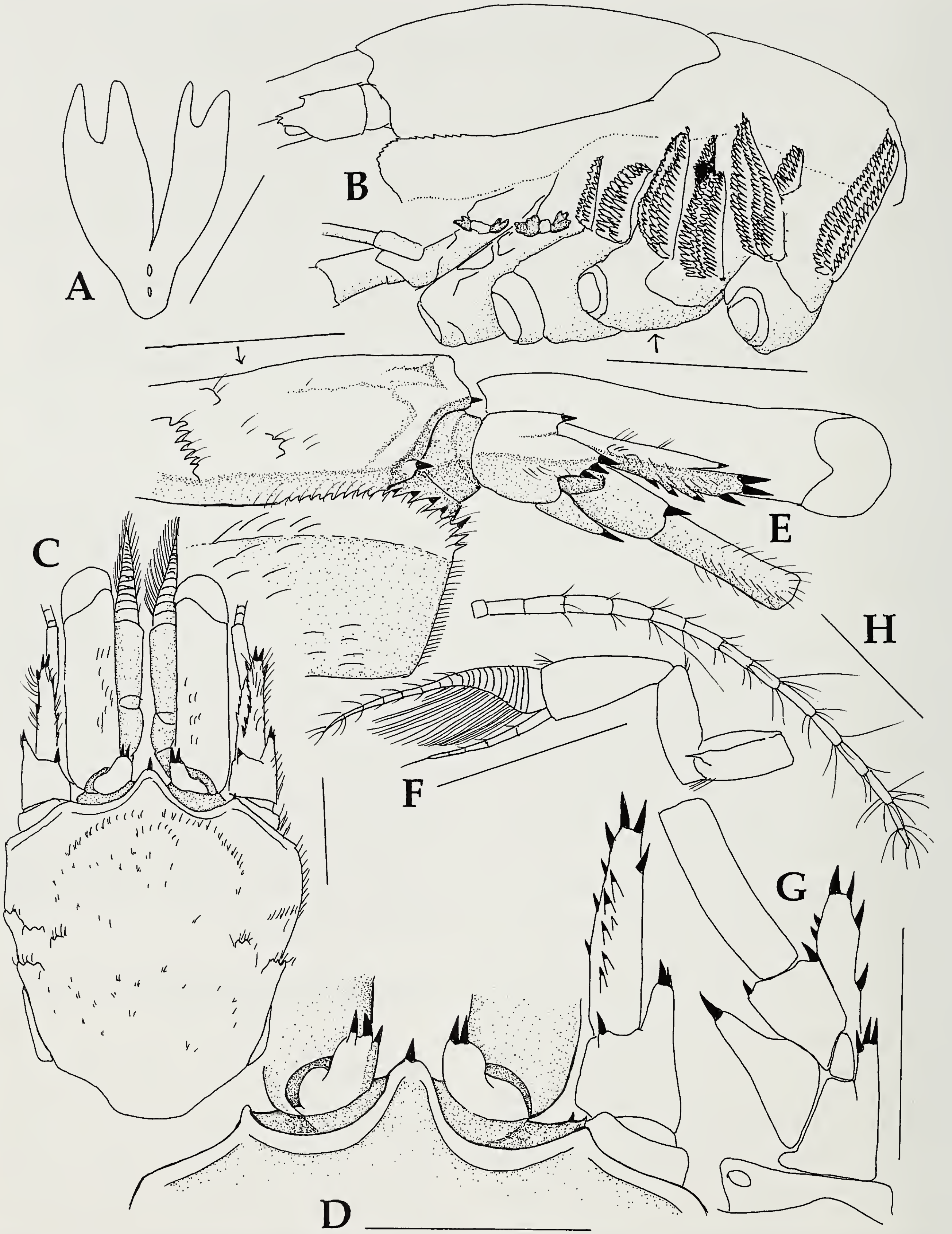

Fig. 1. *Pseudopaguristes bollandi,* new species, holotype male (CBM-ZC 6442), SL = 3.2 mm, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow. A, arthrobranch gill lamella; B, position and shape of gills; C, shield and cephalic appendages; D, ocular acicles and anterior portion of shield; E, right lateral view of ocular peduncle, antenna and anterior portions of branchiostegite and shield; F, left antennule, lateral view; G, left antenna, lateral view; H, antennal flagellum. Scales equal 0.33 mm (A) and 1 mm (B–H).

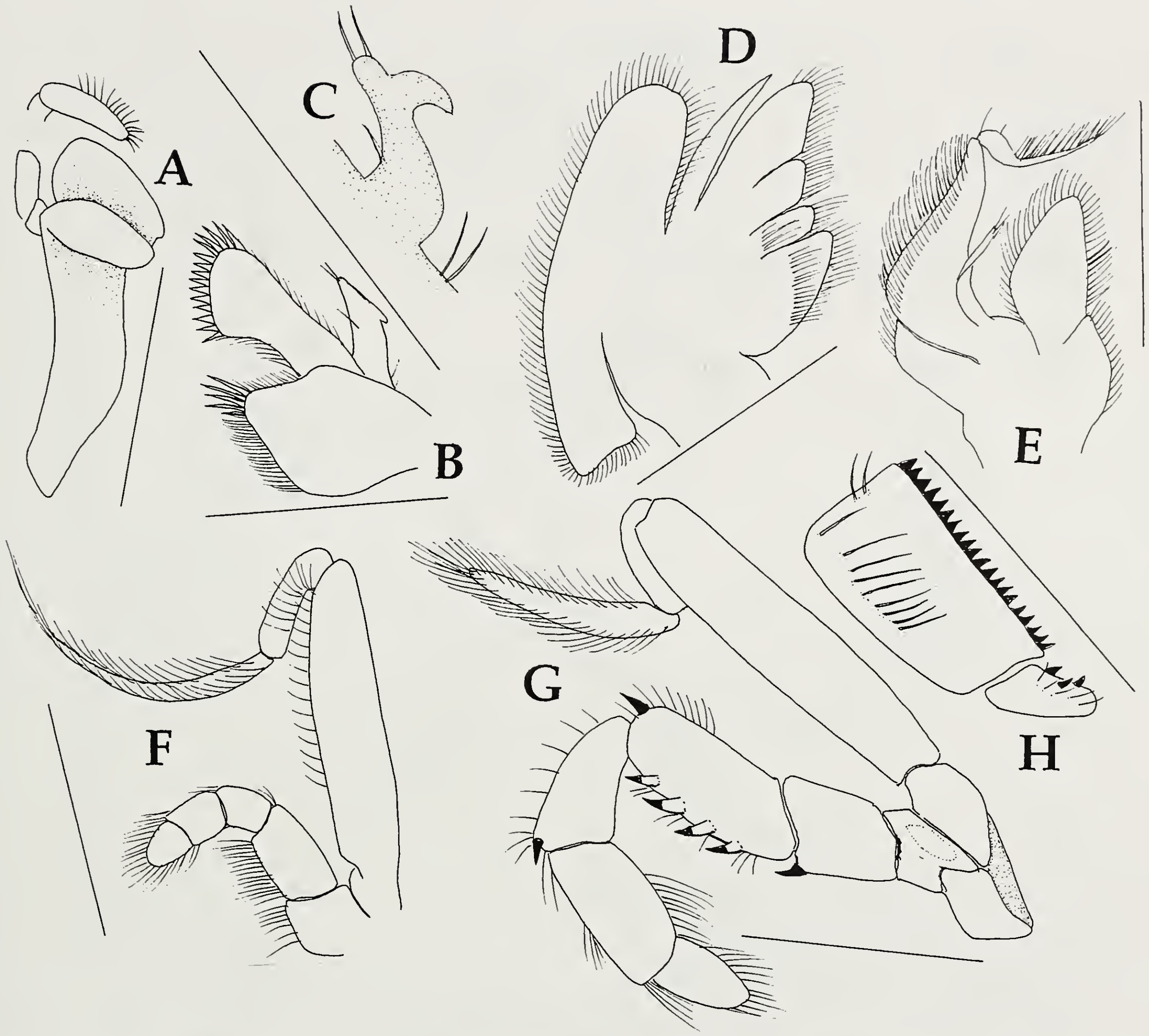

Fig. 2. *Pseudopaguristes bollandi,* new species, holotype male (CBM-ZC 6442), SL = 3.2 mm, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow. Left mouthparts: A, mandible, external; B, maxillule, external; C, same, endopod; D, maxilla, internal; E, first maxilliped, internal; F, second maxilliped, external; G, third maxilliped, external; H, ischium and basis of same, internal. Scales equal 1 mm.

in dorsal view); lateral margins straight; posterior margin truncate; dorsal surface slightly convex, with scattered tufts of short setae and 1 or 2 short ridges laterally. Rostrum (Fig. 1D) prominent, triangular, produced beyond bases of ocular acicles, with terminal corneous spine. Accessory portions of shield (Fig. 1C) small, well calcified, unarmed. Branchiostegites (Fig. 1E) partially calcified anterodorsally, with row of acute, slender spines, several corneous-tipped, on dorsodistal and anterodorsal margins.

Ocular peduncles (Fig. 1C) moderately short, 0.6 length of shield. Corneas (Fig. 1C, E) very slightly dilated. Ocular acicles (Fig. 1D) with 2 (right) or 3 (left) strong corneous spines on distal margin; separated basally by more than breadth of rostrum.

Antennular peduncles (Fig. 1C, F) stout; when fully extended, distal margins of ultimate segments very slightly exceeding distal margins of corneas; ultimate and penultimate segments each with tuft of setae dorsodistally; basal segment with acute spine laterally.

Antennal peduncles (Fig. 1C–E, G) moderately long, when fully extended, reaching bases of corneas; fifth segment with row of setae dorsally and laterally; fourth segment

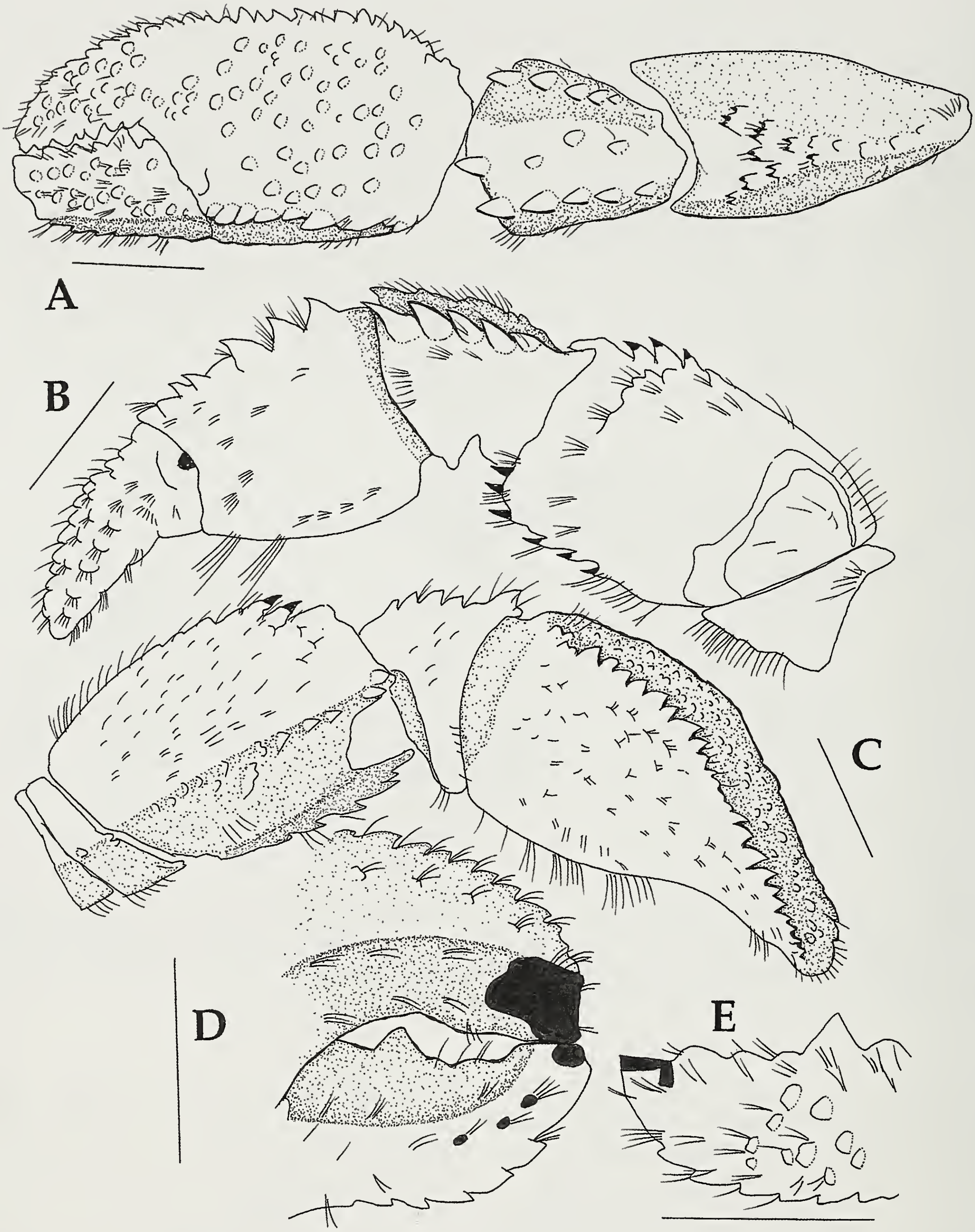

Fig. 3. *Pseudopaguristes bollandi,* new species, holotype male (CBM-ZC 6442), SL = 3.2 mm, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow. Right cheliped: A, dorsal; B, mesial; C, lateral; D, dactyl and fixed finger, ventral; E, fixed finger, dorsal. Scales equal 1 mm.

with strong corneous spine at dorsodistal margin and another corneous spine at ventrodistal margin; third segment with prominent corneous spine at ventrodistal margin; second segment with dorsolateral distal angle produced, bearing 3 strong corneous spines, dorsomesial distal angle with acute corneous spine; first segment unarmed. Antennal acicles moderately long, straight; laterally compressed; dorsomesial and ventro-

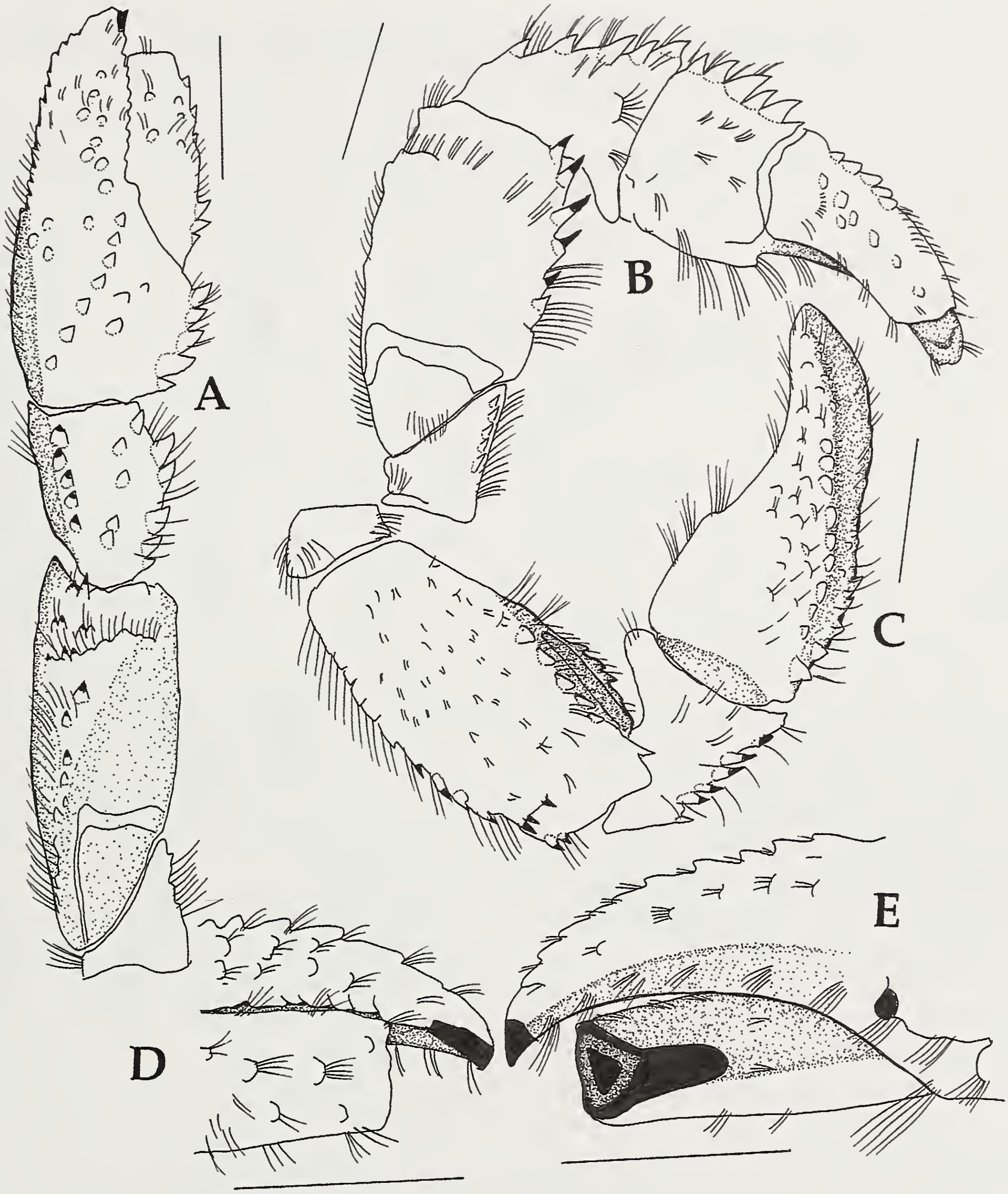

Fig. 4. *Pseudopaguristes bollandi,* new species, holotype male (CBM-ZC 6442), SL = 3.2 mm, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow. Left cheliped: A, dorsal; B, mesial; C, lateral; D, anterior portions of dactyl (tip broken) and fixed finger, dorsal; E, same, ventral. Scales equal 1 mm.

mesial margins each with row of corneous-tipped slender spines; distal margins each with 3 strong corneous spines; lateral margins each with strong, subdistal corneous spine. Antennal flagella (Fig. 1H) consisting of about 15 articles, each article with several setae of various lengths.

Mandible (Fig. 2A) without distinguishing characters. Maxillule (Fig. 2B, C) with external lobe of endopod recurved, internal lobe with 2 bristles. Maxilla (Fig. 2D) with moderately narrow scaphognathite. First maxilliped (Fig. 2E) with well developed, setose epipod. Second maxilliped (Fig. 2F) without distinguishing characters. Third maxilliped (Figs. 2G, H, 7A) with dorsodistal margin of carpus bearing acute corneous spine; merus with ventral margin bearing row of slender corneous-tipped spines, and dorsodistal margin bearing acute corneous spine; ischium with well-developed crista dentata, no accessory tooth, strong corneous spine at ventrodistal margin; basis with few corneous spines.

Right cheliped (Fig. 3) larger than left. Dactyl 0.4 length of palm; terminal margin slightly convex, with very broad corneous claw (Fig. 3D); dorsal face flat, with scattered tubercles; cutting edge with 1 strong and 4 broad, low calcareous teeth. Fixed finger terminating in small corneous-claw (Fig. 3E); ventral face with row of 3 corneous tubercles (Fig. 3D); dorsal face flat, with scattered tubercles; cutting edge with 7 strong calcareous teeth. Palm 1.5 length of carpus; dorsal surface flat, with scattered tubercles; dorsomesial margin with row of very strong spines; dorsolateral margin with row of spines. Carpus 0.6 length of merus; dorsal face with scattered spines, dorsolateral and dorsomesial margins each with row of very strong spines. Merus with numerous spines, some corneous-tipped, on distal half of dorsal face; ventromesial margin with strong corneous or corneous-tipped spines; ventrolateral margin with row of spines or tubercles. Coxa (Fig. 7B) with strong corneous spine ventromesially.

Left cheliped (Fig. 4) with armature much weaker than right. Dactyl (terminal portion broken off) (Fig. 4D, E) with dorsal face flat, bearing few tubercles; cutting edge generally straight. Fixed finger terminating in broad corneous claw (Fig. 4D, E); dorsal face flat, with few tubercles; cutting edge with small, blunt calcareous teeth. Palm 1.3 length of carpus; dorsal surface flat, with scattered tubercles, dorsomesial margin with row of strong spines, dorsolateral margin with row of spines, some corneous-tipped. Carpus 0.5 length of merus; dorsal face with scattered spines, several corneous-tipped; ventrolateral and ventromesial margins each with row of spines. Merus with numerous spines, most corneous-tipped on dorsal face; ventromesial margin with row of spines, subdistal spine sharp; ventrolateral margin with row of spines. Ischium (Fig. 4B) with row of small spines and sparse setae on ventromesial margin. Coxa (Fig. 7B) with strong corneous spine ventromesially.

Second pereopods (Fig. 5A–C) similar from left to right. Dactyls 1.1 length of propodi, each terminating in strong corneous claw; mesial faces each with row of corneous or corneous-tipped spines dorsally (Fig. 5B); ventral margins each with row of 9 (left) or 10 (right) strong corneous spines. Propodi 1.8 length of carpi, each with row of 10 (left) or 12 (right) strong corneous spines on dorsal margin and 1 (right) or 2 (left) acute corneous spines at ventromesial distal margin (Fig. 5B). Carpi 0.6 length of meri, each with strong, corneous-tipped, slender spine at dorsodistal angle and row of 5 (left) or 4 (right) slender, corneous-tipped spines on dorsal face mesially (Fig. 5C). Meri with ventral margins each bearing acute subdistal spine and row of slender corneous-tipped spines; dorsal margins each with proximal row of corneous-tipped spines. Ischia each with few, slender corneous-tipped spines dorsally. Coxae (Fig. 7B) unarmed.

Third pereopods (Fig. 6A, B) similar from left to right. Dactyls 1.1 length of propodi, each terminating in strong corneous claw; mesial faces each with row of small corneous spines ventrally (Fig. 6B); dorsal margins unarmed; ventral margins each with row of 10 (left) or 11 (right) strong corneous spines. Propodi 1.6–1.7 length of carpi; dorsal faces unarmed; acute corneous spine at each ventromesial distal angle (Fig. 6B). Carpi 0.6 length of meri, each with strong, corneous-tipped slender spine at dorsodistal angle; other portions unarmed. Meri with ventral margins each bearing small, subdistal corneous spine; dorsal margins each with row of corneous spines. Ischia each with few slender, corneous-tipped spines dorsally and acute corneous spine ventrally. Coxae (Fig. 7B) unarmed.

Sternite of third pereopods (Fig. 7B) with anterior lobe rectangular, unarmed.

Fourth pereopod (Fig. 6C, D) subchelate. Dactyl terminating in strong corneous claw;

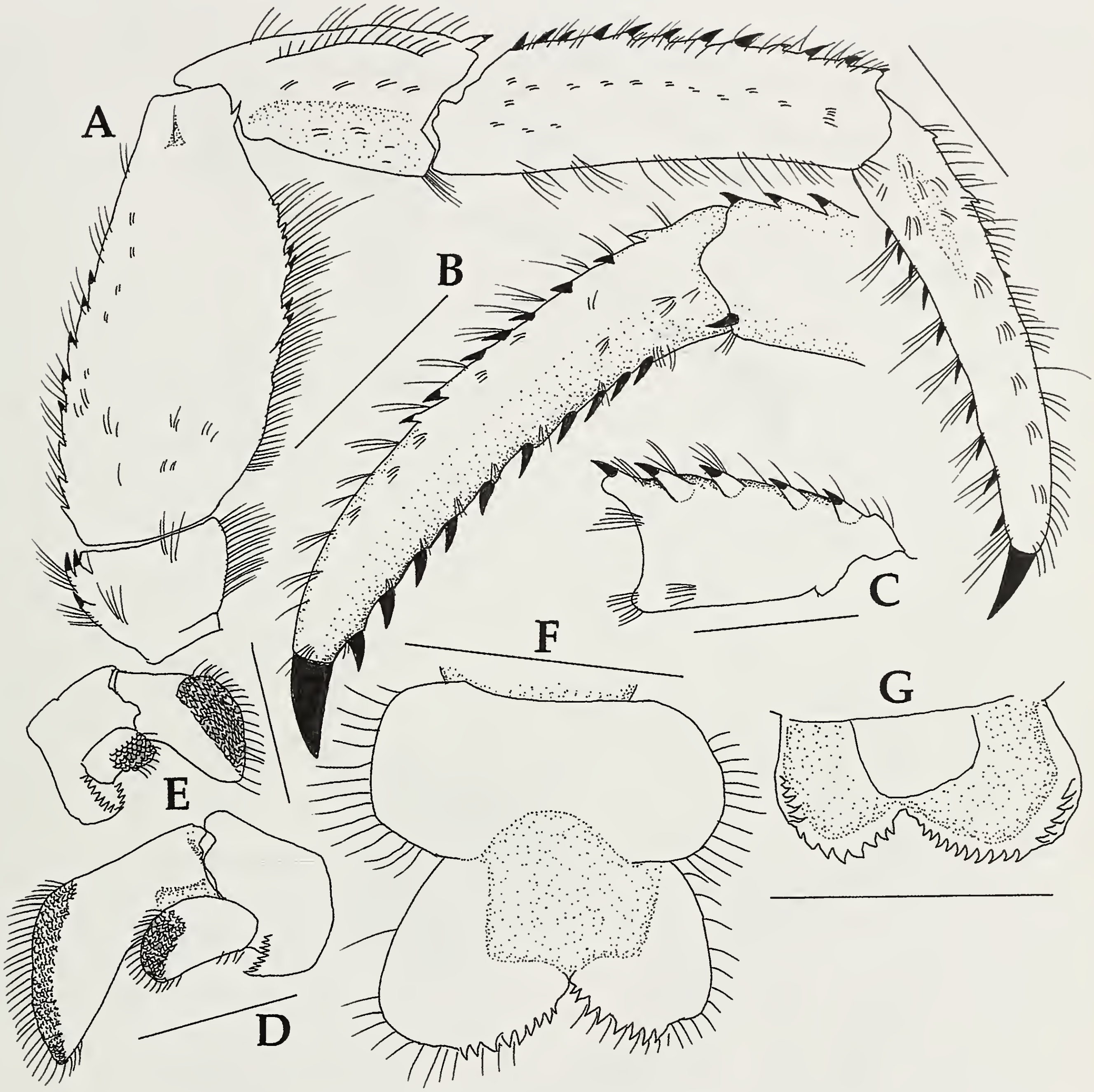

Fig. 5. *Pseudopaguristes bollandi,* new species, holotype male (CBM-ZC 6442), SL = 3.2 mm, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow. A, second right pereopod, lateral; B, dactyl and distal portion of propodus of same, mesial; C, carpus of same, mesial; D, left uropod; E, right uropod; F, telson, dorsal; G, posterior lobes of same, ventral. Scales equal 1 mm.

no preungual process; ventral face with 2 corneous spines slightly laterally. Propodal rasp with 2 rows of corneous scales. Carpus with large dorsodistal spine directed slightly mesially; ventral face with long, simple setae and clump of long capsulate setae (Fig. 6D).

Fifth pereopod (Fig. 6E) chelate; dactyl and propodus with well-developed rasps; carpus with dorsodistal spine.

Male first pleopods (Fig. 7B–D) paired, modified as gonopods; basal lobe bearing few setae at superior mesial angle; inferior lamella with distal margin bearing row of short, hooked spines, and lateral margin with row of setae; internal lobe with row of setae on mesial margin; external lobe distinctly exceeding inferior lamella in distal extension. Second pleopods (Fig. 7B, E, F) paired, modified as gonopods; basal seg-

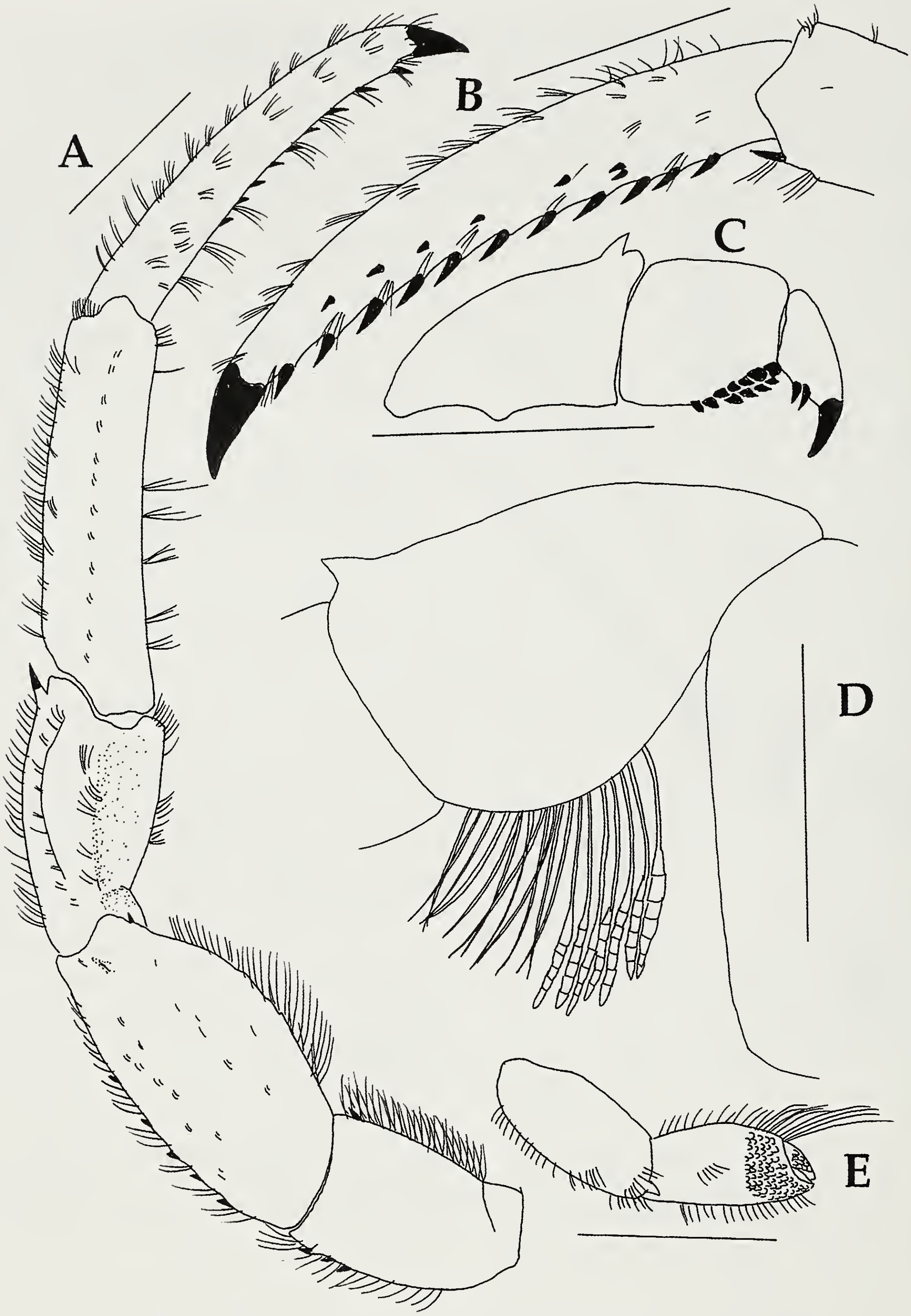

Fig. 6. *Pseudopaguristes bollandi,* new species, holotype male (CBM-ZC 6442), SL = 3.2 mm, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow. A, third right pereopod, B, dactyl and distal portion of propodus of same, mesial; C, fourth right pereopod, lateral; D, carpus and ventral setae of same, mesial; E, fifth right pereopod. Scales equal 1 mm (A–C, E) and 0.5 mm (D).

ment naked; endopod with several long setae; appendix masculina strongly twisted; lateral and distal margins and inferior face with moderately long setae. Third (Fig. 7G) to fifth left pleopods each with exopod well developed, endopod reduced.

Uropods (Fig. 5D, E) asymmetrical, left larger than right; rasps of exopods and en-

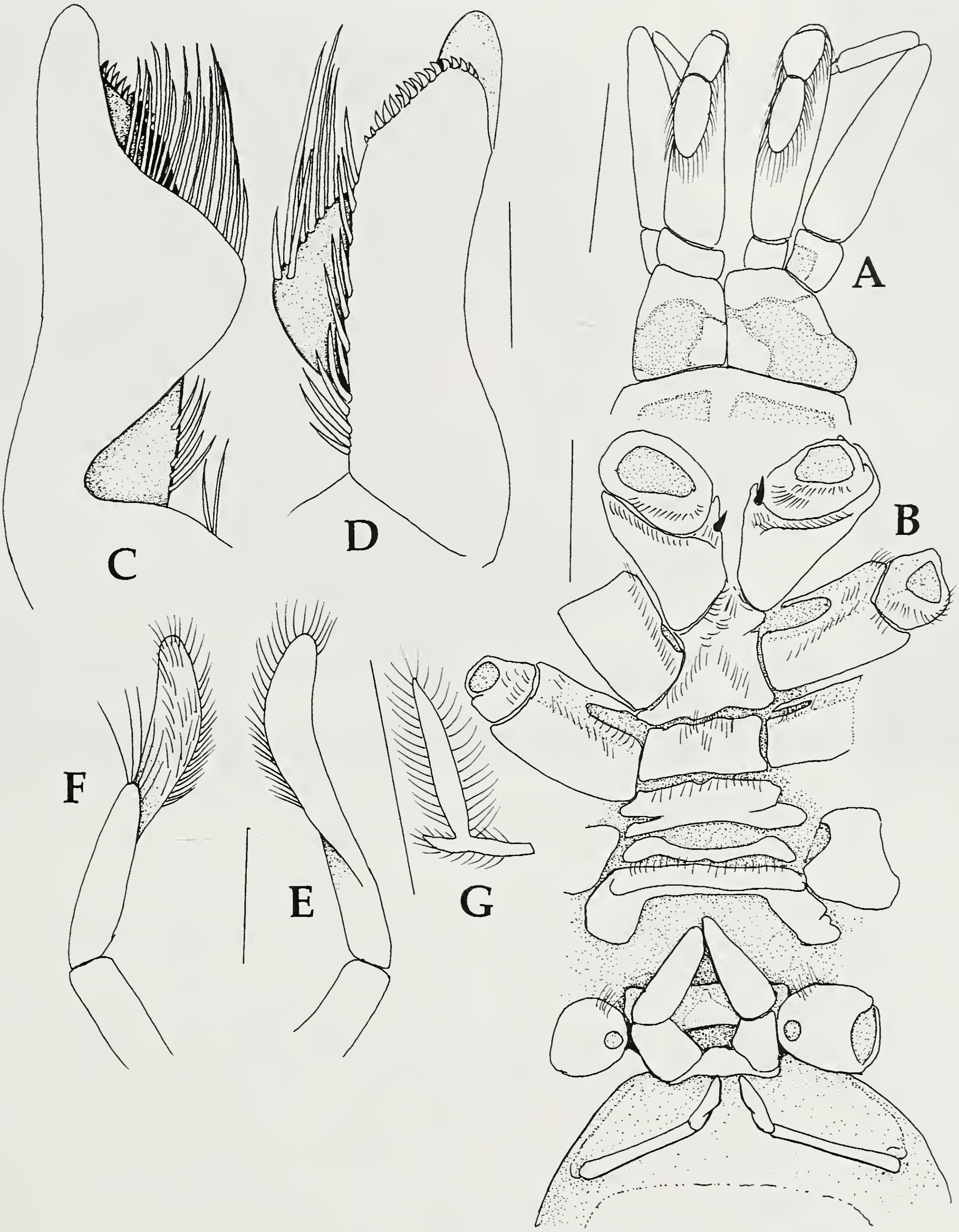

Fig. 7. *Pseudopaguristes bollandi,* new species, holotype male (CBM-ZC 6442), SL = 3.2 mm, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow. A, third maxillipeds, ventral; B, ventral view of cephalothorax and anterior portion of abdomen; C, first pleopod, external; D, first pleopod, internal; E, second pleopod, external; F, second pleopod, internal; G, third pleopod. Scales equal 1 mm (A, B, G) and 0.2 mm (C–F).

dopods well developed; protopods each with row of spines posteriorly.

Telson (Fig. 5F, G) with lateral constrictions; anterior portion unarmed; posterior lobes separated by moderately deep median cleft, left lobe larger than right, terminal margins fringed with spines.

Color in life.—Shield white; antennular flagella yellow; antennal flagella with alternative red and white bands; antennular, oc-

Fig. 8. *Pseudopaguristes bollandi,* new species: holotype male (CBM-ZC 6442), SL = 3.2 mm, Seragaki, Onna-son, Kunigami-gun, Okinawa-hontow. Photo by Robert F. Bolland.

ular and antennal peduncles red; corneas yellow; second and third maxillipeds, chelipeds and second and third pereopods uniform red (Fig. 8).

Etymology.—This species is named for Professor Robert F. Bolland who collected the specimen.

Distribution.—Known only from the type locality.

Remarks.—Morphologically, *P. bollandi* new species is quite similar to *P. janetkae* but minor differences are seen between them. Although the general shapes of the shield and cephalic appendages are quite comparable between *P. janetkae* and *P. bollandi,* the majority of the spines of *P. janetkae* lack the corneous tips found in *P. bollandi.* That the dorsal surfaces of the chelae are provided with spines in *P. janetkae* but only tubercles in *P. bollandi* may be diagnostic, or may be attributable to intraspecific variations, such as observed in many hermit crab species. However, with so few specimens known it is not possible to evaluate variability. The minor differences in the armature of the ambulatory legs and telson seen in the males of these species may also reflect simple variability. One distinct difference between these two species is seen in the dactyls of the fourth pereopods. In *P. janetkae* a very prominent preungual process is developed at the base of the claw, giving the dactyl a quasi-chelate appearance. No preungual process is present in the holotype and only known specimen of *P. bollandi.*

Despite their general similarities in morphology, the two species are readily distinguished in life by differences in coloration of the ambulatory legs. These appendages are uniformly red in *P. bollandi,* whereas the carpi, propodi and dactyls of *P. janetkae* are light cream, tinged with yellow. Differences in color of the ocular and antennal peduncles also have been observed. The peduncles of both are similarly uniform red in *P. bollandi,* while those of *P. janetkae* are cranberry-red proximally, but yellow-orange in the distal 0.7 of the ocular peduncles and yellow in the distal three segments of the antennal peduncles.

The morphology of the female of *P. bollandi* is unknown.

Acknowledgments

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Literature Cited

Dana, J. D. 1851. Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe republicae foederatae duce, lexit et descript.—(Preprint from) Proceedings of the Academy of Natural Sciences, Philadelphia 5: 267–272.

McLaughlin, P. A. 1974. The hermit crabs (Crustacea, Decapoda, Paguridae) of northwestern North America.—Zoologische Verhandelingen 130:1–396.

McLaughlin, P. A. 1997. Crustacea Decapoda: hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. *In* A. Crosnier and P. Bouchet, eds., Résultats des Campagnes MUSORSTOM, 16.—Mémoires du Muséum national d'Histoire naturelle, 172:433–572.

McLaughlin, P. A. 2002. *Pseudopaguristes,* a new and aberrant genus of hermit crabs (Anomura: Paguridea: Diogenidae).—Micronesica 34(2):185–199.

McLaughlin, P. A., & M. de Saint Laurent. 1998. A new genus for four species of hermit crabs formerly assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae).—Proceedings of the Biological Society of Washington 111:158–187.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(2):464–486. 2003.

Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with descriptions of new genera and species. Addendum and taxonomic summary

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Abstract.—The discovery of two new species, *Enallopagurus provenzanoi,* and *Enallopaguropsis williamsi,* has required an addendum and concluding part to the revisionary study of the "*Pylopagurus-Tomopagurus*" group of genera. The diagnoses of *Enallopagurus* McLaughlin and *Enallopaguropsis* McLaughlin, are emended, and a corrected key to the genera is provided. The discovery of additional specimens of *Phimochirus randalli* (Provenzano) from the Gulf of Mexico has provided supplemental information on the morphology, color, and distribution of this uncommon species; it is rediagnosed and illustrated. Also provided is a summary of the original taxonomic assignments in part 1 (published in 1981) of this revisionary study, and the subsequent changes, corrections, deletions, and additions that have occurred since then. An updated list of the 13 genera, two subgenera, and 64 valid species currently recognized in the "*Pylopagurus-Tomopagurus*" group, is presented.

McLaughlin (1981a) proposed the new genera *Enallopagurus* McLaughlin, 1981a and *Enallopaguropsis* McLaughlin, 1981a, for five relatively uncommon eastern Pacific hermit crab species that had been included by earlier authors in the genus *Pylopagurus* A. Milne-Edwards & Bouvier, 1891. To *Enallopagurus,* McLaughlin (1981a) assigned *Pylopagurus affinis* Faxon, 1893, *P. coronatus* (Benedict, 1892), and *P. spinicarpus* Glassell, 1938; *Enallopaguropsis* included *P. guatemoci* Glassell, 1937, and *Pylopagurus hancocki* Walton, 1954. One of the primary characters that McLaughlin (1981a) used to differentiate between *Enallopagurus* and *Enallopaguropsis* was the rows of scales on the propodal rasp of the fourth pereopod. In a subsequent, more detailed account of these two genera, McLaughlin (1982) placed *Enallopaguropsis hancocki* in synonymy with *E. guatemoci* and added the new species *E. janetae* McLaughlin, 1982. In the present addendum and concluding part of the revision of the "*Pylopagurus-Tomopagurus*" group of genera, two new species, one each of *Enallopagurus,* and *Enallopaguropsis,* are described.

Recent sampling off the Louisiana coast in the northern Gulf of Mexico has yielded a number of additional specimens of *Phimochirus randalli* (Provenzano, 1961), a species discussed by McLaughlin (1981b) and at the time known only from the Bahamas Islands and Caribbean region. Examination of these Gulf of Mexico specimens revealed a number of morphological details that complement previous definitions of *P. randalli.* Furthermore, Provenzano's (1961:161) color description was incomplete as it was based on faded, preserved specimens, whereas for this study live specimens from the Gulf of Mexico were available and photographed (D. L. Felder, pers. comm.). *Phimochirus randalli* is herein rediagnosed, and illustrated.

Since the publication of part 1 (McLaughlin 1981a) of the six-part revisionary study of the "*Pylopagurus-Tomopagurus*" group of genera, several new species have been added that have necessitated emendations of generic diagnoses, and two new genera have been erected. Some of the taxonomic assignments made in part 1 have been changed in light of new evidence gleaned from direct examination of type materials not initially available. In some cases, new morphological discoveries, such as the existence of short sexual tubes in some species of *Pylopagurus* sensu stricto (see McLaughlin & Lemaitre 2001), or the existence of short protrusions of the vas deferentia in the form of tubular papillae in *Agaricochirus* McLaughlin, 1981a, *Enallopagurus,* and *Enallopaguropsis* (see McLaughlin 2003, this study), have required adjustments to our concept of these genera. In the new species of the latter two genera herein described, the morphology of the terminal margin of the telson has been found to deviate from the original generic diagnoses. As this margin shape was used as a character in the updated generic key provided by McLaughlin & Lemaitre (2001:480), that key now requires corrections. Also, several taxa have been synonymized since part 1 was published, whereas *Pylopagurus liochele* Barnard, 1947, a taxon tentatively assigned in parts 1 and 2 (McLaughlin 1981a, 1981b) to *Phimochirus* McLaughlin, 1981a, was transferred by McLaughlin (1988) to *Pagurus* Fabricius, 1775, a genus not considered part of the "*Pylopagurus-Tomopagurus*" group. McLaughlin's (1981a) genus *Australeremus* was reduced by de Saint Laurent & McLaughlin (2000) to a subgenus of *Lophopagurus* McLaughlin, 1981a. Thus, it was felt useful to have in a single convenient publication, a summary of the taxonomic assignments, changes, corrections, and additions that have occurred during the 21+ years that have elapsed since the appearance of part 1 of the revision of this group. There are currently 13 genera, two subgenera, and 64 valid species known in this group (see Table 1).

Materials used in this study are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), and University of Louisiana at Lafayette (ULLZ). The specimens of the new species of *Enallopagurus* and *Enallopaguropsis* were collected by Dr. Anthony J. Provenzano, Jr. aboard the R/V *John Elliott Pillsbury,* of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida. The new material of *Phimochirus randalli* was collected by Dr. Darryl L. Felder aboard the R/V *Pelican,* of the Louisiana Universities Marine Consortium, Cocodrie. The interpretation of the ocular acicle is used in accordance with Forest et al. (2000), rather than that of Boyko & Harvey (1999). A single measurement, shield length (sl), measured from the tip of the rostrum to the midpoint of the posterior margin of the shield provides an indication of animal size. Other abbreviations used are: ovig, ovigerous female; sta, station.

Enallopagurus McLaughlin, 1981a

Pylopagurus: Walton, 1954:140 (in part).—Scanland & Hopkins, 1969:257 (in part) [Not *Pylopagurus* A. Milne-Edwards & Bouvier, 1891].

Enallopagurus McLaughlin, 1981a:7; 1982: 843; 2003:122.

Emended diagnosis.—Eleven pairs of biserial gills. Ocular acicle triangular or subovate, usually with strong submarginal spine. Sternite of third maxillipeds with spine on either side of midline. Third maxillipeds each with well-developed crista dentata, 1 accessory tooth; merus with or without dorsodistal spine. Maxillule with internal lobe moderately well produced, with 1 terminal bristle; external lobe weakly produced.

Table 1.—List of valid names of ''*Pylopagurus-Tomopagurus*'' group of taxa.

Pylopagurus A. Mine-Edwards & Bouvier, 1891 sensu stricto

P. discoidalis (A. Milne-Edwards, 1880)
P. holmesi Schmitt, 1921
P. pattiae Lemaitre & Campos, 1993
P. macgeorgei McLaughlin & Lemaitre, 2001
P. gorei McLaughlin & Lemaitre, 2001

Lophopagurus (*Lophopagurus*) McLaughlin, 1981a

L. (*L.*) *foresti* McLaughlin & Gunn, 1992
L. (*L.*) *lacertosus* (Henderson, 1888)
L. (*L.*) *nanus* (Henderson, 1888)
L. (*L.*) *nodulosus* McLaughlin & Gunn, 1992
L. (*L.*) *pumilus* de Saint Laurent & McLaughlin (2000)
L. (*L.*) *thompsoni* (Filhol, 1885)

Lophopagurus (*Australeremus*) McLaughlin, 1981a

L. (*A.*) *cookii* (Filhol, 1883)
L. (*A.*) *eltaninae* McLaughlin & Gunn, 1992
L. (*A.*) *cristatus* (H. Milne Edwards, 1836)
L. (*A.*) *kirkii* (Filhol, 1883)
L. (*A.*) *laurentae* (McLaughlin & Gunn, 1992)
L. (*A.*) *stewarti* (Filhol, 1883)
L. (*A.*) *triserratus* (Ortmann, 1892)

Rhodochirus McLaughlin, 1981a

R. rosaceus (A. Milne-Edwards & Bouvier, 1893)
R. hirtimanus (Faxon, 1893)

Phimochirus McLaughlin, 1981a

P. operculatus (Stimpson, 1859)
P. californiensis (Benedict, 1892)
P. venustus (Bouvier, 1898)
P. roseus (Benedict, 1892)
P. randalli (Provenzano, 1961)
P. holthuisi (Provenzano, 1961)
P. occlusus (Henderson, 1888)
P. leurocarpus McLaughlin, 1981b

Haigia McLaughlin, 1981a

H. diegensis (Scanland & Hopkins, 1969)

Agaricochirus McLaughlin, 1981a

A. boletifer (A. Milne-Edwards & Bouvier, 1893)
A. alexandri (A. Milne-Edwards & Bouvier, 1893)
A. cavimanus (Chace, 1939)
A. erosus (A. Milne-Edwards, 1880)
A. gibbosimanus (A. Milne-Edwards, 1880)
A. hispidus (Benedict, 1892)
A. echinatus McLaughlin, 1982
A. acanthinus McLaughlin, 1982

Anisopagurus McLaughlin, 1981a

A. bartletti (A. Milne-Edwards, 1880)
A. pygmaeus (Bouvier, 1918)
A. vossi Lemaitre & McLaughlin, 1996
A. actinophorus Lemaitre & McLaughlin, 1996
A. hopkinsi Lemaitre & McLaughlin, 1996

Table 1.—Continued.

Manucomplanus McLaughlin, 1981a
M. cervicornis (Benedict, 1892)
M. spinulosus (Holthuis, 1959)
M. longimanus (Faxon, 1893)
M. varians (Benedict, 1892)
M. ungulatus (Studer, 1883)
Enallopagurus McLaughlin, 1981a
E. spinicarpus (Glassell, 1938)
E. affinis (Faxon, 1893)
E. coronatus (Benedict, 1892)
E. provenzanoi, new species
Enallopaguropsis McLaughlin, 1981a
E. guatemoci (Glassell, 1937)
E. janetae McLaughlin, 1982
E. williamsi, new species
Tomopagurus A. Milne-Edwards & Bouvier, 1893
T. rubropunctatus A. Milne-Edwards & Bouvier, 1893
T. cokeri (Hay, 1917)
T. maclaughlinae Haig, 1976
T. cubensis (Wass, 1963)
T. wassi McLaughlin, 1981a
T. purpuratus (Benedict, 1892)
T. merimaculosus (Glassell, 1937)
T. chacei (Wass, 1963)
Protoniopagurus Lemaitre & McLaughlin, 1996
P. bioperculatus Lemaitre & McLaughlin, 1996
Pylopaguridium McLaughlin & Lemaitre, 2001
P. markhami McLaughlin & Lemaitre, 2001

Right cheliped with subovate or subrectangular chela. Left cheliped with chela triangular in cross-section, but dorsal surface not elevated into prominent keel or crest. Dorsodistal spine of carpi of second and third pereopods lacking. Sternite of third pereopods with subcircular, subovate or subquadrate anterior lobe. Sternites of third to fifth pereopods often with capsulate setae. Fourth pereopod with propodal rasp consisting of single row of corneous scales; dactyl with small preungual process usually present.

Males with paired gonopores, no distinct sexual tubes but occasionally with vas deferens protruded to form short tubular papilla, usually on right; without paired pleopods, with 3 uniramous or weakly biramous left pleopods on somites 3–5. Females with paired gonopores, paired first pleopods modified as gonopods, 4 unpaired left pleopods, second to fourth with both rami well-developed, fifth usually uniramous.

Uropods symmetrical or asymmetrical. Telson without indication of division into anterior and posterior portions; terminal margin entire or with inconspicuous median indentation, unarmed.

Remarks.—Faxon (1893, 1895: pl. 12, fig. 2e) reported that his single male specimen of *Pylopagurus affinis* (= *Enallopagurus affinis*) had the vas deferentia extruded as "small threads" from both gonopores. McLaughlin (1982) reexamined Faxon's (1893) specimen and concluded that while there were slight protrusions, these were more probably an artifact of preservation rather than actual, very small sexual tubes. Since McLaughlin's (1982) study, our information on and understanding of sexual tubes in the Paguridae has increased substantially. Among the "*Pylopagurus-Tomopagurus*" group, species of *Enallopaguropsis* and *Agaricochirus* can also have the vas deferentia protruded as tubular papillae, albeit not as a distinct sexual tube. In other Paguridae, similar protrusions are known to occur in genera such as *Discorsopagurus* McLaughlin, 1974, *Paguritta* Melin, 1939, and *Pagurus* (see de Saint Laurent 1970, McLaughlin & Lemaitre 1993, McLaughlin 2003). However, as reported by McLaughlin & Lemaitre (2001), short but distinct sexual tubes are present in some species of *Pylopagurus* sensu stricto. Recently, McLaughlin & Jensen (1996) found a very small sexual tube developed on the right coxa of males of *Parapagurodes hartae* McLaughlin & Jensen, 1996, and Komai (1998) provisionally transferred two Japanese species formerly assigned to *Pagurus* (*P. gracilipes* Stimpson, 1858 and *P. nipponensis* Yokoya, 1933), to *Parapagurodes* McLaughlin & Haig, 1973, because of the observed small sexual tubes in males of both species.

McLaughlin (1981a, 1982) included Faxon's (1893) *Pylopagurus affinis* in *Enallopagurus,* despite the fact that Faxon described the propodal rasp of the fourth pereopod as "multiserial". The type specimen has been reexamined, and Faxon's description and subsequent illustration (Faxon 1895: pl 12, fig. 2d) found to be in error; the propodal rasp of the fourth pereopod actually has a single row of scales. This species is retained in *Enallopagurus,* although this generic assignment is still provisional given that *E. affinis* is known only from the male holotype.

Until the discovery of the new species of *Enallopagurus* described herein, the genus had been considered exclusively an eastern Pacific taxon. Although the right cheliped of this new species lacks the operculate-like conformation seen in the other three species assigned to the genus, the unarmed carpi of the second and third pereopods, the single row of scales on the propodal rasp of the fourth pereopod, and the presence in females of paired first gonopods, support its placement in the genus. The terminal margin of the telson in this new species of *Enallopagurus* has a minute median indentation and is not clearly entire as described in the original generic diagnosis (McLaughlin 1981a, 1982); thus, the need for the emendation. An updated key to the species of *Enallopagurus* is provided following the description of this new species.

Enallopagurus provenzanoi, new species
Figs. 1, 2

Holotype.—Ovig. ♀ (sl = 2.40 mm), R/V *John Elliott Pillsbury,* sta 581, 21°05′N, 86°23′W, Arrowsmith Bank, 146–265 m, 22 May 1967, USNM 1007525.

Paratype.—1 ♂ in poor condition (sl = 1.80 mm), same data as holotype, USNM 1007526.

Description.—Shield (Fig. 1a) longer than broad; anterior margin between rostrum and lateral projections slightly concave; anterolateral margins sloping; posterior margin truncate, dorsal surface glabrous. Rostrum triangular, terminating acutely. Lateral projections rounded, unarmed.

Ocular peduncle approximately 0.65 length of shield, moderately stout, with cornea slightly dilated; ocular acicles subtriangular, each terminating subacutely, with moderately well-developed submarginal spine (not always visible in dorsal view); separated basally by approximately basal width of 1 acicle.

Antennular peduncle overreaching ocular peduncle by 0.35–0.50 length of ultimate segment; ultimate and penultimate segments unarmed; basal segment with small spine on lateral face.

Antennal peduncle slightly shorter to equaling length of ocular peduncle. Fifth and fourth segments with scattered short se-

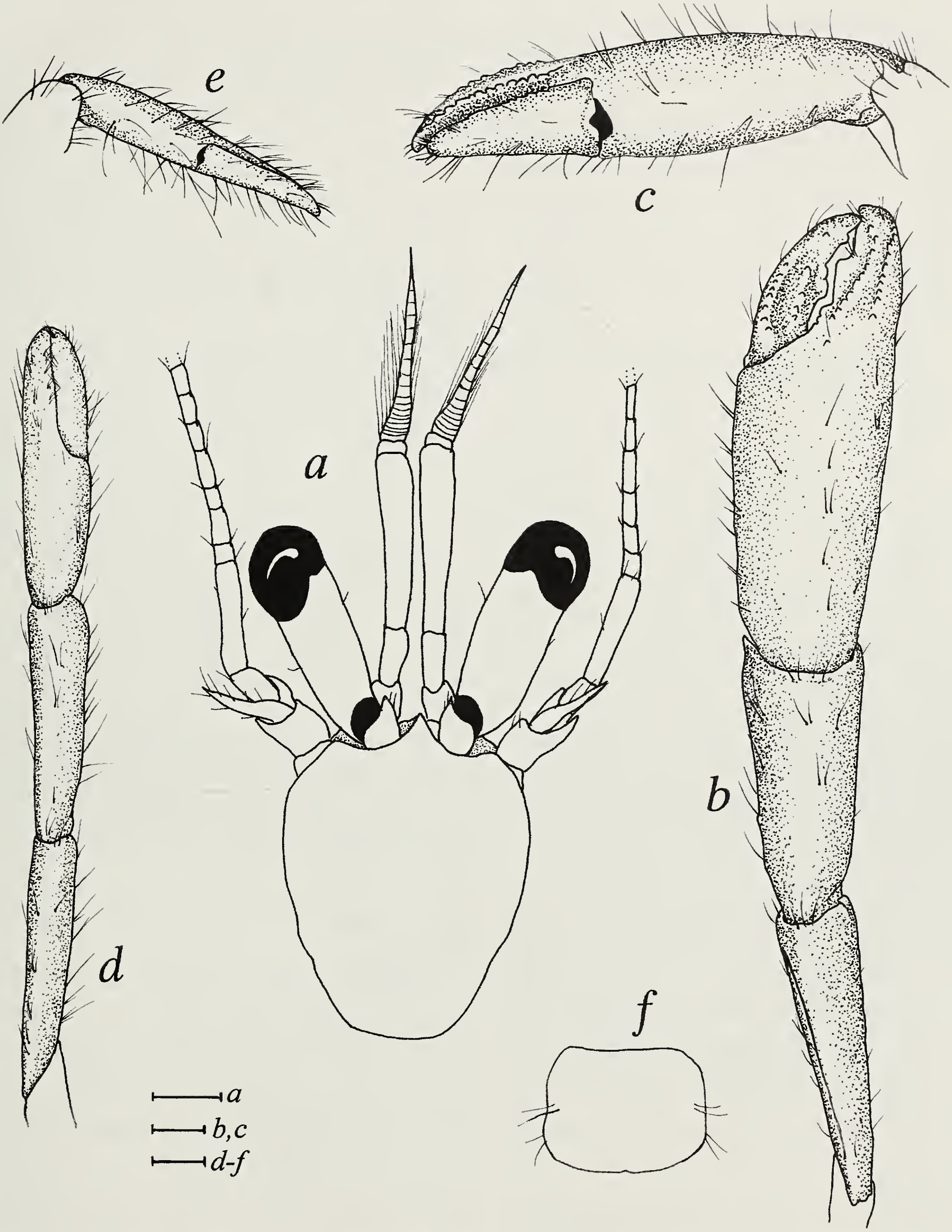

Fig. 1.—*Enallopagurus provenzanoi,* new species, holotype ovig ♀ (sl = 2.40 mm), northwestern Caribbean, R/V *John Elliott Pillsbury,* sta 581, USNM 1007525. a, shield and cephalic appendages, dorsal; b, right cheliped, dorsal; c, chela of same, mesial; d, left cheliped, dorsal; e, chela of same, mesial; f, telson, dorsal. Scales equal 0.50 mm (a), 1.00 mm (b, c), and 0.5 mm (d–f).

tae. Third segment with acute spine at ventrodistal angle. Second segment with dorsolateral distal angle produced, terminating in small spine; dorsomesial distal angle with small spine. First segment produced ventrally and with acute spine on ventrolateral margin. Antennal acicle moderately short, reaching only to distal margin of fourth peduncular segment. Flagellum long, with 1 or 2 short setae every several articles.

Sternite of third maxillipeds with strong spine on either side of midline.

Right cheliped (Figs. 1b, c) elongate, slender, overreaching left by length of dactyl. Dactyl approximately 0.75 length of palm, with row of small spines on proximal half of dorsomesial margin, separated from similar short row near cutting edge by shallow sulcus; cutting edge with 1 prominent double tooth in proximal half and single prominent tooth in distal half; mesial and ventral surfaces with few short setae. Palm exceeding carpus by approximately 0.20 own length; dorsal surface convex, unarmed, but with sparse tufts of setae, dorsomesial and dorsolateral margins not delimited; mesial, lateral and ventral surfaces also with sparse tufts of setae; fixed finger with row of low spines on dorsolateral margin and second row adjacent to cutting edge; latter with 2 or 3 small and 1 large broad calcareous teeth. Carpus slightly shorter than merus, subtriangular; dorsomesial and dorsolateral margins not delimited, surfaces unarmed but with scattered setae, 1 prominent spine on distomesial margin. Merus triangular, margins and surfaces unarmed, but with scattered short setae. Ischium unarmed.

Left cheliped (Figs. 1d, e) with dactyl approximately as long as palm; surfaces of dactyl, fixed finger and palm all unarmed but with sparse tufts of setae. Carpus only slightly shorter than merus; surfaces of both segments and ischium unarmed but with scattered short to moderately long setae.

Second and third pereopods (Figs. 2a, b) long and slender. Dactyls longer than propodi; dorsal surfaces with few short setae; ventral margins each with row of 10–12 corneous spines and few short setae. Propodi approximately twice as long as carpi; dorsal surfaces with few setae; ventral margins each with 3 or 4 corneous spines, longest on third pereopod. Carpi less than half length of meri, unarmed, but with scattered setae dorsally and ventrally. Meri and ischia unarmed, but with dorsal and ventral sparse tufts of setae.

Fourth pereopod (Fig. 2d) with small preungual process on dactyl.

Sternite of third pereopods with reduced, slender anterior lobe. Sternites of fourth and fifth pereopods with capsulate setae (Fig. 2c). Telson (Fig. 1f) without indications of division into anterior and posterior portions; terminal margin broadly rounded, with inconspicuous median indentation, unarmed.

Color.—Overall body and appendage color very pale yellow. Ocular peduncles with white and yellow chromatophores and dark red longitudinal stripe on ventromesial and ventrolateral surfaces forming an elongate U-shaped pattern; corneas black with "frosted" overtone. Chelipeds each with few scattered orange spots. Dactyls of second and third pereopods with 2 extremely faint yellow bands, most apparent on second. (From A. J. Provenzano, Jr., field notes).

Affinities.—This species, known from only two specimens, bears certain habitat and morphological similarities to *Pylopagurus pattiae* Lemaitre & Campos, 1993. Both have been found living in membranous tubes and both have similarly elongate and weakly armed chelipeds. However, in addition to differences in generic characters, *E. provenzanoi* is easily distinguished from *P. pattiae* by the armature of the dactyl and fixed finger of the right chela, greater number of spines on the ventral margins of the dactyls of the second and third pereopods, unarmed ambulatory carpi, and structure of the telson.

Habitat.—The holotype was found living in a semi-transparent polychaete tube.

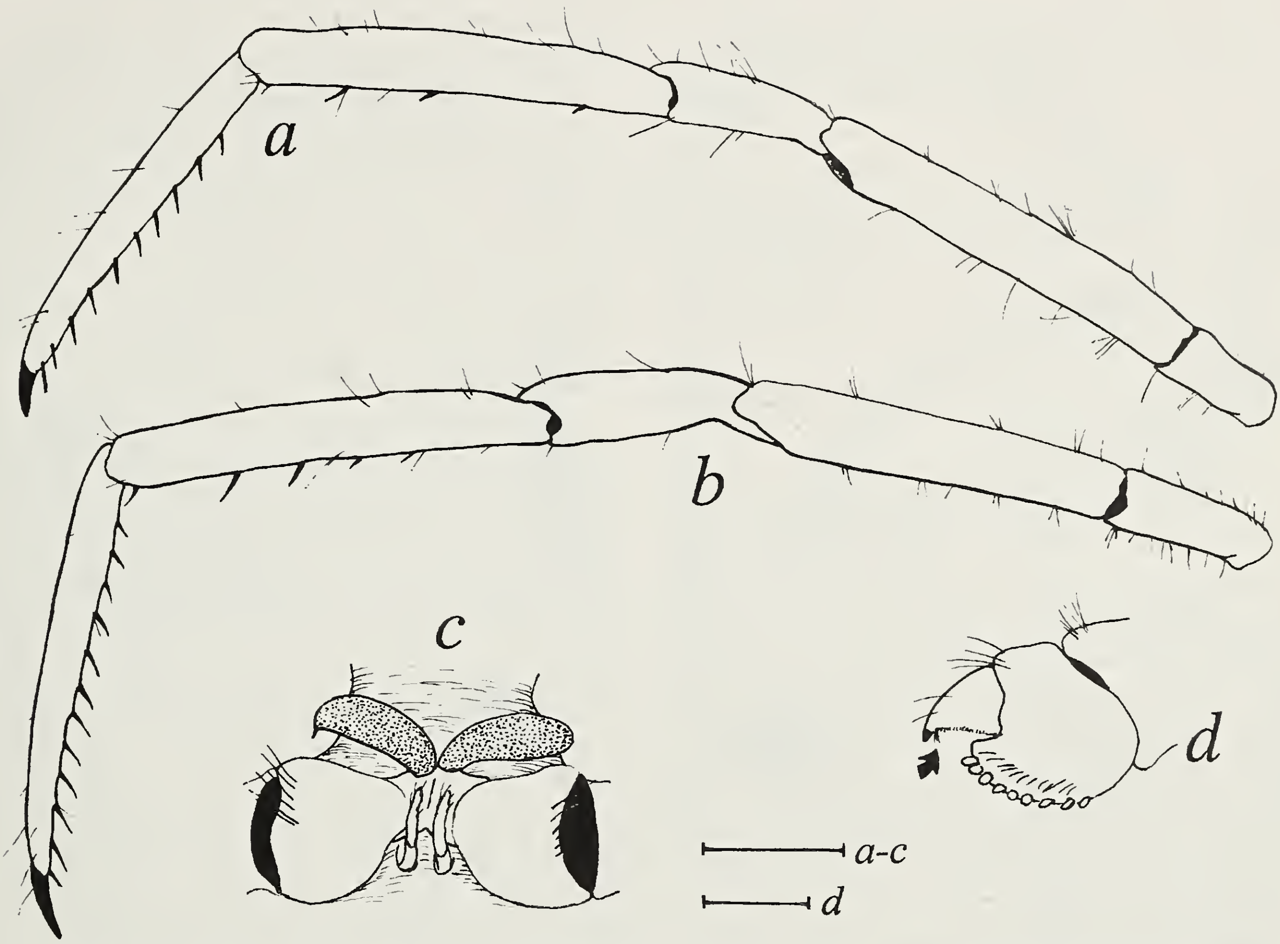

Fig. 2.—*Enallopagurus provenzanoi,* new species, holotype ovig ♀ (sl = 2.40 mm), northwestern Caribbean, R/V *John Elliott Pillsbury,* sta 581, USNM 1007525. a, left second pereopod, lateral; b, left third pereopod, lateral; c, coxae and sternite of fifth pereopods with capsulate setae (stippled), and part of abdomen (lower) showing first pleopods; d, propodus and dactyl of left fourth pereopod with preungual process (arrow), lateral. Scales equal 1.00 mm (a, b), 0.50 mm (c), and 0.10 mm (d).

Distribution.—Known at present only from the type locality, off Arrowsmith Bank, in the northwestern Caribbean; 146–265 m.

Etymology.—This species is named for Dr. Anthony J. Provenzano, Jr., whose pioneering work on western Atlantic hermit crabs provided the basis for the study of the "*Pylopagurus-Tomopagurus*" group of genera.

Remarks.—As previously indicated, *Enallopagurus provenzanoi,* new species, is the first recognized representative of the genus in the western Atlantic. Unlike some species of *Phimochirus* (another of the "*Pylopagurus-Tomopagurus*" group of genera), which is represented in both oceans by geminate pairs (cf. McLaughlin 1981b), *E. provenzanoi* appears to be related to the two eastern Pacific species only through major generic characters.

Key to Species of *Enallopagurus*

1. Dorsoproximal margin of right chela armed with strong spines; eastern Pacific .... *E. coronatus*
– Dorsoproximal margin of right chela unarmed 2
2. Dorsal surface of palm of right chela with relatively closely-spaced small spines or spinules; eastern Pacific .... *E. affinis*
– Dorsal surface of palm of right chela unarmed or rarely slightly tuberculate ... 3
3. Carpus of right cheliped with two or three spines on dorsomesial margin separated by concavity from prominent dorsodistal spine; eastern Pacific .... *E. spinicarpus*

– Carpus of right cheliped with unarmed dorsomesial margin; Caribbean Sea . . . . *E. provenzanoi*, new species

Enallopaguropsis McLaughlin, 1981a

Pylopagurus: Walton, 1954:140 (in part).—Scanland & Hopkins, 1969:257 (in part) [Not *Pylopagurus* A. Milne-Edwards & Bouvier, 1891].

Enallopaguropsis McLaughlin 1981a:7; 1982:848; 2003:121.

Emended diagnosis.—Eleven pairs of biserial gills. Ocular acicle acutely triangular, with moderate to well-developed submarginal spine. Sternite of third maxillipeds with prominent spine on either side of midline. Third maxilliped with well-developed crista dentata and 1 accessory tooth. Maxillule with internal lobe of endopod moderately well-developed, and with 1 stiff bristle terminally; posterior lobe somewhat produced, not recurved.

Right cheliped with suboperculate chela. Left chela subtriangular in cross-section, but dorsal surface not produced into prominent keel or crest. Dorsodistal spine of carpi of second and third pereopods lacking. Anterior lobe of sternite of third pereopods represented by 1 or 2 capsulate setae. Sternites of fourth and fifth pereopods often with 1 to several large capsulate setae. Fourth pereopod with propodal rasp consisting of multiple rows of corneous scales.

Males with paired gonopores, no distinct sexual tubes but occasionally with vas deferentia produced to form short tubular papillae on one or both coxae; no paired pleopods; 3 unpaired left pleopods with endopods reduced or absent. Females with paired gonopores, paired first pleopods modified as gonopods, 4 unpaired left pleopods, second to fourth with both rami well-developed, fifth with endopod reduced or absent.

Abdomen straight or slightly flexed, usually moderately long; uropods symmetrical or asymmetrical. Telson without indication of division into anterior and posterior portions; terminal margin convex, entire or with shallow median concavity, unarmed.

Remarks.—The original diagnosis of *Enallopaguropsis* indicated that the terminal margin of the telson was entire in all the species. In the new species described herein, however, the terminal margin is divided into nearly symmetrical lobes by a shallow median concavity, and the diagnosis of the genus has been corrected accordingly.

With the addition of the new species of *Enallopaguropsis* described herein, the genus is now represented by two eastern Pacific and one western Atlantic species. An updated key to the species is provided following the description of this new species.

Enallopaguropsis williamsi, new species

Figs. 3, 4

Holotype.—♂ (sl = 1.70 mm), R/V *John Elliott Pillsbury,* sta 421, 09°32.1′N, 78°33.5′W, Golfo de San Blas, Panamá, 53–58 m, 19 Jul 1966, USNM 1007523.

Description.—Shield (Fig. 3a) longer than broad; anterior margin between rostrum and lateral projections slightly concave; anterolateral margins sloping; posterior margin truncate, dorsal surface with few setae. Rostrum triangular, with terminal spinule. Lateral projections triangular, each with terminal spine or spinule.

Ocular peduncle approximately 0.85 length of shield, moderately stout, with cornea slightly dilated. Ocular acicles subtriangular, each terminating subacutely, with well-developed submarginal spine; separated basally by slightly more than basal width of 1 acicle.

Antennular peduncle overreaching ocular peduncle by approximately 0.50 length of ultimate segment; ultimate and penultimate segments unarmed; basal segment unarmed.

Antennal peduncle slightly shorter to equaling length of ocular peduncle. Fifth and fourth segments with scattered setae. Third segment with acute spine at ventrodistal angle. Second segment with dorsolateral distal angle prominently produced, ter-

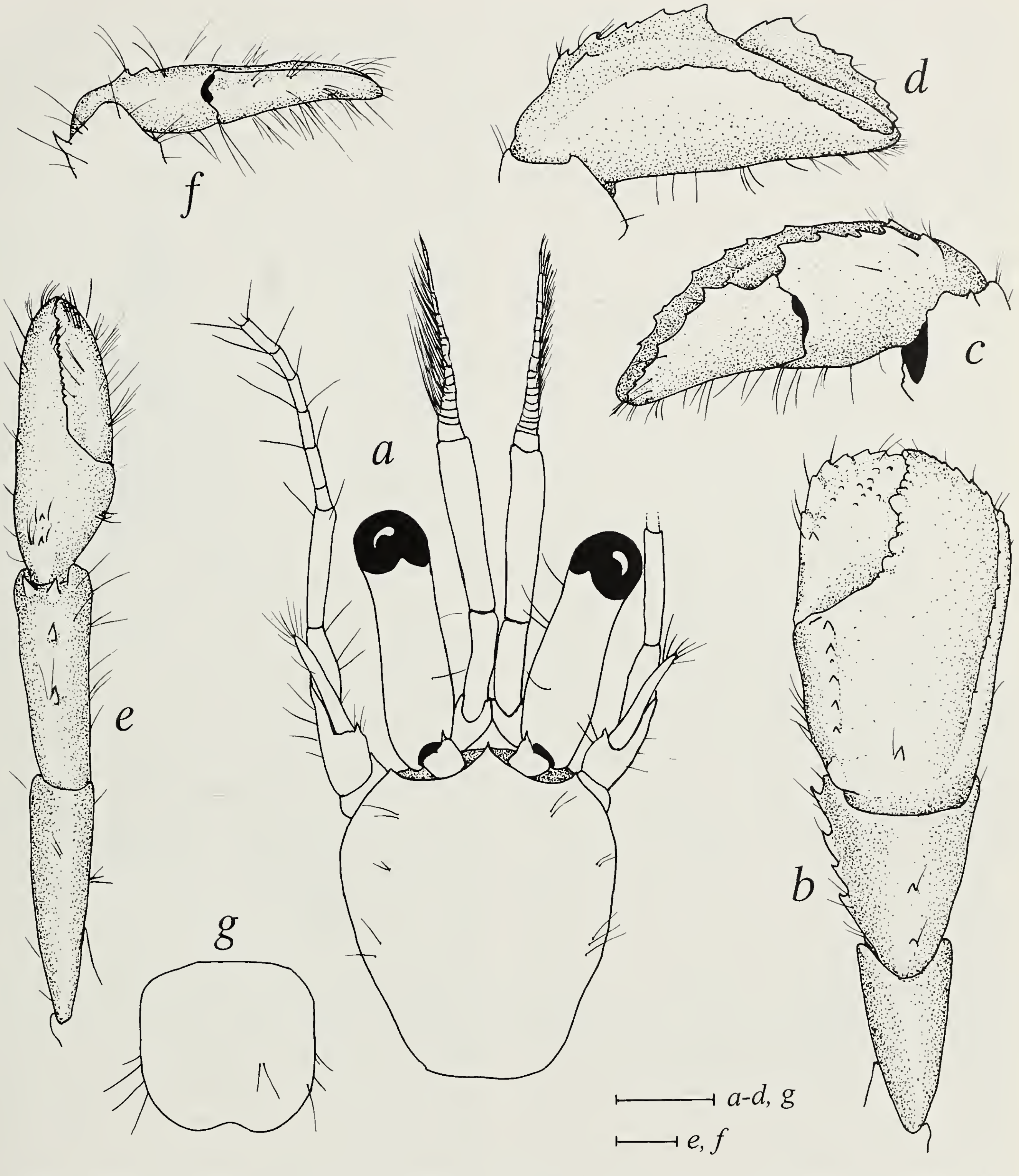

Fig. 3.—*Enallopaguropsis williamsi,* new species, holotype ♂ (sl = 1.70 mm), southwestern Caribbean, R/V *John Elliott Pillsbury,* sta 421, Golfo de San Blas, Panamá, USNM 1007523. a, shield and cephalic appendages (right antennal flagellum missing), dorsal; b, right cheliped, dorsal; c, chela of same, mesial; d, same, lateral; e, left cheliped, dorsal; f, chela of same, mesial; f, telson, dorsal. Scales equal 0.50 mm (a–d, g) and 0.25 mm (e, f).

minating in small spine; dorsomesial distal angle with small spine. First segment produced ventrally and with acute spine on ventrolateral margin distally. Antennal acicle moderately short, reaching only to distal margin of fourth peduncular segment. Flagellum with short setae ≥1 article in length in most articles, and moderately long setae 2 or 3 articles in length every 2 articles.

Right cheliped (Figs. 3b–d) with suboperculate chela. Dactyl approximately 0.80 length of palm, approximately equal to fixed finger in width, with row of spines on distal 0.75 of elevated dorsomesial margin, dorsal surface with few small tubercles in distal half; cutting edge with row of moderately large teeth; mesial, lateral and ventral surfaces with scattered short setae. Palm slightly exceeding length of carpus; dorsal surface weakly convex, armed with only 1 small spine slightly mesiad of midline in proximal half, elevated dorsomesial margin forming spinose crest, dorsolateral margin also elevated as low ridge proximally becoming more pronounced and weakly serrate distally and on fixed finger; cutting edge of fixed finger with row of distinct teeth; mesial, lateral and ventral surfaces with sparse tufts of setae. Carpus approximately equal to length of merus, subtrapezoidal; dorsomesial margin with row of 4 prominent spines, dorsolateral margin not delimited, dorsal surface with longitudinal row of 2 spinose protuberances proximally, otherwise surfaces unarmed, but with few scattered setae. Merus triangular, margins and surfaces unarmed but with scattered, short setae. Ischium unarmed.

Left cheliped (Figs. 3e, f) with dactyl approximately as long as palm; surfaces of dactyl and fixed finger unarmed but with sparse tufts of setae, dorsal surface of palm with 2 small spines in midline proximally. Carpus only slightly shorter than merus; dorsal surface with longitudinal row of 2 spines medially, and 2 additional spines on distal margin; mesial, lateral and ventral surfaces unarmed but with few scattered setae. Merus and ischium with only scattered short to moderately long setae on all surfaces.

Second and third pereopods (Figs. 4a, b) moderately long and slender. Dactyls equal to or slightly longer than propodi; dorsal surfaces with few short setae; ventral margins each with row of 6 or 7 long corneous spines and few short setae. Propodi approximately 1.50 to nearly twice as long as carpi; dorsal surfaces with few setae; with 1 or 2 ventrodistal spiniform bristles, and 1 or 2 additional slightly shorter spiniform bristles on each ventral margin distally. Carpi 0.45–0.75 length of meri, unarmed, but with scattered setae dorsally and ventrally. Meri and ischia unarmed, but with dorsal and ventral sparse tufts of setae.

Fourth pereopod (Fig. 4d) with propodal rasps consisting of 3 rows of corneous scales. Dactyl lacking preungual process.

Sternites of third, fourth, and fifth pereopods (Fig. 4c) each with 3, 4, and 2 capsulate setae, respectively. Coxae of fifth pereopods with vas deferentia slightly produced forming short tubular papillae on right and left sides (Fig. 4c).

Uropods nearly symmetrical. Telson (Fig. 3g) without indications of division into anterior and posterior portions; terminal margin with broad median concavity, unarmed.

Color.—Shield weakly mottled orange with large darker orange spot on each side laterally and few smaller spots and patches in distal half. Ocular peduncles mottled light orange with scattered darker orange specks. Antennal peduncles with band of light orange on second segments superimposed with few darker orange specks; antennal acicles with few patches of light orange. Chelipeds each generally light orange with few scattered darker orange patches; dactyls each with proximal darker orange band. Dactyls of second and third pereopods each with orange band in proximal half; propodi with scattered orange spots and orange band at mid-length; carpi very light orange, that of third with at least scattered darker orange specks; meri faint orange, darker proximally and with numerous darker orange specks. (From notes by B. Stolen, artist for A. J. Provenzano, Jr.).

Etymology.—This species is dedicated to the memory of Dr. Austin B. Williams (1919–1999, see Lemaitre & Collette 2000), esteemed colleague who during many years of work at the Systematics Laboratory, National Marine Fisheries Service, contributed greatly to our knowledge of western Atlantic decapod crustaceans.

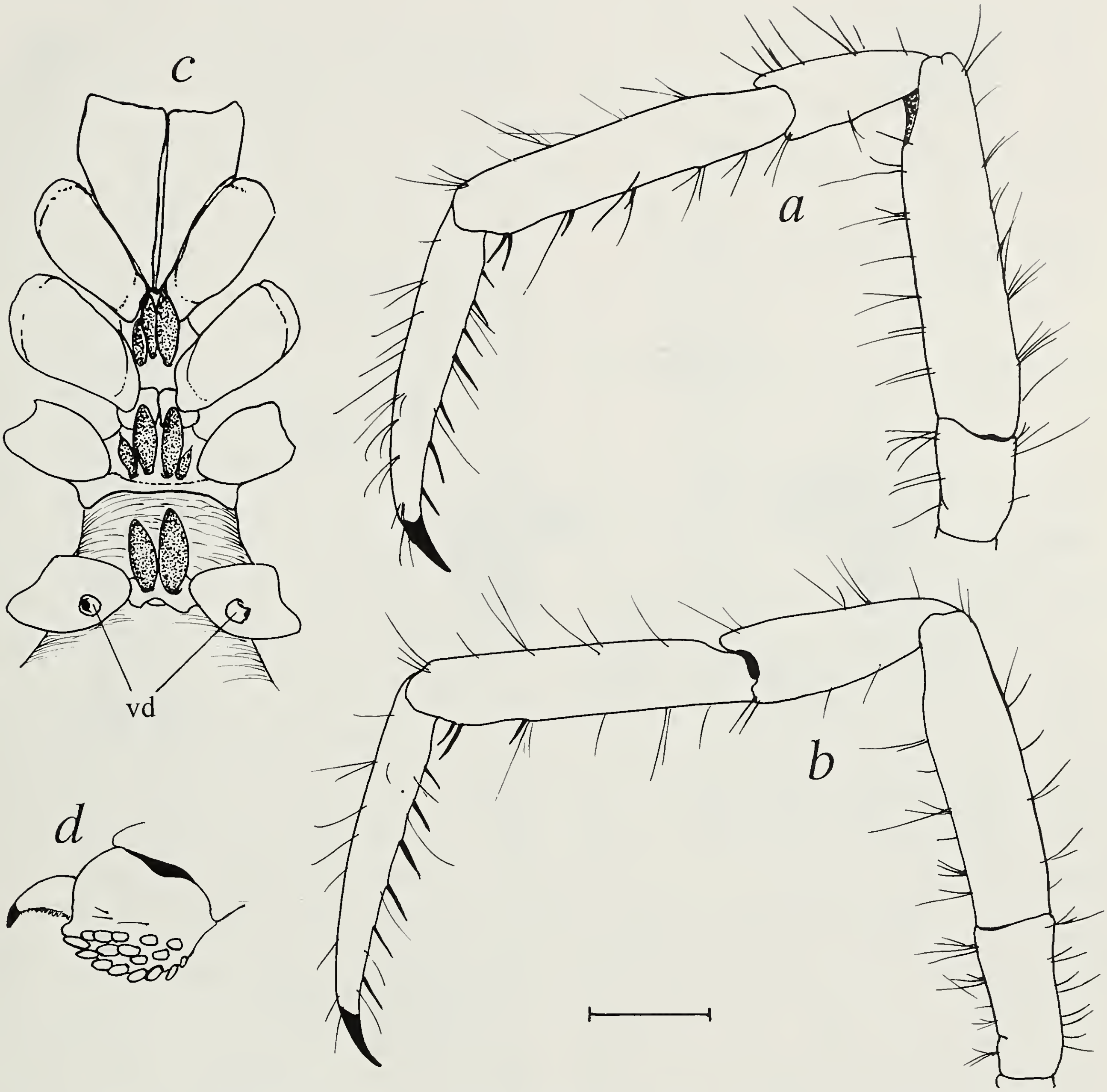

Fig. 4.—*Enallopaguropsis williamsi,* new species, holotype ♂ (sl = 1.70 mm), southwestern Caribbean, R/V *John Elliott Pillsbury,* sta 421, Golfo de San Blas, Panamá, USNM 1007523. a, left second pereopod, lateral; b, left third pereopod, lateral; c, coxae and sternites of first to fifth pereopods with capsulate setae (stippled), and protruded vas deferens (vd), ventral; d, propodus and dactyl of left fourth pereopod, lateral. Scale equals 0.50 mm (a–c) and 0.25 mm (d).

Habitat.—Housing unknown. Bottom where found consisted of "coralline plates and broken shells" (Voss 1966).

Distribution.—Known only from the type locality, Golfo de San Blas, on the Caribbean coast of Panamá.

Remarks.—Because *Enallopaguropsis williamsi,* new species, is known from only the male holotype, this species can only provisionally be assigned to *Enallopaguropsis.* The telson of *E. williamsi* bears some resemblance to species of *Agaricochirus.* However, the morphology of the right cheliped and propodal rasp suggests that this new species belongs in *Enallopaguropsis.*

Key to Species of *Enallopaguropsis*

1. Palm of left chela with row of spines on dorsolateral margin 2

– Palm of left chela with unarmed dorsolateral margin; Caribbean Sea .... *E. williamsi*, new species

2. Dorsal surface of right chela covered with closely-spaced corneous-tipped spinules or granules; eastern Pacific ... . *E. guatemoci*

– Dorsal surface of right chela with scattered tubercles; eastern Pacific .... *E. janetae*

Phimochirus randalli (Provenzano, 1961)
Figs. 5–7

Pylopagurus randalli Provenzano, 1961: 159, fig. 2 (type locality: ridge 5 miles southeast of Lameshur Bay, St. John, Virgin Islands).

Phimochirus randalli: McLaughlin, 1981a: 5; 1981b:340, figs. 4b, 5b, 7b.—Williams et al., 1989:32.—McLaughlin et al., 2003:125.

Holotype.—♂ (sl = 6.20 mm), SE Lameshur Bay, St. John, Virgin Islands, 20 m, 5 Feb 1960, colls. J. Randall and T. Chess, USNM 106353.

Material examined.—Northern Gulf of Mexico, R/V *Pelican,* U.S. Department of Energy project: 1 ♂ (sl = 6.70 mm) + exuvia, 27°48.717′N, 93°02.880′W, dredged at night, calcareous rubble, 16 Aug 1998, USNM 276157 (photo voucher).—1 ♀ ovig (sl = 5.9 mm), dredge sta 10-3, 28°05.999′N, 91°02.289′W, 57 m, 27 May 2000, ULLZ 4678 (photo voucher).—1 ♂ (sl = 2.80 mm), dredge sta 7-2, 91°02.481′W, 57–60 m, 1 Jul 2001, ULLZ 4551 (photo voucher).

Diagnosis.—Shield (Fig. 5a) longer than broad; dorsal surface with several short transverse or oblique rows of bristle-like setae; rostrum prominent, acutely triangular; with minute terminal spine; lateral projections obsolete or broadly triangular, usually with minute terminal spine. Ocular peduncles stout, about 0.60 times length of shield, with corneas strongly dilated. Ocular acicles elongate, acutely triangular; dorsal surfaces concave distally; each usually with small, submarginal spine terminally; separately basally by basal width of 1 acicle.

Antennular peduncle exceeding distal margin of cornea by about 0.30 length of ultimate segment. Antennal peduncle exceeding distal margin of cornea by about 0.30 length of fifth segment; second segment with dorsolateral distal angle produced, terminating in strong spine, dorsomesial distal angle with small spine; first segment unarmed; acicle elongate, weakly arcuate, reaching to about midpoint of fifth antennal segment, terminating in spine, unarmed. Antennal flagella moderately long; with short setae every 3 or 4 articles, each seta about 1 flagellar article in length.

Right cheliped (Fig. 6) sparsely setose. Chela operculate, dorsoventrally compressed (more markedly so laterally and mesially); dorsal surfaces of palm and fingers covered with low, mushroom-like tubercles replaced medially on palm by 2 longitudinal, rectangular or ovate granular patches separated by narrow tuberculate area; patches slightly depressed, with granules arranged in irregular, transverse rows. Fixed finger broad basally, with up to 6 blunt spines dorsally more prominent than surrounding tubercles. Dactyl about as long or slightly shorter than length of palm; mesial margin with blunt spines; dorsal surface with 2 (1 distal, 1 proximal) blunt spines standing out from surrounding tubercles. Carpus with granules or low tubercles on dorsal, lateral and mesial surfaces, dorsomesial margin with row of irregular, corneous-tipped spines; mesial surface concave distally. Merus with row of small spines or spinulose tubercles on ventromesial and ventrolateral margins; dorsodistal margin with row of 4–6 corneous-tipped spines.

Left cheliped (Fig. 5b) with surfaces of carpus and chela usually covered with small, flattened tubercles or granules. Palm with longitudinal, often ridge-like elevation in midline armed with row of spines or spinules, and flanked on each side by subrectangular or ovate area nearly smooth or with

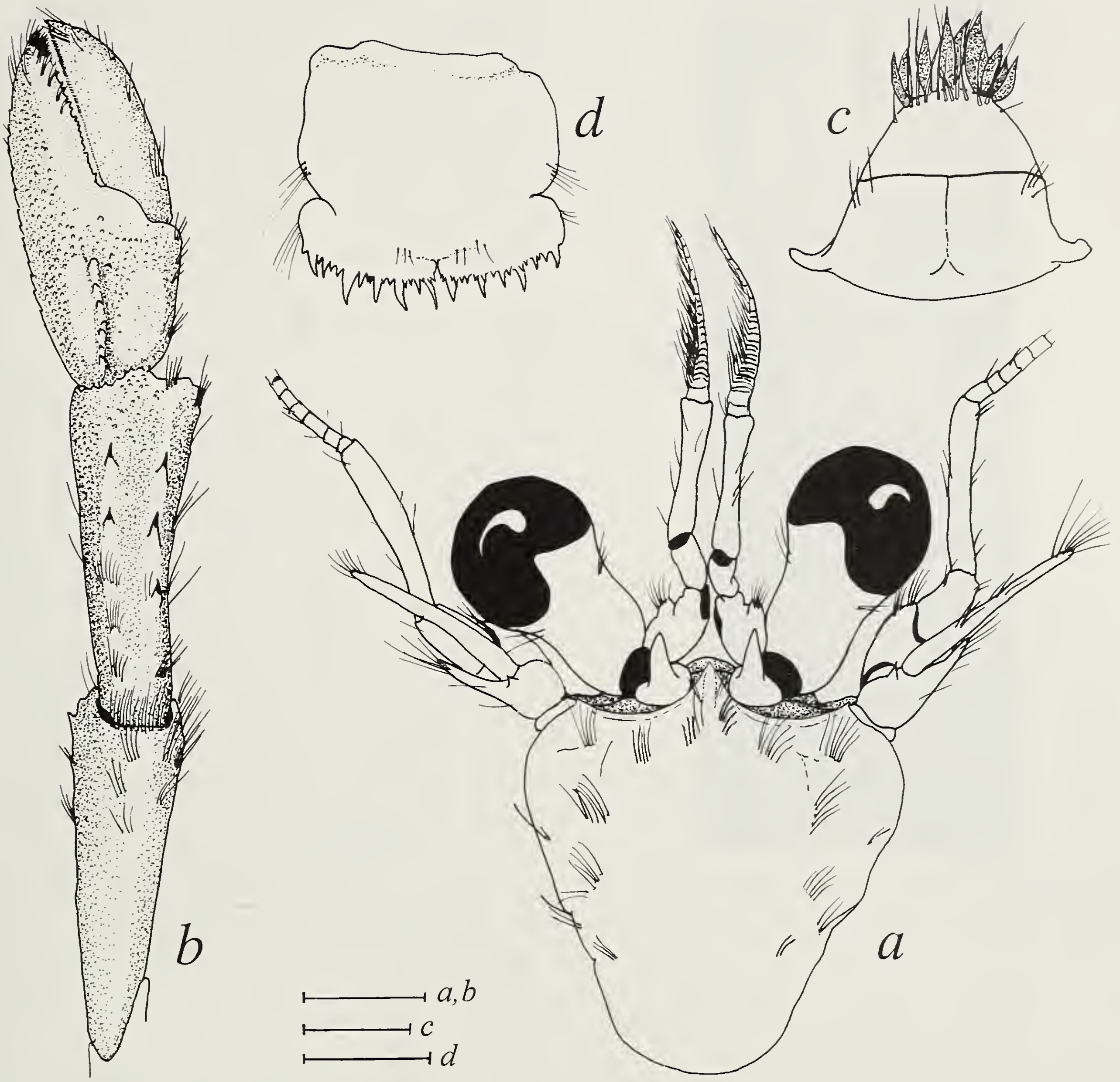

Fig. 5.—*Phimochirus randalli* (Provenzano, 1961), northern Gulf of Mexico, R/V *Pelican,* M (sl = 6.70 mm), USNM 276157. a, shield and cephalic appendages, dorsal; b, left cheliped, dorsal; c, sternite of third pereopods, ventral; d, telson, dorsal. Scales equal 2.00 mm (a, b), and 1.00 mm (c, d).

scattered small granules. Carpus with dorsolateral and dorsomesial margins each with irregular row of 2–4 corneous-tipped spines; dorsodistal margin minutely spinulose.

Second and third pereopods (Fig. 7a–d) with meri, carpi, propodi and dactyls setose dorsally. Dactyls moderately short, about 1.20–1.40 times as long as dorsal margins of propodi; dorsal and dorsomesial distal margins with small corneous spines interspersed with setae; ventral margins each with row of 7–9 corneous spines. Propodi with dorsal surfaces spinulose or tuberculate, ventral margins each with row of 2–4 corneous spines in addition to pair of corneous spines on distal angle. Carpi each with prominent dorsodistal spine.

Fourth pereopod (Fig. 7e) with distinct preungual process on dactyl surrounded by dense, circularly arranged setae.

Sternite of third pereopods (Fig. 5c) with subquadrate to semicircular anterior lobe; sternites of third to fifth pereopods frequently with capsulate setae.

Telson (Fig. 5d) with distinct transverse

Fig. 6.—*Phimochirus randalli* (Provenzano, 1961), northern Gulf of Mexico, R/V *Pelican*, M (sl = 6.70 mm), USNM 276157. Right cheliped (× 3.97).

indentation; terminal margin nearly straight or broadly rounded, divided into left and right lobes by V-shaped cleft, each portion armed with several elongate spines interspersed with shorter spines.

Color.—Generally amber or brownish. Anterior half of shield mottled with white patches. Branchiostegites with white patches surrounded by brownish to purple. Ocular peduncles with irregular white patches basally, turning to uneven tints of amber distally; each peduncle with distinct, light purple spot on dorsomesial surface near cornea. Basal segments of antennules purple, penultimate segments and flagella white, remaining parts amber or brownish. Right cheliped amber or brownish except for few white spines on dorsal surface of fingers and dorsodistal surface of carpus; carpus with band of white patches on dorsal surface proximally; merus with band of white patches surrounded by light purple tint on dorsodistal surface. Left cheliped also amber or brownish except for scattered white patches on carpus; merus similar in color to that of right cheliped. Second and third pereopods with distal halves of dactyls white and amber proximally; propodi white on distal thirds, with white patches proximally, otherwise amber; carpi each with white dorsodistal spine having light purplish tint basally, elsewhere with scattered white patches over amber; meri with many white patches on lateroventral surfaces surrounded by light purplish tint, otherwise amber. Fourth and fifth pereopods amber with white patches. (Based on photographs of live specimens taken by D. L. Felder).

Habitat.—Found in gastropod shells. According to Provenzano (1961) the holotype was found in a shell of the gastropod *Semicassis granulata* (Born).

Distribution.—Bahama Islands; Straits of Florida; northern Gulf of Mexico; eastern and western Caribbean. Depth: 15–91 m.

Remarks.—McLaughlin's (1981b:340, fig. 5b) diagnosis and illustration of the right chela of *P. randalli* describe a median "ridge" that separates two longitudinal, slightly depressed, granular patches. This "ridge" was used by McLaughlin (1981b: 336, couplet 1) in her key to separate *P. randalli* from all other congeners. Based on the study of the Gulf of Mexico specimens herein reported, and a reexamination of some of the specimens used by McLaughlin (1981b), we have found that the use of this ridge as a key diagnostic character may lead to confusion. In some individuals the ridge does appear somewhat elevated as result of the two depressed patches, whereas in others the patches are hardly if at all depressed, and no distinct ridge is apparent. Actually, it is the presence of granular patches that more clearly serve to separate *P. randalli* from other congeners. The tubercles that cover the other portions of the dorsal surface of the right palm can also vary in strength and size. Given the variation ob-

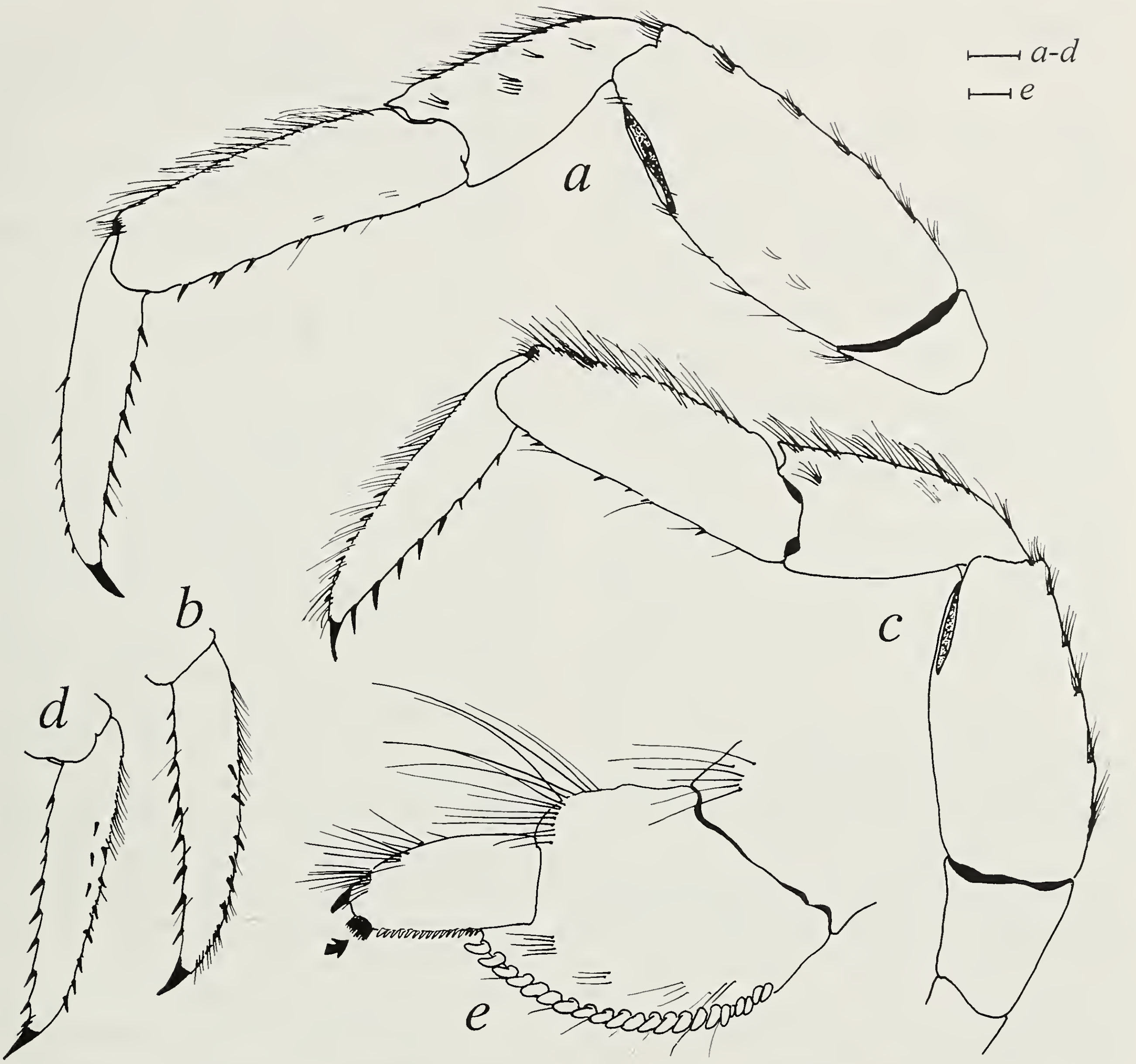

Fig. 7.—*Phimochirus randalli* (Provenzano, 1961), northern Gulf of Mexico, R/V *Pelican*, ♂ (sl = 6.70 mm), USNM 276157. a, left second pereopod, lateral; b, dactyl of same, mesial; c, left third pereopod, lateral; d, dactyl of same, mesial; e, propodus and dactyl of left fourth pereopod with preungual process (arrow), lateral. Scales equal 0.50 mm (a–d) and 0.25 mm (e).

served on the right palm of *P. randalli*, which requires a modification of couplet 1 of McLaughlin's (1981b) key, and the removal by McLaughlin (1988) of *Phimochirus liochele* to *Pagurus*, an updated key to the species is presented.

Updated Key to Species of *Phimochirus*

1. Palm of right chela with two longitudinal, rectangular or ovate granular patches; western Atlantic .... *P. randalli*
– Palm of right chela without longitudinal granular patches 2
2. Dorsal surface of dactyl of right chela with median ridge or row of tubercles or spines 3
– Dorsal surface of dactyl of right chela without median ridge or row of tubercles or spines 7
3. Dorsal surface of palm and fixed finger of right chela with strong or moderately strong tubercles, at least distally 4
– Dorsal surface of palm and fixed finger of right chela smooth, granular or weakly tuberculate 5
4. Exopod of left uropod with dense tuft of long setae; eastern Pacific .... *P. californiensis*

– Exopod of left uropod without dense tuft of long setae; western Atlantic .... *P. holthuisi*

5. Dorsal surface of carpus of right cheliped unarmed; western Atlantic .... *P. leurocarpus*

– Dorsal surface of carpus of right cheliped tuberculate, spinose or spinulose .. 6

6. Palm of left chela with dorsal midline unarmed or with few spinules or tubercles proximally; eastern Pacific .... *P. venustus*

– Palm of left chela with dorsomedial row of small spines or tubercles extending to base of dactyl; western Atlantic .... *P. operculatus*

7. Exopod of left uropod with dense tuft of long setae; eastern Pacific ...... *P. roseus*

– Exopod of left uropod without dense tuft of long setae; western Atlantic .... *P. occlusus*

Taxonomic Summary of the "*Pylopagurus-Tomopagurus*" Group of Taxa, from the Publication of Part 1 in 1981 to the Present

(Taxa listed in same order discussed during revision of group; see Table 1 for list of current valid names)

Genus *Tomopagurus* A. Milne-Edwards & Bouvier, 1893

Species assigned by McLaughlin (1981a).—*Tomopagurus rubropunctatus* A. Milne-Edwards & Bouvier, 1893, *T. cokeri* (Hay, 1917), *T. maclaughlinae* Haig, 1976, *T. cubensis* (Wass, 1963), *T. wassi* McLaughlin, 1981a, *Pagurus purpuratus* (Benedict, 1892), *P. merimaculosus* Glassell, 1937, and *Pylopagurus chacei* Wass, 1963.

Changes and additions since McLaughlin (1981a).—None.

Species discussion.—See McLaughlin (1981a).

Genus *Rhodochirus* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—*Pylopagurus rosaceus* A. Milne-Edwards & Bouvier, 1893, *Pylopagurus hirtimanus* Faxon, 1893. McLaughlin (1981a) also considered *P. acutus* Forest & de Saint Laurent, 1968, a synonym of *Rhodochirus rosaceus.*

Changes and additions since McLaughlin (1981a).—None.

Species discussion.—See McLaughlin (1981b).

Genus *Phimochirus* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—*Pylopagurus operculatus* (Stimpson, 1859), *P. californiensis* (Benedict, 1892), *P. mexicanus* (Benedict, 1892), *P. venustus* (Bouvier, 1898), *P. roseus* (Benedict, 1892), *P. randalli* Provenzano, 1961, and *P. holthuisi* Provenzano, 1961. Questionably assigned were *P. occlusus* (Henderson, 1888) and *P. liochele* Barnard, 1947.

Changes and additions since McLaughlin (1981a).—McLaughlin (1981b:349) synonymized *Pylopagurus mexicanus* with *Phimochirus californiensis,* and described *P. leurocarpus.* McLaughlin (1988:6) transferred *Phimochirus liochele* to *Pagurus.*

Species discussion.—See McLaughlin (1981b, 1988), and this study.

Genus *Agaricochirus* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—*Pylopagurus boletifer* A. Milne-Edwards & Bouvier, 1893, *P. alexandri* A. Milne-Edwards & Bouvier, 1893, *P. cavimanus* Chace, 1939, *P. erosus* (A. Milne-Edwards, 1880), *P. gibbosimanus* (A. Milne-Edwards, 1880), and *Pagurus hispidus* (Benedict, 1892).

Changes and additions since McLaughlin (1981a).—McLaughlin (1982:838, 841) described *Agaricochirus acanthinus* and *A. echinatus.*

Species discussion.—See McLaughlin (1982).

Genus *Enallopagurus* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—*Pylopagurus spinicarpus* Glassell, 1938, *P. affinis* Faxon, 1893, and *P. coronatus* (Benedict, 1892).

Changes and additions since McLaughlin (1981a).—Enallopagurus provenzanoi is described in this study.

Species discussion.—See McLaughlin (1982), and this study.

Genus *Enallopaguropsis* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—Pylopagurus guatemoci Glassell, 1937, and *P. hancocki* Walton 1954.

Changes and additions since McLaughlin (1981a).—McLaughlin (1982:849, 851) synonymized *Enallopaguropsis hancocki* with *E. guatemoci,* and described *E. janetae. Enallopaguropsis williamsi* is described in this study.

Species discussion.—See McLaughlin (1982), and this study.

Genus *Lophopagurus* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—Pylopagurus thompsoni (Filhol, 1885), *P. lacertosus* (Henderson, 1888), *P. nanus* (Henderson, 1888), *P. crenatus* (Borradaile, 1916), and questionably *P. cristatus* (H. Milne Edwards, 1836).

Changes and additions since McLaughlin (1981a).—McLaughlin & Gunn (1992:52, 55) described *Lophopagurus foresti,* and *L. nodulosus*; de Saint Laurent & McLaughlin (2000:150) described *L. pumilus.*

De Saint Laurent & McLaughlin (2000: 148) reduced McLaughlin's (1981a) genus *Australeremus* to subgeneric status within *Lophopagurus.* The subgenus *Lophopagurus* then became the nominal subgenus. The following species were assigned by de Saint Laurent & McLaughlin (2000:149) to *Lophopagurus* (*Lophopagurus*): *L.* (*L.*) *foresti, L.* (*L.*) *lacertosus, L.* (*L.*) *nanus, L.* (*L.*) *nodulosus, L.* (*L.*) *pumilus,* and *L.* (*L.*) *thompsoni.* De Saint Laurent & McLaughlin (2000:153) also synonymized *L.* (*L.*) *crenatus* with *L.* (*L.*) *lacertosus.*

Species discussion.—See McLaughlin & Gunn (1992), and de Saint Laurent & McLaughlin (2000).

Genus *Australeremus* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—Pylopagurus cooki (Filhol, 1883), and *P. kirki* (Filhol, 1883).

Changes and additions since McLaughlin (1981a).—McLaughlin & Gunn (1992:68) assigned *Pylopagurus stewarti* and *P. serpulophilus* to *Australeremus,* and considered the latter species a junior synonym of *Australeremus triserratus* (Ortmann, 1892). McLaughlin & Gunn (1992:74, 77, 92) also described *Australeremus laurentae* and *A. eltaninae,* and added *A. cristatus* (H. Milne Edwards, 1836).

McLaughlin's (1981a) genus *Australeremus* was reduced by de Saint Laurent & McLaughlin (2000:148) to subgeneric rank within *Lophopagurus.* The following species were assigned by de Saint Laurent & McLaughlin (2000:166) to *Lophopagurus* (*Australeremus*): *L.* (*A.*) *cookii* [also corrected spelling], *L.* (*A.*) *eltaninae, L.* (*A.*) *cristatus, L.* (*A.*) *kirkii* [also corrected spelling], *L.* (*A.*) *laurentae, L.* (*A.*) *stewarti,* and *L.* (*A.*) *triserratus.*

Species discussion.—See McLaughlin & Gunn (1992), and de Saint Laurent & McLaughlin (2000).

Genus *Anisopagurus* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—Pylopagurus bartletti A. Milne-Edwards, 1880, and *P. pygmaeus* (Bouvier, 1918).

Changes and additions since McLaughlin (1981a).—Lemaitre & McLaughlin (1996: 95, 101, 108) described *Anisopagurus actinophorus, A. hopkinsi,* and *A. vossi.*

Species discussion.—See Lemaitre & McLaughlin (1996).

Genus *Manucomplanus* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—Pylopagurus corallinus (Benedict, 1892), *P. cervicornis* (Benedict, 1892), *P. spinulosus* Holthuis, 1959, *P. longimanus* Faxon, 1893, *P. varians* (Benedict, 1892), and questionably *P. ungulatus* (Studer, 1883).

Changes and additions since McLaughlin (1981a).—Lemaitre & McLaughlin (1996: 113) synonymized *Manucomplanus corallinus* with *M. ungulatus.*

Species discussion.—See Lemaitre & McLaughlin (1996).

Genus *Protoniopagurus* Lemaitre & McLaughlin, 1996

Species assigned.—Monotypic: *Protoniopagurus bioperculatus* Lemaitre & McLaughlin, 1996.

Species discussion.—See Lemaitre & McLaughlin (1996).

Genus *Pylopagurus* A. Mine-Edwards & Bouvier, 1891 *sensu stricto*

Species assigned by McLaughlin (1981a).—*Pylopagurus discoidalis* (A. Milne-Edwards, 1880), *P. holmesi* Schmitt, 1921, *P. longicarpus* Walton, 1954, *P. stewarti* (Filhol, 1883), and *P. serpulophilus* Miyake, 1978.

Changes and additions since McLaughlin (1981a).—As mentioned under *Australeremus,* McLaughlin & Gunn (1992:68) transferred *Pylopagurus stewarti* and *P. serpulophilus* to *Australeremus* McLaughlin, 1981a, and considered the latter species a junior synonym of *A. triserratus* (Ortmann, 1892).

Pylopagurus longicarpus was shown to be a junior synonym of *P. holmesi* by McLaughlin & Lemaitre (2001:459).

Lemaitre & Campos (1993:554) described *Pylopagurus pattiae,* and McLaughlin & Lemaitre (2001:464, 468) described *P. macgeorgei* and *P. gorei.*

Species discussion.—See Lemaitre & Campos (1993), and McLaughlin & Lemaitre (2001).

Genus *Haigia* McLaughlin, 1981a

Species assigned by McLaughlin (1981a).—Monotypic: *Pylopagurus diegensis* Scanland & Hopkins, 1969.

Changes and additions since McLaughlin (1981a).—None.

Species discussion.—See McLaughlin & Lemaitre (2001).

Genus *Pylopaguridium* McLaughlin & Lemaitre, 2001

Species assigned.—Monotypic: *Pylopaguridium markhami* McLaughlin & Lemaitre (2001).

Species discussion.—See McLaughlin & Lemaitre (2001).

Corrected Key to Genera of the "*Pylopagurus-Tomopagurus*" Group

In light of the morphology of the telson in the new species *Enallopagurus provenzanoi* and *Enallopaguropsis williamsi,* the key provided by McLaughlin & Lemaitre (2001:480) must be modified as follows:

1\. Abdomen reduced; males without unpaired pleopods; females with unpaired pleopods 2–4 .... *Protoniopagurus*

– Abdomen not reduced; males with some unpaired pleopods; females with unpaired pleopods 2–5 2

2 Protopods of uropods prominently produced posteriorly; dorsal surface of right chela commonly with characteristic covering of mushroom-shaped tubercles .... *Agaricochirus*

– Protopods of uropods not prominently produced posteriorly; dorsal surface of right chela usually without characteristic covering of mushroom-shaped tubercles 3

3\. Spines on dorsal surfaces of chelae with basal rosettes .... *Rhodochirus*

– Spines on dorsal surfaces of chelae without basal rosettes 4

4\. Propodal rasps of fourth pereopods each with more than one row of corneous scales 5

– Propodal rasps of fourth pereopods

each with one row of corneous scales 7
5. Left chela triangular or subtriangular in cross-section, dactyl and fixed finger not dorsoventrally flattened 6
– Left chela not triangular or subtriangular in cross-section, dactyl and fixed finger dorsoventrally flattened . . . . *Manucomplanus*
6. Telson with lateral indentations suggesting division into anterior and posterior portions . . . . *Anisopagurus*
– Telson without lateral indentations suggesting division into anterior and posterior portions . . . . *Enallopaguropsis*
7. Ocular acicles simple; coxae of male fifth pereopods symmetrical 8
– Ocular acicles multispinose; coxae of male fifth pereopods asymmetrical . . . . *Pylopaguridium*
8. Telson with lateral indentations suggesting division into anterior and posterior portions 9
– Telson without lateral indentations suggesting division into anterior and posterior portions . . . . *Enallopagurus*
9. Chela of right cheliped subovate to subcircular, margins unarmed, weakly tuberculate or minutely crenulate and/or serrate, but never armed with prominent, blunt or acute spines 10
– Chela of right cheliped variable, margins armed with prominent, blunt or acute spines or tubercles 11
10. Fourth pereopods with large, very prominent preungual process at base of claw . . . . *Phimochirus*
– Fourth pereopod without large, very prominent preungual process at base of claw . . . . *Pylopagurus*
11. Dactyl and fixed finger of left chela excavated ventral, presenting "spoon-shaped" appearance . . . . *Tomopagurus*
– Dactyl and fixed finger of left chela not excavated ventrally and not presenting spoon-shaped appearance 12
12. Left cheliped with rotation of propodal-carpal articulation 45°–90° from horizontal plane . . . . *Lophopagurus* (*Australeremus*)
– Left cheliped with rotation of propodal-carpal articulation much less than 45° from horizontal plane 13
13. Left chela with midline elevated into prominent keel or crest . . . . *Lophopagurus* (*Lophopagurus*)
– Left chela with midline sometimes elevated, but not into prominent keel or crest . . . . *Haigia*

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Literature Cited

Barnard, K. H. 1947. Descriptions of new species of South African decapod Crustacea, with notes on synonymy and new records.—The Annals and Magazine of Natural History (11)13:361–392.

Benedict, J. D. 1892. Preliminary descriptions of thirty-seven new species of hermit crabs of the genus *Eupagurus* in the U.S. National Museum.—Proceedings of the United States National Museum 15:1–26.

Borradaile, L. A. 1916. Crustacea, part 1. Decapoda. British Antarctic ("Terra Nova") Expedition, 1910.—Natural History Report, Zoology 3(2): 75–110.

Bouvier, E.-L. 1898. Sur quelques Crustacés anomoures et brachyures recueillis par M. Diguet en Basse-Californie.—Bulletin du Muséum d'Histoire Naturelle, Paris 4:371–384.

———. 1918. Sur une petite collection de Crustacés de Cuba offerte au Muséum par M. de Boury.—Bulletin du Muséum d'Histoire Naturelle, Paris 24:6–15.

Boyko, C. B., & A. W. Harvey, 1999. Crustacea Decapoda: Albuneidae and Hippidae of the tropical Indo-West Pacific region. *In* A. Crosnier (ed.), Résults des Campagnes MUSORSTOM, vol. 20.—Mémoirs du Muséum national d'Histoire naturelle 180:379–460.

Chace, F. A., Jr. 1939. Reports on the scientific results of the Atlantis expedition to the West Indies, under the joint auspices of the University of Havana and Harvard University. Preliminary descriptions of one new genus and seventeen new species of decapod and stomatopod Crustacea.—Memorias de la Sociedad Cubana de Historia Natural 13:31–54.

Fabricius, J. C. 1775. Systema Entomologiae, sistens insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus i–xxxii, 1–832. Flensburgi et Lipsiae: Officina Libraria Kortii.

Faxon, W. 1893. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried out by the U.S. Fish Commission steamer "Albatross" during 1891, Lieut.-Commander Z. L. Tanner, U.S.N., commanding. VI. Preliminary descriptions of new species of Crustacea.—Bulletin of the Museum of Comparative Zoology at Harvard College 24:149–220.

———. 1895. Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut.-Commander Z.L. Tanner, U.S.N., commanding. XV. The stalk-eyed Crustacea.—Memoirs of the Museum of Comparative Zoology at Harvard College 18:1–292.

Filhol, H. 1883. Note sur quelques espèces nouvelles d'*Eupagurus* recueillies en Nouvelle-Zélande.—Bulletin de la Société Philomatique de Paris (7)8(2):66–68.

———. 1885. Considérations relatives à la faune des Crustacés de la Nouvelle-Zélande.—Bibliothéque de l'École des Hautes Études, Section des Sciences Naturelles 30:3–60.

Forest, J., & M. de Saint Laurent. 1968. Résultats scientifiques des campagnes de la "Calypso", part VII. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961–1962). 6. Crustacés Décapodes: Pagurides.—Annales de l'Institut Océanographique de Monaco, n.s. 45(2):45–172.

———, M. de Saint Laurent, P. A. McLaughlin, and R. Lemaitre. 2000. The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae.—National Institute of Water and Atmospheric Research Biodiversity Memoir 114:1–250.

Glassell, S. A. 1937. The Templeton Crocker Expedition. XI. Hermit crabs from the Gulf of California and the west coast of Lower California.—Zoologica 22(3):241–263.

———. 1938. Three new anomuran crabs from the Gulf of California.—Allan Hancock Pacific Expeditions 5:1–6.

Haig, J. 1976. *Tomopagurus maclaughlinae,* a new hermit crab from the eastern Pacific (Crustacea, Anomura, Paguridae).—Bulletin of Marine Science 26:27–32.

Hay, W. P. 1917. Preliminary descriptions of five new species of crustaceans from the coast of North Carolina.—Proceedings of the Biological Society of Washington 30:71–74.

Henderson, J. R. 1888. Report on the Anomura collected by H.M.S. Challenger during the years 1873–1876. Report on the scientific results of the voyage of H.M.S. Challenger, Zoology 23: 1–221.

Holthuis, L. B. 1959. The Crustacea Decapoda of Suriname (Dutch Guiana).—Zoologische Verhandelingen 44:1–296, pls. 1–16.

Komai, T. 1998. The taxonomic position of *Pagurus gracilipes* (Stimpson, 1858) and *Pagurus nipponensis* (Yokoya, 1933), and description of a new species of *Pagurus* (Decapoda, Anomura, Paguridae) from Japan.—Zoosystema 20:265–288.

Lemaitre, R., & N. H. Campos. 1993. Two new hermit crabs (Crustacea: Decapoda: Paguridae) from the Caribbean Sea.—Proceedings of the Biological Society of Washington 106(3):554–565.

———, & B. B. Collette. 2000. Austin Beatty Williams (17 October 1919–27 October 1999). Biographical summary.—Proceedings of the Biological Society of Washington 113(1):2–13.

———, & P. A. McLaughlin. 1996. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: part V. *Anisopagurus* McLaughlin, *Manucomplanus* McLaughlin, and *Protoniopagurus* new genus.—Proceedings of the Biological Society of Washington 114(2): 444–483.

McLaughlin, P. A. 1974. The hermit crabs (Crustacea Decapoda, Paguroidea) of northwestern North America.—Zoologische Verhandelingen 130: 1396, pl. 1.

———. 1981a. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: part I. Ten new genera of the Paguridae and a redescription of *Tomopagurus* A. Milne Edwards and Bouvier.—Bulletin of Marine Science 3:1–30.

———. 1981b. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: part II. *Rhodochirus* McLaughlin and *Phimo-*

chirus McLaughlin.—Bulletin of Marine Science 31:329–365.

———. 1982. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: part III. *Agaricochirus* McLaughlin, *Enallopagurus* McLaughlin, and *Enallopaguropsis* McLaughlin.—Bulletin of Marine Science 32: 823–855.

———. 1988. The taxonomic position of *Pylopagurus liochele* Barnard (Decapoda, Paguroidea).—Crustaceana 54(1):5–12.

———. 2003. Illustrated keys to the families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with supplemental diagnoses of genera of the Paguridae.—Memoirs of Museum Victoria 60(1):111–144.

———, & S. W. Gunn. 1992. Revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with the descriptions of new genera and species: part IV. *Lophopagurus* McLaughlin and *Australeremus* McLaughlin.—Memoirs of the Museum of Victoria 53(1):43–99.

———, & J. Haig. 1973. On the status of *Pagurus mertensii* Brandt, with descriptions of a new genus and two new species from California (Crustacea: Decapoda: Paguridae).—Bulletin of the Southern California Academy of Sciences 72: 113–136,

———, & G. S. Jensen. 1996. A new hermit crab species of the genus *Parapagurodes* from the eastern Pacific, with a description of its first zoeal stage.—Journal of Natural History 30: 841–854.

———, & R. Lemaitre. 1993. A review of the hermit crab genus *Paguritta* (Decapoda: Anomura: Paguridae) with descriptions of three new species.—The Raffles Bulletin of Zoology 41(1): 1–29.

———, & ———. 2001. The revision of *Pylopagurus* and *Tomopagurus* (Crustacea: Decapoda: Paguridae), with descriptions of new genera and species, part VI. *Pylopagurus* Milne Edwards & Bouvier, 1891, *Haigia* McLaughlin, 1981, and *Pylopaguridium*, new genus.—Proceedings of the Biological Society of Washington 114(2): 444–483.

———, D. K. Camp, L. G. Eldredge, D. L. Felder, J. W. Goy, H. H. Hobbs, III, B. A. Kensley, R. Lemaitre, & J. W. Martin. 2003. Decapoda. *In* D. D. Turdgeon & D. K. Camp (eds.), Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Crustacea. American Fisheries Society Special Publication (in press).

Melin, G. 1939. Paguriden und Galatheiden von Prof. Dr. Sixten Bocks Expedition nacj den Bonin-Inseln, 1914.—Kongliga Svenska Vetenskapsakademiens Hanglinar (3)18(2):1–119.

Milne-Edwards, A. 1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico, and in the Caribbean Sea, 1877, 78, 79, by the United States Coast Survey steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. VIII. Études préliminaires sur les Crustacés.—Bulletin of the Museum of Comparative Zoölogy, Harvard College 8(1):1–68.

Milne-Edwards, A., & E. -L. Bouvier. 1891. Observations générales sur les paguriens recueillis dans la mer des Antilles et le Golfe du Mexique, par le Blake et le Hassler, sous la direction de M. Alexandre Agassiz.—Bulletin de la Société Philomatique de Paris (8)3:102–110.

———, & ———. 1893. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic coast of the United States (1880), by the U.S. Coast Survey Steamer "Blake", Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., commanding. XXXIII. Description des Crustacés de la famille des paguriens recueillis pendant l'expédition.—Memoirs of the Museum of Comparative Zoölogy, Harvard College 14(3):5–172.

Milne Edwards, H. 1836. Observations zoologiques sur les Pagures et description d'un nouveau genre de la tribu des Paguriens.—Annales des Sciences Naturelle, Zoologie (2)6:257–288.

Miyake, S. 1978. The crustacean Anomura of Sagami Bay: 1–200 (English), 1–161 (Japanese). Tokyo: Hoikusha Publishing Co.

Ortmann, A. 1892. Die Decapoden-Krebse des Strassburger Museum, mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. IV. Die Abtheilungen Galatheidea und Paguridea.—Zoologischen Jahrbüchern. Abtheilung für Systematik, Geographie und Biologie der Thiere 6:241–326.

Provenzano, A. J., Jr. 1961. Pagurid crabs (Decapoda Anomura) from St. John, Virgin Islands, with descriptions of three new species.—Crustaceana 3:151–166.

Saint Laurent, M. de. 1970. Révision des genres *Catapaguroides* et *Cestopagurus* et description de quatre genres nouveaux. V. *Trichopagurus* de Saint Laurent (Crustacés Décapodes Paguridae). VI. Conclusion.—Bulletin du Muséum national d'Histoire naturelle, Paris, 2e séries, No 1, 42: 210–222.

———, & P. A. McLaughlin. 2000. Superfamily Paguroidea. Family Paguridae. Pp. 104–209 *in* J. Forest, M. de Saint Laurent, P. A. McLaughlin, & R. Lemaitre, The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae. National Institute of Water and Atmospheric Research Biodiversity Memoir 114:1–250.

Scanland, T. B., & T. S. Hopkins. 1969. A new species of hermit crab, *Pylopagurus diegensis* (Decapoda: Anomura), with a key for the genus in the eastern Pacific.—Pacific Science 23:257–260.

Schmitt, W. L. 1921. The marine decapod Crustacea of California with special reference to the decapod Crustacea collected by the United States Bureau of Fisheries Steamer "Albatross" in connection with the biological survey of San Francisco Bay during the years 1912–1913.—University of California Publications in Zoology 23:1–470.

Stimpson, W. 1858. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. W. Stimpson. Pars VII. Crustacea Anomoura. [Preprint (December 1858) from].—Proceedings of the Academy of Natural Sciences of Philadelphia 10:225–252.

———. 1959. Notes on North American Crustacea.—[Preprint from] Annals of the Lyceum of Natural History in New York 7:49–93.

Studer, T. 1883. Verzeichniss der während der Reise S. M. S. Gazelle an der Wesküste von Africa, Ascension und dem Cap der guten Hoffnung gesammelten Crustaceen.—Abhandlungen der K. Preussischen Akademie der Wissenschaften (Berlin), 2(1882):1–32, pls. 1, 2.

Voss, G. L. 1966. Narrative of cruise P-6607 to the southwestern Caribbean conducted by the Institute of Marine Science, University of Miami aboard R/V *John Elliott Pillsbury* July 7–22, 1966. [Unpublished report].

Walton, B. C. 1954. The genus *Pylopagurus* (Crustacea, Anomura) in the Pacific with descriptions of two new species.—Allan Hancock Pacific Expeditions 15:139–172.

Wass, M. L. 1963. New species of hermit crabs (Decapoda, Paguridae) from the western Atlantic.—Crustaceana 6(2):133–157.

Williams, A. B., L. G. Abele, D. L. Felder, H. H. Hobbs, Jr., R. B. Manning, P. A. McLaughlin, & I. Pérez Farfante. 1989. Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Decapod crustaceans.—American Fisheries Society Special Publication 17:i–vii, 1–77 + 4 unnumbered pls.

Yokoya, Y. 1933. On the distribution of decapod Crustacea inhabiting the continental shelf around Japan, chiefly based upon the materials collected by S.S. "Soyo Maru" during the years 1923–1930.—Journal of College of Agriculture, Imperial University of Tokyo 12(1):1–226.

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A new species of the genus *Periclimenes* Costa, 1844 (Crustacea: Decapoda: Palaemonidae) from the Ryukyu Islands, southern Japan

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Abstract.—A new species of pontoniinid shrimp, *Periclimenes dolichosternum,* is described and illustrated on the basis of 21 specimens collected from sublittoral zones of the Ryukyu Islands at depths of 1.5–30 m. This new species may be readily distinguished from all previously known species of *Periclimenes* Costa, 1844 by the long third thoracic sternite, and long intermediate segment of the antennular peduncle.

Shrimps of the genus *Periclimenes* Costa, 1844, are widely distributed through tropical to warm-temperate marine and brackish waters worldwide (Chace & Bruce 1993). Most species of the genus are associated with a range of marine invertebrates, although considerable numbers are free-living (Bruce 1994). Chace & Bruce (1993) recognized 165 valid species of *Periclimenes* at the time, and subsequently 17 additional species have been described: four from the Atlantic Ocean (see Heard & Spotte 1991, 1997; d'Udekem d'Acoz 1999; Li 2000), two from the Mediterranean Sea (see d'Udekem d'Acoz 1999, Li 2000), one from the eastern Pacific region (see Vargas 2000) and ten from the Indo-West Pacific region (see Berggren 1994, Bruce & Coombes 1997, Bruce 1998, Li 2000, Hayashi & Otomi 2001, Okuno & Nomura 2002). Bruce (1994) transferred three species, *P. gorgonicola* Bruce, 1969, *P. franklini* Bruce, 1990a, and *P. setirostris* Bruce, 1991 to the newly erected genus *Paraclimenes* Bruce, 1994 on the basis of absence of the antennal spine. *Periclimenes denticulatus* Nobili, 1906 and *P. sibogae* Holthuis, 1952 have been transferred to the genus *Exoclimenella* Bruce, 1994, and *P. petitthouarsii* (Audouin, 1826) and *P. spiniferus* De Man, 1902 to the genus *Periclimenella* Bruce, 1994 (see Duris & Bruce 1995). More recently, Wicksten (1995) and Spotte (1999) pointed out that *Periclimenes anthophilus* Holthuis and Eibl-Eibesfeldt, 1964 should be considered as a junior synonym of *P. pedersoni* Chace, 1958. Thus, currently there is a total of 174 valid species of *Periclimenes* known worldwide. On the basis of a bibliographic survey, Li (2000) provided illustrations for 148 of these species.

In 1998, an ovigerous female shrimp of an unfamiliar free-living pontoniinid species was found. The specimen was collected from the sublittoral zone (4.0 m depth) of Iriomote Island (southwestern Ryukyu Islands). Subsequently, additional specimens collected from Kume Island and Iriomote Island, the Ryukyu Islands were examined. These specimens clearly belong to an undescribed species of *Periclimenes,* and are here described as a new species.

Illustrations were made with the aid of a camera lucida mounted on both dissecting microscope and compound microscope. For microstructural observations under the scanning electron microscope (SEM), the telson and appendages of two of the specimens (NSMT-Cr 1988, 1989) were dissected and freeze dried. The postorbital carapace length is abbreviated as CL in the text. The term 'bec ocellaire' is used for the anteromedian process on the ophthalmic somite. The specimens examined in this study are deposited in the Coastal Branch of Natural History Museum and Institute, Chiba (CMNH), Nationaal Natuurhistorisch Museum, Leiden (RMNH), National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), National Science Museum, Tokyo (NSMT), and the Queensland Museum, South Brisbane (QM).

Family Palaemonidae Rafinesque, 1815
Subfamily Pontoniinae Kingsley, 1878
Genus *Periclimenes* Costa, 1844
Periclimenes dolichosternum, new species
Figs. 1–5

Type series.—Holotype: ♀ CL 2.6 mm, Ou-shima Harbor, Kume Island, Ryukyu Islands, 26°20.1′N, 126°49.2′E, 1.5 m, 19 Dec 2001, coll. J. Okuno and T. Takahashi, CMNH-ZC 00855. Paratypes: Ryukyu Islands. 1 ovig. ♀ CL 2.4 mm, 1 ♀ CL 1.5 mm, same locality as holotype, 12 Jul 2001, coll. T. Kawamoto, CMNH-ZC 00791; 1 ♂ CL 2.1 mm, CMNH-ZC 00802, 1 ♀ CL 2.2 mm, CMNH-ZC 00801, 1 ♂ CL 2.0 mm, 1 ♀ CL 1.9 mm, RMNH-D 49858, same locality as holotype, 19 Oct 2001, coll. T. Kawamoto; 2 ♂ CL 1.6, 2.8 mm, CMNH-ZC 00856, 1 ♀ CL 2.4 mm, QM-W 26570, same data as holotype; 1 ovig. ♀ CL 2.3 mm, Amitori Bay, Iriomote Island, Yaeyama Group, 24°19.6′N, 123°42.2′E, 4 m, 25 May 1998, coll. R. Minemizu, CMNH-ZC 00767; 1 ovig. ♀ CL 3.1 mm, CMNH-ZC 00931, 1 ♂ CL 2.6 mm, 2 ♀ CL 2.1, 2.9 mm, 4 ovig. ♀ CL 2.2–4.1 mm, NSMT-Cr 1981, 1 ovig. ♀ CL 3.6 mm, NSMT-Cr 1988, 1 ovig. ♀ CL 3.7 mm, NSMT-Cr 1989, 1 ♀ CL 3.0 mm, 1 ovig. ♀ CL 4.4 mm, USNM 1006977, Amitori Bay, 25–30 m, 2 Jul 2000, coll. Y. Ikeda and K. Hagiwara.

Diagnosis.—Size small (CL 1.5–4.4 mm), body slender. Carapace usually armed with epigastric spine. Rostrum slender, straight, falling slightly short of distal margin of proximal segment of antennular peduncle, dorsal margin dentate, ventral margin with 0–2 vestigial teeth subapically. Third thoracic sternite about 3 times as long as fourth sternite. Third abdominal somite with median carina posterodorsally produced. Sixth somite distinctly longer than postorbital carapace length. Intermediate segment of antennular peduncle about twice as long as distal segment. Third maxilliped without arthrobranch. First and second pereiopods slender, each with carpus considerably longer than chela. Chela of second pereiopod with fingers about twice as long as palm, cutting edges armed mesially with numerous recurved fine teeth. Third to fifth pereiopods slender, with dactyli biunguiculate. Endopod of male first pleopod without appendix interna.

Description.—Carapace (Fig. 1) smooth, glabrous, lacking supraorbital spine; orbit feebly developed, inferior orbital margin strongly produced, semiquadrate; antennal spine well developed, slender, submarginal, arising distinctly ventral to orbital margin; hepatic spine large, arising slightly ventral to level of antennal spine; epigastric spine usually present, feebly articulated with median carina; pterygostomian margin rounded.

Rostrum (Fig. 2A, B) slender, straight, 0.5–0.6 times as long as carapace, falling short of level of distal margin of proximal segment of antennular peduncle; dorsal blade low, with 5–7 (usually 6) equidistantly spaced, small, acute teeth, interspaced by short setae; ventral blade poorly developed, proximally with row of short setae, with 0–2 vestigial or minute teeth subapically.

Second thoracic sternite (Fig. 2C) with median longitudinal ridge; third sternite

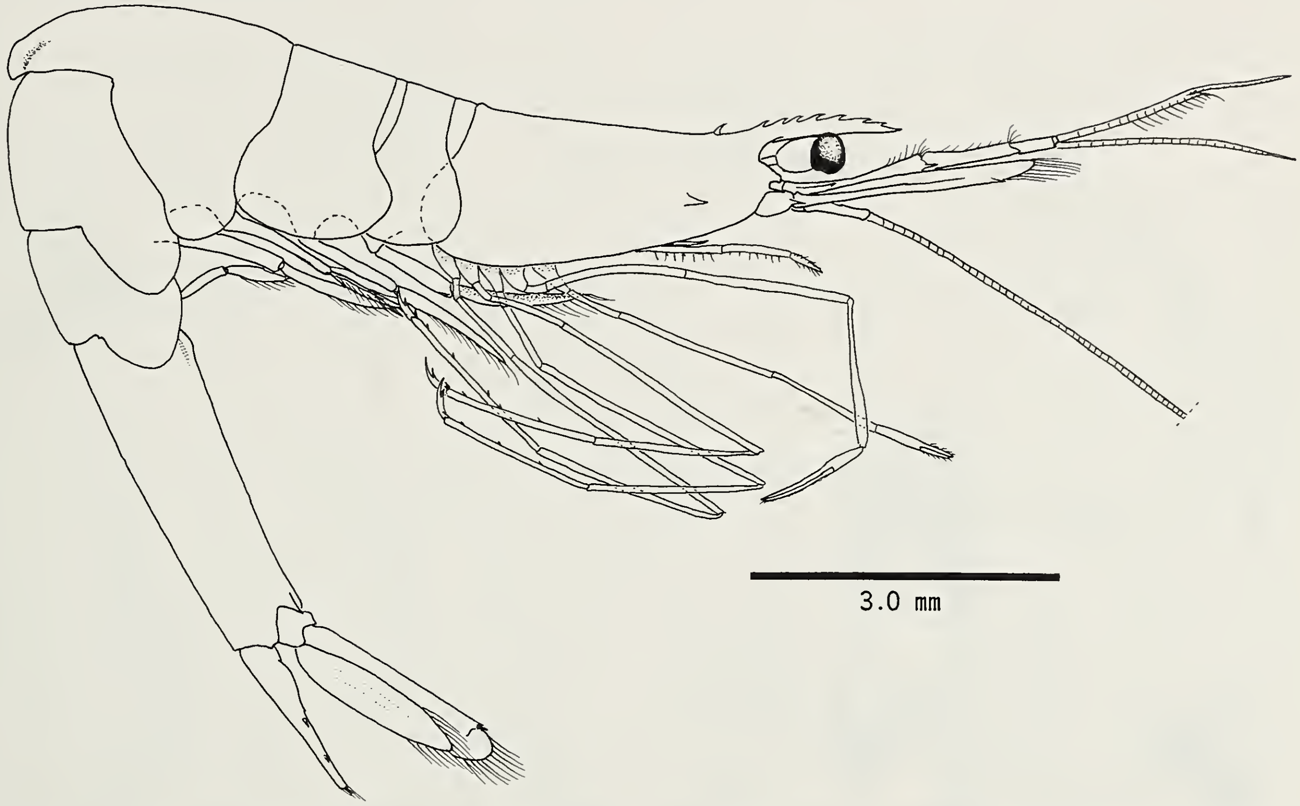

Fig. 1. *Periclimenes dolichosternum,* new species. Holotype female, CMNH-ZC 00855. Entire animal in lateral view.

about 1.5 times as long as second, 3 times as long as fourth; fourth to eighth sternites (Fig. 2D) unarmed, fourth sternite with low transverse ridge, median notch shallow.

Abdomen (Fig. 1) smooth, glabrous; pleura of first to third somites broad, rounded; those of fourth and fifth somites posteriorly produced, but blunt; posterodorsal tergum of third somite produced posteriorly, slightly elevated dorsally, compressed laterally (Fig. 2E); sixth somite slender, elongate, 1.2–1.8 times as long as carapace, posterolateral process blunt, posterolateral margin produced. Telson (Fig. 2F) tapering posteriorly, posterior margin convex, with 3 pairs of spines, intermediate pair longest, mesialmost pair plumose, lateral and intermediate pairs simple (Fig. 5A); 2 pairs of small, subequal dorsolateral spines positioned midlength of telson and midway between these spines and posterior margin of telson.

Ophthalmic somite without 'bec ocellaire'. Eye (Fig. 2A) with large, globular, pigmented cornea, bearing small ocellus; stalk slightly longer than maximum corneal diameter, maximum width less than maximum corneal diameter.

Antennular peduncle (Fig. 2A) slender, slightly overreaching apex of lamella of scaphocerite; proximal segment with distolateral margin strongly produced, lateral margin straight, terminating distally in large acute tooth, slightly overreaching distolateral margin; ventromesial margin armed with small acute tooth; stylocerite short, slender, acute, reaching level of proximal third of length of proximal segment; statocyst well developed, rounded; intermediate segment about twice as long as distal segment, with distolateral margin strongly produced, lateral lobe well developed, slightly depressed, laterally setose; distal segment short, feebly setose mesially. Upper flagellum biramous, proximal 11 or 12 segments fused, shorter free ramus 3 or 4 segmented; lower flagellum more slender than upper flagellum.

Antenna with stout basicerite armed ventrolaterally with acute tooth, dorsal margin

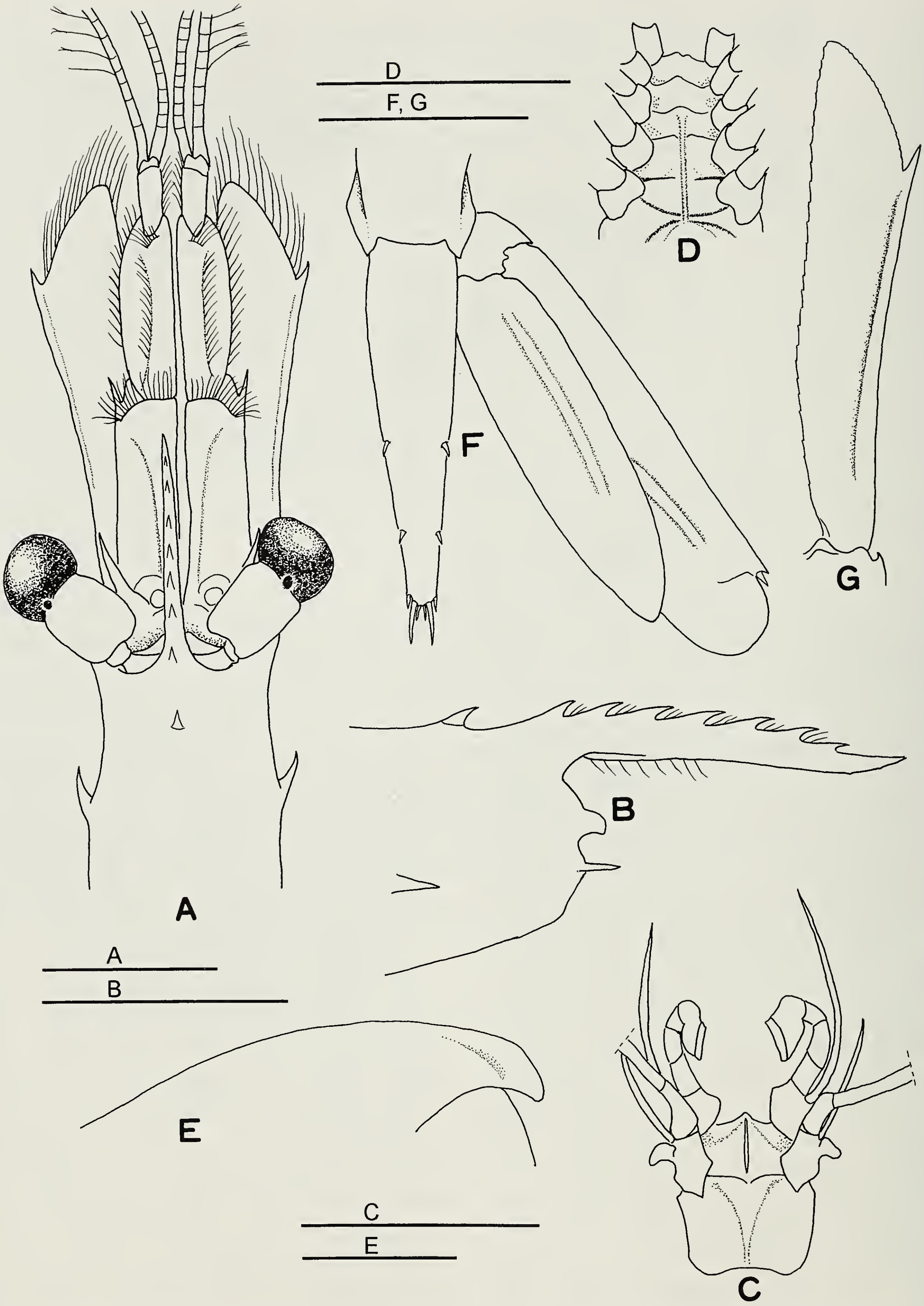

Fig. 2. *Periclimenes dolichosternum,* new species. A, B, F, G, holotype female, CMNH-ZC 00855; D, male paratype, CMNH-ZC 00802; C, E, ovigerous female paratype, CMNH-ZC 00931. A, anterior carapace, rostrum and cephalic appendages, dorsal; B, anterior carapace and rostrum, lateral; C, second and third thoracic sternites, ventral; D, fourth to eighth thoracic sternites, ventral; E, dorsal part of third abdominal somites, lateral; F, telson and right uropod, dorsal; G, right antennal scaphocerite, dorsal. C, D, F, G, setae omitted. Scales: 1.0 mm.

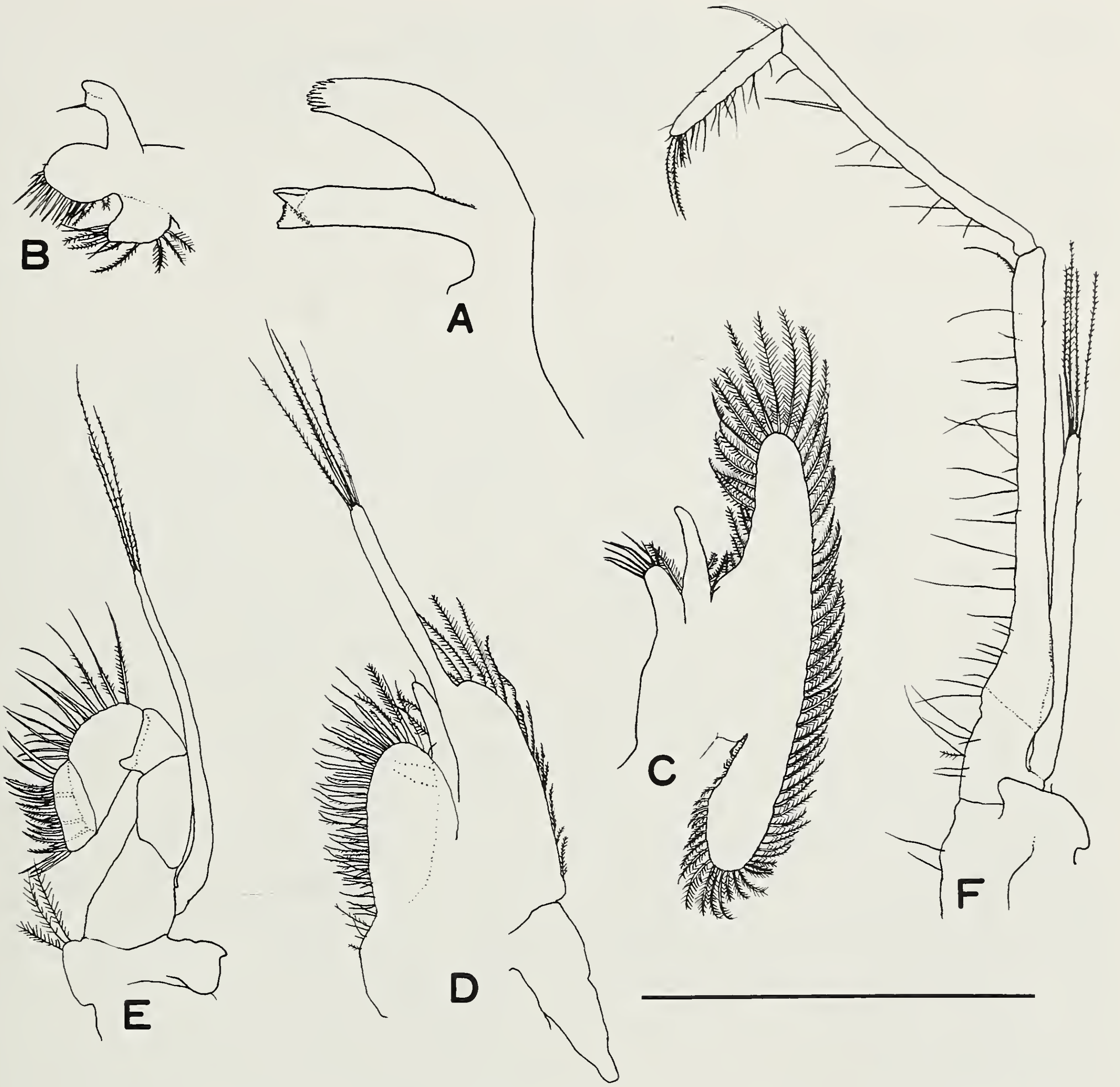

Fig. 3. *Periclimenes dolichosternum*, new species. Female paratype, NSMT-Cr 1988. A, left mandible, external; B, left maxillule, external; C, left maxilla, external; D, left first maxilliped, external; E, left second maxilliped, external; F, left third maxilliped, lateral. Scale: A, 0.5 mm; B–F, 1.0 mm.

with small raised lobe; scaphocerite (Fig. 2G) slender, with lateral margin feebly concave, terminating in strong tooth reaching distal fifth of length of scaphocerite, lamella strongly tapering distomesially in dorsal view, 3.4–5.4 times as long as width at base of lateral tooth; carpocerite reaching proximal fourth of length of scaphocerite.

Epistome unarmed.

Mandible (Fig. 3A) without palp; incisor process well developed, distal margin truncated, armed with 7 or 8 small teeth; molar process truncated distally, with stout teeth. Maxillule (Fig. 3B) with feebly bilobed palp, inner lobe with long simple seta; upper lacinia broad, distal margin truncated, armed with simple spines and few simple setae; lower lacinia sparsely furnished with plumose setae marginally. Maxilla (Fig. 3C) with slender, tapering palp; distal endite developed, simple, narrow, distally furnished with sparse simple setae; proximal endite obsolete; scaphognathite well developed, marginally furnished with numerous plumose setae, anterior lobe slightly tapering distally. First maxilliped (Fig. 3D) with

Table 1.—*Periclimenes dolichosternum,* new species. Branchial formula.

	Maxillipeds			Pereiopods				
	I	II	III	I	II	III	IV	V
Pleurobranchs	—	—	—	1	1	1	1	1
Arthrobranchs	—	—	—	—	—	—	—	—
Podobranchs	—	—	—	—	—	—	—	—
Epipods	1	1	—	—	—	—	—	—
Exopods	1	1	1	—	—	—	—	—

long, slender, simple palp; distal endite furnished with long, simple and plumose setae; proximal endite developed, rounded; caridean lobe broad, low; exopod with well developed flagellum; epipod large, feebly bilobed. Second maxilliped (Fig. 3E) with normal endopod; ischium and basis fused; exopod with well developed flagellum; coxa inflated mesially; epipod small, subquadrate, without podobranch. Third maxilliped (Fig. 3F) with endopod slender, overreaching distal margin of antennal basicerite by full length of ultimate segment; ultimate segment tapering distally, ventral surface with 5 transverse rows of simple setae; penultimate segment 1.7–2.3 times as long as ultimate segment, sparsely with simple setae mesially; antepenultimate segment with tufts of long simple setae on ventral surface; coxal plate semiquadrate; arthrobranch absent.

Branchial formula as in Table 1.

First pereiopod (Fig. 4A) slender, falling slightly short of distal end of scaphocerite. Chela (Fig. 5B) 0.2–0.3 times as long as carapace; palm slightly compressed, slightly longer than dactylus, with 3 transverse rows of short serrulate glooming setae proximally, with sparse setae anterior to rows of glooming setae; fingers each terminating in small, hooked unguis, cutting edges situated laterally, entire. Carpus 1.6–2.2 times as long as chela, slightly widened distally, with longitudinal row of serrulate glooming setae distomesially. Merus unarmed, 1.1–1.3 times as long as carpus.

Second pereiopods (Fig. 4B) slender, similar, overreaching distal margin of scaphocerite by length of dactyli. Chela well developed, small, 0.4–0.6 times as long as carapace; palm slightly swollen; dactylus (Fig. 5C) elongate, 2.2–2.3 times as long as palm, terminating in hooked, acutely pointed unguis, cutting edge with large, acute subterminal tooth and 43–76 laterally situated, recurved, fine teeth; fixed finger (Fig. 5C) similar to dactylus. Carpus elongate, slightly widened distally, unarmed, 1.1–2.0 times as long as chela. Merus elongate, unarmed, 1.05–1.14 times as long as carpus. Ischium slender, unarmed 0.9–1.0 times as long as carpus.

Third pereiopod (Fig. 4C) slender, overreaching distal margin of scaphocerite by distal half of propodus and dactylus. Dactylus (Fig. 5D) slender, ventral margin armed with 1 accessory tooth, unguis not clearly demarcated, about 2.5 times as long as accessory tooth. Propodus (Fig. 4C) 0.8–1.0 times as long as carpus, 4.0 times as long as dactylus, with 2 long distoventral spines and equidistantly spaced set of 3 spines on ventral surface, dorsal surface with few short setae. Carpus unarmed. Merus 1.4–1.5 times as long as carpus. Fourth and fifth pereiopods similar in form to third.

Endopod of male first pleopod (Fig. 4D) short, slender, tapering distally, reaching proximal fifth of exopod, without appendix interna. Endopod of male second pleopod (Fig. 4E) with appendices interna and masculina arising from proximal third of mesial margin; appendix interna slender, slightly overreaching tip of appendix masculina, with few distal cincinnuli; appendix masculina slender, distally with 2 long setae with fine setules.

Uropod (Fig. 2F) with protopodite pos-

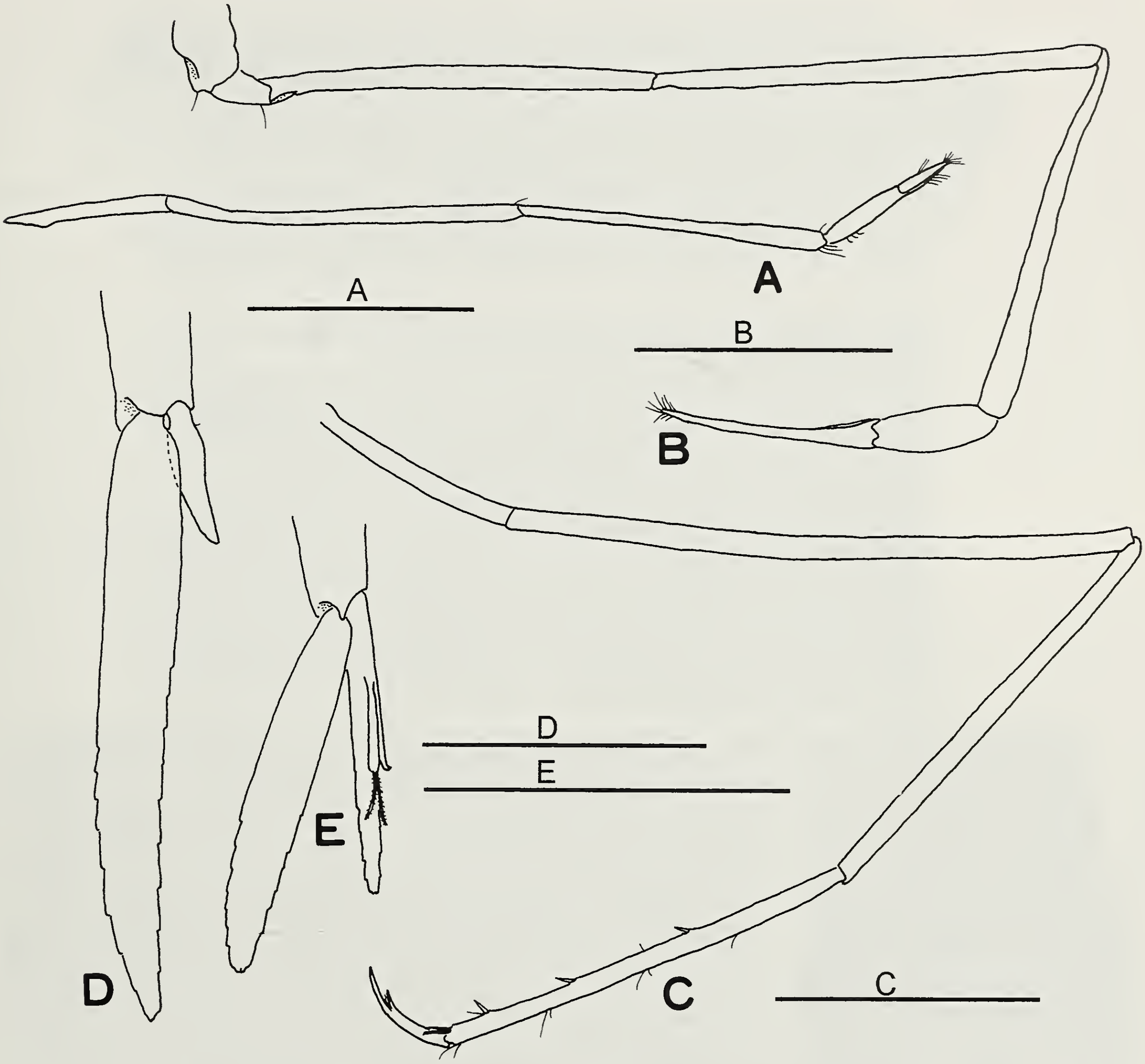

Fig. 4. *Periclimenes dolichosternum*, new species. A–C, holotype female, CMNH-ZC 00855; D, E, male paratype, CMNH-ZC 00802. A, right first pereiopod, lateral; B, right second pereiopod, lateral; C, right third pereiopod, lateral; D, male right first pleopod, dorsal; E, male second pleopod, dorsal. D, E, marginal setae omitted. Scales: A–C, E, 1.0 mm; D, 0.5 mm.

terolaterally produced; exopod broad, distinctly overreaching posterior margin of telson, lateral margin straight, terminating in small acute tooth, with larger mobile spine proximesial to distolateral tooth; endopod oval, slightly shorter than exopod.

Color in life.—Body and appendages generally transparent. Lateral part of carapace with oblique white band. Dorsal surface of median carina of third abdominal somite with large, white semiquadrate circle. Posterior margin of sixth abdominal somite white. Antennular peduncle yellowish brown. Scaphocerite whitish yellow, covered with dark brown spots. Posterior part of uropods white.

Etymology.—From the Greek, *dolichos* meaning long and the Greek *sternon* meaning breast, in reference to the characteristic, long third thoracic sternite of the new species.

Ecological notes.—Field notes taken at Kume Island show the following: the species lives beneath large pieces of coral rubbles (about 20 cm diameter) on a silty bottom at a depth of 1.5 m. Any sessile invertebrates possibly being the host of shrimps do not appear on surface or vicinity of the

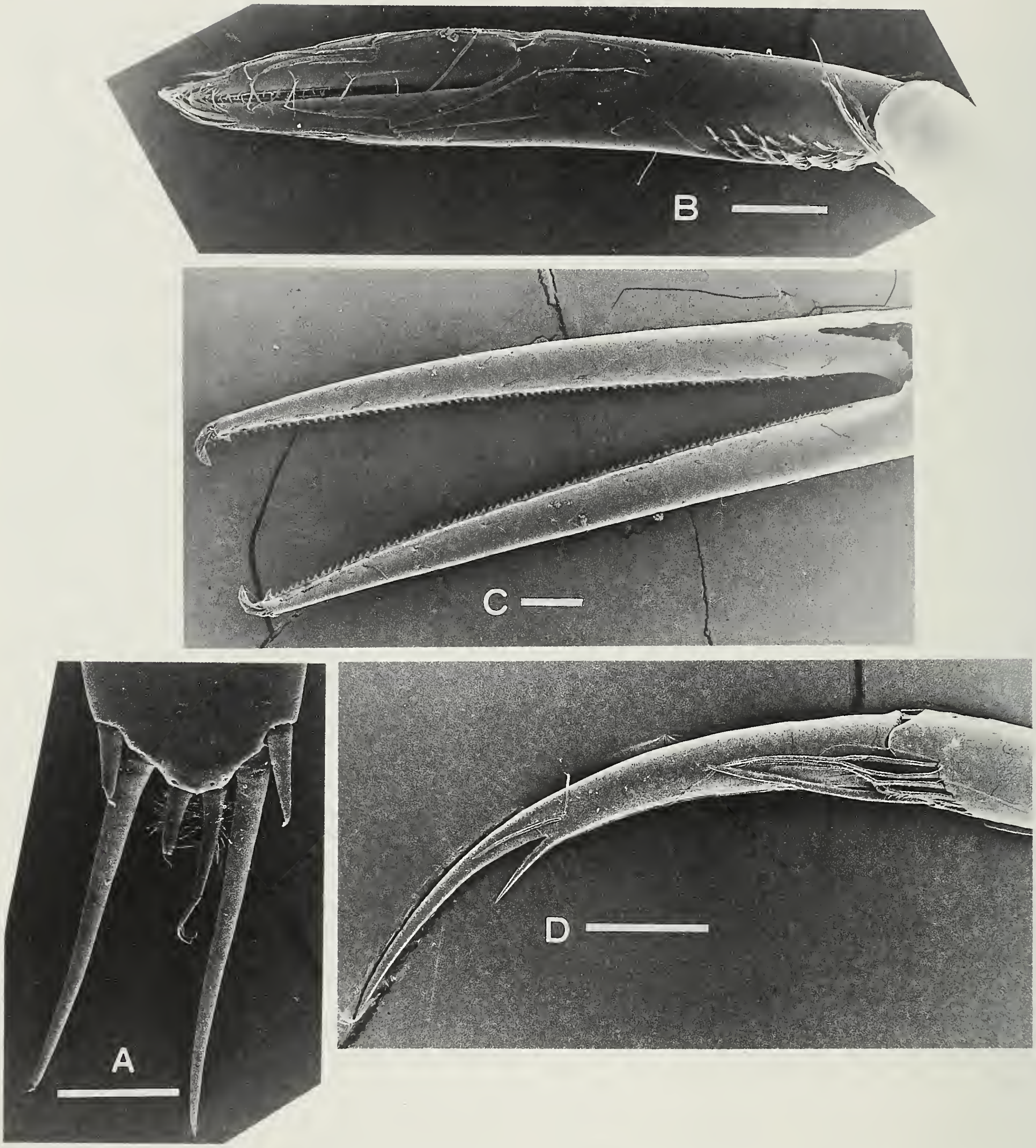

Fig. 5. *Periclimenes dolichosternum,* new species. A, ovigerous female paratype, NSMT-Cr 1989; B–D, ovigerous female paratype, NSMT-Cr 1988. A, tip of telson, dorsal; B, chela of right first pereiopod, mesial; C, fingers of right second pereiopod, mesial; D, dactylus of right third pereiopod, mesial. Scales: 100 μm.

rubble. One to four individuals were found underneath one piece of rubble. When the rubble was removed, shrimps always clung to the underside. The small and transparent body of the shrimp is almost invisible in muddy water. The specimens collected from Iriomote Island in 2000 lived around the *Halimeda* green algae bed on sandy bottom at depths of 25–30 m.

Distribution.—Known only from the Ryukyu Islands, southern Japan.

Remarks.—Currently, the genus *Periclimenes* is morphologically distinguished from other pontoniinid genera by the following features (see Chace & Bruce 1993, Bruce 1994, Holthuis 1993): body slightly compressed laterally; carapace armed with well developed antennal and fixed hepatic spines; dorsal and ventral blades of rostrum dentate, with proximal part of rostrum not forming a supraorbital eave; pleura of first five abdominal somites lacking acute posteroventral angles; mandible lacking palp; third maxilliped with 0 or 1 arthrobranch; exopod of third maxilliped well developed; dactyli of third to fifth pereiopods lacking hoof-like protuberances.

Periclimenes dolichosternum can be separated from other species of *Periclimenes* by the long third thoracic sternite, and long intermediate segment of the antennular peduncle. The third thoracic sternite is about four times as long as the fourth somite; therefore, in lateral view, the interval between the third maxilliped and first pereiopod is wide. Although the length of third thoracic sternite has previously been overlooked, the space between third maxilliped and first pereiopod can be used to distinguish *P. dolichosternum* from other congeneric species. The intermediate segment of the antennular peduncle is about twice as long as the distal segment, and the antennular peduncle overreaches the distal margin of the scaphocerite.

The posterior protrusion of the tergum of the third abdominal somite is found in some *Periclimenes* species of the '*P. aesopius* species group' (see Bruce 1990b, Okuno & Nomura 2002). In addition to the features mentioned above, *P. dolichosternum* is readily distinguished from species of '*P. aesopius* species group' by having the longer and slenderer pereiopods, numerous recurved teeth on the cutting edges of the second pereiopodal fingers, the considerably wider corneal diameter than maximum width of eyestalk, and lacking a reflected inner flange on the inferior orbital angle. Thus, we did not consider *P. dolichosternum* as the member of the '*P. aesopius* species group'.

Acknowledgments

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Literature Cited

Audouin, V. 1826. Explication sommaire des planches de Crustacés de l'Égypte et de la Syrie, publiées par Jules-César Savigny, membre de l'Institut; offrant un exposé des caractèeres naturels des genres, avec la distinction des espèces. Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'Expédition de l'Armée Française.—Histoire Naturelle 1:77–98. (not seen)

Berggren, M. 1994. *Periclimenes nomadophila* and *Tureariocaris sarec*, two new species of pontoniine shrimps (Decapoda: Pontoniinae), from Inhaca Island, Moçambique.—Journal of Crustacean Biology 14:782–802.

Bruce, A. J. 1969. Preliminary descriptions of sixteen new species of the genus *Periclimenes* Costa, 1844 (Crustacea, Decapoda, Natantia, Pontoniinae).—Zoologische Mededelingen 43:253–278.

———. 1990a. *Periclimenes franklini* sp. nov., a new deep-sea shrimp from the Coral Sea (Crustacea: Decapoda: Palaemonidae).—The Beagle, Records of the Northern Territory Museum of Arts and Sciences 7:55–64.

———. 1990b. A new cnidarian-associated palaemonid shrimp from Port Essington, Cobourg Peninsula, Australia.—Indo-Malayan Zoology 6: 229–243.

———. 1991. Crustacea Decapoda: further deep-sea palaemonid shrimps from New Caledonian waters. Pp. 299–411 *in* A. Crosnier, ed., Résultats des Campagnes MUSORSTOM, 9. Mémoires Muséum National d'Histoire Naturelle, (A) 152, 520 pp.

———. 1994. A synopsis of the Indo-West Pacific genera of the Pontoniinae (Crustacea: Decapoda: Palaemonidae). Koeltz Scientific Books, Konigstein, 172 pp.

———. 1998. Pontoniine shrimps from Moreton Bay, Queensland (Crustacea: Decapoda: Pontoniinae).—Memoirs of the Queensland Museum 42:387–398.

———, & K. E. Coombes. 1997. An annotated checklist of the caridean shrimps (Crustacea: Decapoda) of Darwin Harbour, with descriptions of three new species of *Periclimenes* (Palaemonidae: Pontoniinae). Pp. 301–337 *in* J. R. Hanley, G. Caswell, G. Megirian, and H. K. Larson, eds., Proceedings of the Sixth International Marine Biological Workshop. The marine flora and fauna of Darwin Harbor, Northern Territory, Australia. Museum and Art Galleries of the Northern Territory and the Australian Marine Science Association, Darwin, 466 pp.

Chace, F. A., Jr. 1958. A new shrimp of the genus *Periclimenes* from the West Indies.—Proceedings of the Biological Society of Washington 71:125–130.

———, & A. J. Bruce. 1993. The caridean shrimps (Crustacea: Decapoda) of The Albatross Philippine Expedition 1907–1910, Part 6: Superfamily Palaemonoidea.—Smithsonian Contributions to Zoology 543:i–iiv+1–152.

Costa, O. G. 1844. Su due nouvi generi di Crostacei decapodi Macrouri Nota.—Annali delle Accademia degli Aspiranti Naturalisti, Napoli 2:285–290. (not seen)

De Man, J. G. 1902. Die von Herrn Professor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden. Pp. 467–929, pls. 18–27, *in* W. Kükenthal, ed., Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo. Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft 25:1–988, pls. 1–28.

Duris, Z., & A. J. Bruce. 1995. A revision of the 'petitthouarsii' species-group of the genus *Periclimenes* Costa, 1844 (Crustacea: Decapoda: Palaemonidae).—Journal of Natural History 29: 619–671.

Hayashi, K.-I., & J. Otomi. 2001. A new species of the genus *Periclimenes* (Decapoda: Caridea: Palaemonidae) collected from hydrothermal vent fields in Kagoshima Bay, Japan.—Crustacean Research 30:160–171.

Heard, R. W., & S. Spotte. 1991. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. II. *Periclimenes patae*, new species, a gorgonian associate from shallow reef areas off the Turks and Caicos Islands and Florida Keys.—Proceedings of the Biological Society of Washington 104:40–48.

———, & ———. 1997. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) of the northwest Atlantic. V. *Periclimenes mclellandi*, new species, a gorgonian associate from Pine Cay, Turks and Caicos Islands, British West Indies.—Proceedings of the Biological Society of Washington 110:39–48.

Holthuis, L. B. 1952. The Decapoda of the Siboga Expedition, part XI: the Palaemonidae collected by the Siboga and Snellius Expeditions, with remarks on other species, II. Subfamily Pontoniinae.—Siboga-Expeditie 39a^{10}:1–254.

———. 1993. The recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda): with an appendix of the order Amphionidacea. Nationaal Natuurhistorisch Museum, Leiden, 328 pp.

———, & Eibl-Eibesfeldt. 1964. A new species of the genus *Periclimenes* from Bermuda (Crustacea, Decapoda, Palaemonidae).—Senckenbergiana Biologica 45:185–192.

Li, X.-Z. 2000. Catalog of the genera and species of Pontoniinae Kingsley, 1878 (Decapoda, Palaemonidae). Xueyuan Press, Beijing, 319 pp.

Nobili, G. 1906. Diagnoses préliminaires de Crustacés, Décapodes et Isopodes nouveaux recueillis par M. le Dr G. Seurat aux îles Touamotou.—Bulletin du Muséum d'Histoire Naturelle 12:256–270.

Okuno, J., & K. Nomura. 2002. A new species of the '*Periclimenes aesopius* species group' (Decapoda: Palaemonidae: Pontoniinae) associated with sea anemone from Pacific coast of Honshu, Japan.—Natural History Research 7:83–94.

Spotte, S. 1999. Possible synonymy of the western Atlantic anemone shrimps *Periclimenes pedersoni* and *P. anthophilus* based on morphology.—Bulletin of Marine Science 65:407–417.

Udekem d'Acoz, C. d'. 1999. Inventaire et distribution des crustacés décapodes de l'Atlantique oriental, de la Méditerranée et des eaux continentales adjacentes, au nord de 25°N. Collection Patrimoines Naturels, Múseum National d'Histoire Naturelle, Service du Patrimoine Natural, Paris, 383 pp.

Vargas, R. 2000. *Periclimenes murcielagensis,* a new species of shrimp (Crustacea: Decapoda: Palaemonidae) living on black coral from the Pacific coast of Costa Rica.—Proceedings of the Biological Society of Washington 113:17–23.

Wicksten, M. K. 1995. Within-species variation in *Periclimenes yucatanicus* (Ives), with taxonomic remarks on *P. pedersoni* Chace (Crustacea: Decapoda: Caridea: Palaemonidae).—Proceedings of the Biological Society of Washington 108: 458–464.

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A new genus and species, *Tumidochelia randyi,* from the Gulf of Mexico (Crustacea: Peracarida: Tanaidacea)

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Abstract.—*Tumidochelia randyi,* new genus, new species is described from the continental slope of the northern Gulf of Mexico at depths ranging from 482 to 2974 m. It is distinguished from the other genera and species of Tanaidomorpha by having: an inflated "shield-like" laterally compressed expansion of the inner distal side of the cheliped carpus, and a biramous uropod with a dorsal process on the inner distal margin of the protopod. *Tumidochelia randyi* is placed in the family Colletteidae Larsen & Wilson, although no phylogenetic analysis has been performed to support this designation.

Deep-water tanaidaceans from the Gulf of Mexico have recently been the focus of an intense taxonomic study. Prior to the year 2000, only five species, two apseudomorphans, one neotanaidomorphan, and two tanaidomorphans were known from depths greater than 200 m (see Gardiner 1975, Sieg & Heard 1989, Viskup & Heard 1989, Meyer & Heard 1989). As a result of study conducted on the Tanaidacea of the Gulf of Mexico, within the last year, the number of described deep-water species from the region has nearly tripled (Larsen 2002, Larsen & Heard 2002, 2003; Larsen & Hansknecht 2002).

Recent examination of specimens collected from the deep waters of the northern Gulf of Mexico by personnel of Texas A&M University during a Mineral Management Service sponsored study revealed an undescribed tanaidomorphan tanaidacean having affinities with species of the family Colletteidae Larsen & Wilson, 2002. After further study it was determined that the species was undescribed and represented a new genus. This new genus and species, which is described here, brings the number of tanaidacean taxa described from the deep water (greater than 300 m) in the Gulf of Mexico to 14 species in 11 different genera.

Type material has been deposited in the National Museum of Natural History, Washington, D.C. (USNM), and the Gulf Coast Research Laboratory Museum (GCRL). The terminology used in this study follows that of Dojiri & Sieg (1997) with the exception of the terms sternal and tergal, which have been substituted by ventral and dorsal, respectively.

Tumidochelia, new genus

Diagnosis.—Female: Body elongate. Antennule with 4 articles. Antenna with 6 articles; article 3 without fusion line. Mandible molars of intermediate width between those of *Typhlotanais* and *Leptognathia,* and with ring of small apical spines. Cheliped with inflated "shield-like" laterally compressed expansion of the inner distal side of the carpus. Pereopod 1–3, propodus longer than dactylus and unguis combined. Pereopod 4–6, propodus longer, or as long as dactylus and unguis combined. Marsupium consists of four oostegites. Pleopods present. Uropod biramous, bearing distal process on protopod inner margin; endopod and exopod each with 2 articles. Male unknown.

Remarks.—The short dactylus on pereopods 1–3 and long dactylus on pereopods 4–6 is a condition found in *Tanaella* Norman & Stebbing, 1886, but members of this genus have uniramous uropods and different cheliped structure. The special features of the uropod are similar to these of *Leptognathiella spinicauda* Bird & Holdich, 1984, but this species lacks an inflated carpal lobe on the cheliped. The distinctive uropod and the inflated cheliped carpus are not found in other members of *Leptognathiella* Hansen, 1913. A specialized cheliped similar to that of *Tumidochelia* has been reported for *Stenotanais hamicauda* Bird & Holdich, 1984, *S. crassiseta* Bird & Holdich, 1984, *Paraleptognathia bacescui* Kudinova-Pasternak, 1981, *Akanthophoreus inermis* Sieg, 1986, and to a lesser degree, *Akanthophoreus weddellensis* Sieg, 1986; however, in these species, the uropod is distinctively different from that of *Tumidochelia.* The amount of homoplasy indicated by these conflicting characters is characteristic of the Paratanaidoidea (see Larsen & Wilson, 2002). With the exception of the biarticulated uropodal exopod, *Tumidochelia* fits the diagnosis for Colletteidae, but does not come close to any other family diagnoses within the Tanaidomorpha. *Tumidochelia* is therefore placed within the Colletteidae, although no phylogenetic analyses have been performed to formally support this designation.

Etymology.—Genus named for the inflated cheliped (Latin: inflated + cheliped = tumidus + chelia).

Type species.—*Tumidochelia randyi.*

Tumidochelia randyi, new species
Figs. 1 & 2

Material.—Holotype: 1 non-ovigerous female, USNM 1012109, Station NB3-2, 5 May 2000, 26°33.3912′N, 91°49.4653′W, 1875 m. Paratypes: 1 non-ovigerous female, USNM 1012111, Station C12-2, 2 Jun 2000, 26°22.9752′N, 89°14.4854′W, 2920 m; 1 non-ovigerous female, USNM 1012112, Station AC1-2, 19 May 2000, 26°23.2813′N, 94°33.2633′W, 2450 m; 2 non-ovigerous females, GCRL 2049, Station B3-1, 10 May 2000, 26°09.8667′N, 91°44.1060′W, 2650 m.

Additional material.—1 non-ovigerous female, Station C7-1, 30 May 2000, 27°43.6967′N, 89°58.7782′W, 1080 m; 1 ovigerous female, Station C12-1, 2 Jun 2000, 26°22.7651′N, 89°14.4849′W, 2922 m; 1 non-ovigerous female, Station MT1-2, 17 Jun 2000, 28°32.3703′N, 89°49.7338′W, 482 m; 2 non-ovigerous females, Station NB5-2, 9 May 2000, 26°15.0855′N, 91°12.7524′W, 2060 m; 1 non-ovigerous female, Station S35-2, 11 Jun 2000, 29°19.9897′N, 87°02.9021′W, 667 m; 2 non-ovigerous females, Station S37-1, 13 Jun 2000, 28°33.4054′N, 87°45.7357′W, 2388 m; 1 non-ovigerous female, Station S37-2, 13 Jun 2000, 28°33.4292′N, 87°45.6441′W, 2,382 m; 1 non-ovigerous female, Station S41-1, 8 Jun 2000, 28°00.8463′N, 86°34.5587′W, 2974 m.

Description.—Body sub-cylindrical, elongate, approximately 7.7 times longer than wide. (Figs. 1A, B)

Cephalothorax (Figs. 1A, B): Longer than wide (l/w 1.33) with no pronounced spines or setae.

Pereonites (Figs. 1A, B): All approximately of equal length and width.

Pleon (Figs. 1A, B): Having pleonites all approximately of equal length and width.

Pleotelson (Figs. 1A, B, H): Longer than combined length of 3 pleonites and tapering to a pointed apex.

Antenna 1 (Fig. 1C): With 4 articles. Stout at base tapering distally, approximately 0.65 length of carapace. Article 1 with 1 simple distal seta and 2 subdistal broom setae; article 2 approximately 0.75 length of article 1, with 2 simple distal setae; article 3 approximately 0.3 length of article 2, with

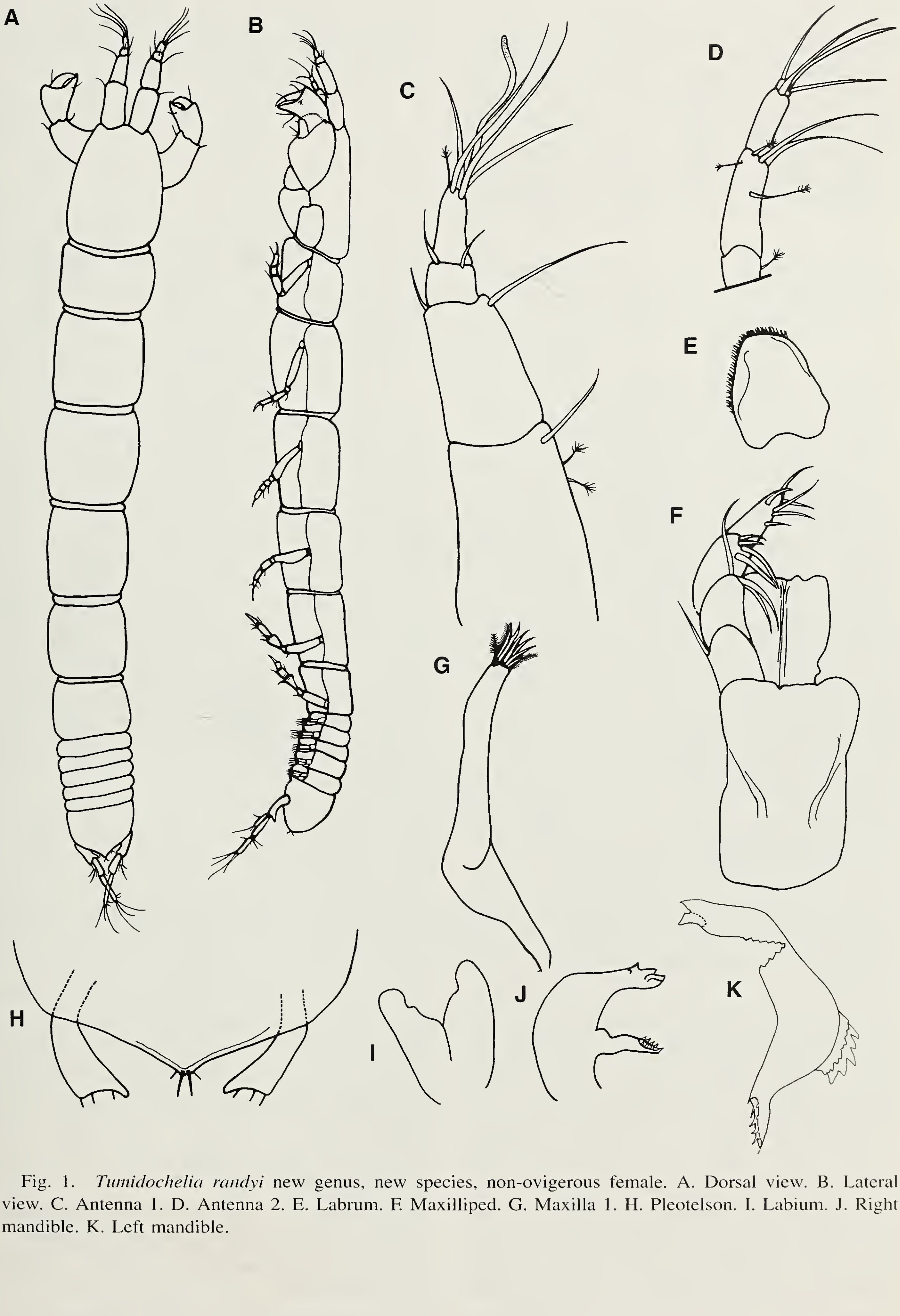

Fig. 1. *Tumidochelia randyi* new genus, new species, non-ovigerous female. A. Dorsal view. B. Lateral view. C. Antenna 1. D. Antenna 2. E. Labrum. F. Maxilliped. G. Maxilla 1. H. Pleotelson. I. Labium. J. Right mandible. K. Left mandible.

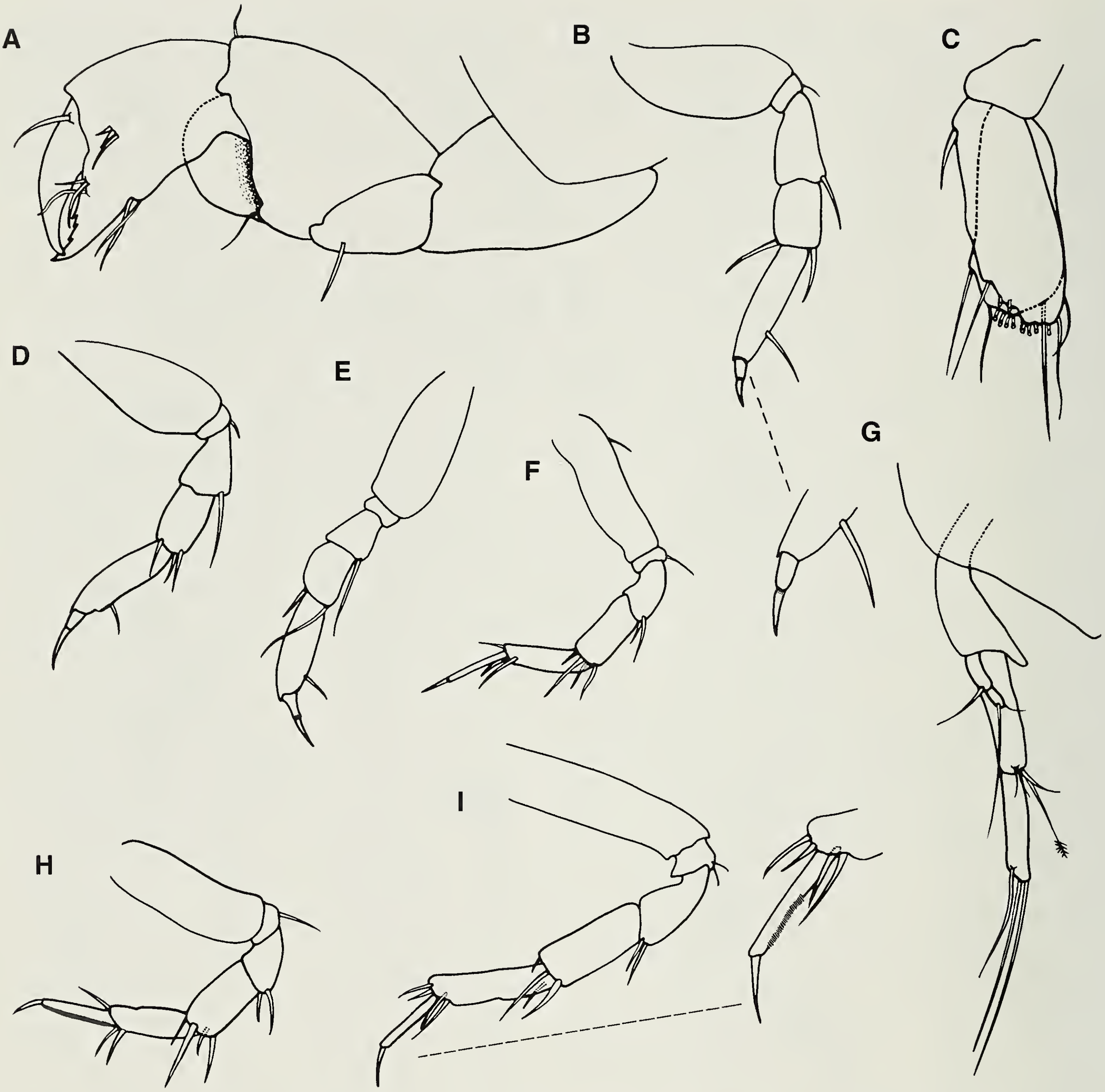

Fig. 2. *Tumidochelia randyi* new genus, new species, non-ovigerous female. A. Left cheliped. B. Pereopod 1 with enlargement of dactylus and unguis. C. Pleopod 1. D. Pereopod 2. E. Pereopod 3. F. Pereopod 4. G. Uropod. H. Pereopod 5. I. Pereopod 6 with enlargement of dactylus and unguis.

2 simple distal setae; article 4 narrowing distally, approximately twice length of article 3, with 4 simple distal setae, 1 distal broom seta, and 1 elongate aesthetasc.

Antenna 2 (Fig. 1D): With 6 articles (observed from undissected specimen). Approximately 0.5 length of antenna 1. Articles 1, 2 and proximal part of article 3 not recovered; distal part of article 3 with 1 broom seta; article 4 approximately same length as articles 5 and 6 combined, with 2 simple distal setae, 2 distal broom setae, and 1 subdistal broom seta; article 5 approximately 0.75 length of article 4, with 1 simple distal seta; article 6 approximately 0.25 length of article 5, with 3 simple distal setae.

Labrum (Fig. 1E): Apex rounded, with numerous setae.

Right Mandible (Fig. 1J): Molar process of intermediate width and tapering distally, with ring of terminal spines; incisor with 4 acute denticles.

Left Mandible (Fig. 1K): Molar as in

right mandible; incisor pointed; lacinia mobilis wider than incisor with flat apex.

Maxilla 1 (Fig. 1G): Endite with 8 terminal spiniform setae of which, 3 are setulose; palp not recovered.

Maxilla 2: not recovered.

Labium (Fig. 1I): Smooth with 2 blunt lobes.

Maxilliped (Fig. 1F): With smooth endites; basis fused; palp articles 1–4 similar in length; palp article 1 with simple outer seta; palp article 2 with 3 simple distal setae; palp article 3 with 4 simple distal setae; palp article 4 with 6 simple distal setae.

Epignath: Not recovered.

Cheliped, left (Fig. 2A): Attachment via sclerite. Basis smooth approximately same length as carpus; merus narrowing distally, with 1 subdistal ventral seta; carpus widening distally, with 1 simple dorsodistal seta, 1 simple ventrodistal seta, distal side inflated, extending distally past articulation; propodus approximately same length as basis with 2 simple ventral setae mid-length, and 3 small distal setae proximal to fixed finger; fixed finger displaying distal notches extending only to mid-length, with 3 medial setae; dactylus large, with 1 dorsoproximal seta.

Pereopod 1 (Fig. 2B): Basis robust with no seta; ischium with 1 simple distal seta; merus widening distally, with 1 simple ventral distal seta; carpus rectangular approximately 0.8 length of merus, with 1 simple dorsal distal seta and 1 simple ventral distal seta; propodus elongate approximately 2 times length of carpus, with 1 simple ventral subdistal seta; dactylus and unguis approximately 0.4 length of propodus, with fine distal notches.

Pereopod 2 (Fig. 2D): Same as pereopod 1, except carpus bearing 1 simple dorsodorsal distal seta and 2 simple ventrodistal setae.

Pereopod 3 (Fig. 2E): Same as pereopod 1, except ischium smooth; merus approximately 0.5 length of merus of pereopod 1; carpus with longer simple ventrodistal seta.

Pereopod 4 (Fig. 2F): Basis elongate with 1 simple ventroproximal seta; ischium with 1 simple ventral seta; merus widening distally, with 2 simple ventrodistal setae; carpus rectangular, slightly longer than merus, with 4 simple distal setae; propodus approximately same length as carpus, with 3 simple distal setae; dactylus (including unguis) approximately same length as propodus.

Pereopod 5 (Fig. 2H): Same as pereopod 4, except basis without seta; dactylus with notches extending the full length of posterior margin.

Pereopod 6 (Fig. 2I): Same as pereopod 4, except basis approximately 0.2 times longer than basis of pereopod 4, without seta; ischium with 2 simple distal setae; merus approximately 0.3 times longer than merus of pereopod 4; carpus approximately two times longer than carpus of pereopod 4; propodus approximately 0.3 times longer than propodus of peroeopod 4, with 4 simple distal setae; dactylus approximately 0.2 times longer than dactylus of pereopod 4, with notches extending 0.75 of length.

Pleopods (Fig. 2C): Protopod smooth; endopod rectangular, with numerous simple distal setae; exopod rectangular, with 1 robust proximal seta, and numerous simple distal setae.

Uropods (Fig. 2G): Biramous, attached to ventrolateral margin in mid-region of pleotelson. Protopod smooth, with dorsomedially directed process on inner distal margin; endopod with 2 articles of approximately equal length; article 1 with 3 simple distal setae and 1 distal broom seta; article 2 with 3 simple distal setae; exopod approximately 0.25 length of endopod, with 2 articles; article 1 approximately twice length of article 2, with 1 simple distal seta; article 2 with 2 simple distal setae.

Remarks.—See remarks for genus.

Etymology.—The species named for Thomas Randell "Randy" Knight, father of the senior author, in appreciation of his support and encouragement of her academic pursuits.

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Literature Cited

Bird, G. J., & D. M. Holdich. 1984. New deep-sea Leptognathiid Tanaids (Crustacea, Tanaidacea) from the North-east Atlantic.—Zoologica Scripta 13:285–315.

Dojiri, M., & J. Sieg. 1997. Chapter 3. The Tanaidacea. Pp. 181–268 *in* J. A. Blake & P. H. Scott, eds., Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel, vol. 11. The Crustacea Part 2. The Isopoda, Cumacea and Tanaidacea. Santa Barbara Museum of Natural History, Santa Barbara, California, 278 pp.

Gardiner, L. F. 1975. The systematics, postmarsupial development, and ecology of the deep-sea family Neotanaidae (Crustacea: Tanaidacea).—Smithsonian Contributions to Zoology 170:1–265.

Hansen, H. J. 1913. Crustacea, Malacostraca. II. Danish Ingolf Expedition 3:1–127.

Kudinova-Pasternak, R. K. 1981. Tanaidacea. Pp. 94–112 *in* A. P. Kusnjezov & A. N. Mironov, eds., Benthos of the submarine mountain Markus Necker and adjacent Pacific regions. Shirshov Institute of Oceanography, Moscow.

Larsen, K. 2002. Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico, X: the question of being male.—Gulf and Caribbean Research 14:53–66.

———, & T. Hansknecht. 2002. New species of the genus *Neotanais*.—Journal of Natural History (in press).

———, & R. W. Heard. 2002. Two new deep-sea tanaidacean genera, *Isopodidus* and *Cetiopyge* (Crustacea: Peracarida) from the Gulf of Mexico.—Proceedings of the Biological Society of Washington 115:403–411.

———, & ———. 2003. Revision of the deep-sea genus *Tanaella* (Crustacea: Tanaidacea).—Journal of Natural History (in press).

———, & G. D. F. Wilson. 2002. Tanaidacean phylogeny. The first step: the superfamily Paratanaidoidea.—Journal of Zoological Systematics and Evolutionary Research 40:205–222.

Meyer, G. H., & R. W. Heard. 1989. Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico. VII. *Atlantapseudes lindae,* n. sp. (Apseudidae) from the continental slope of the northern Gulf of Mexico.—Gulf Research Reports 8:67–105.

Norman, A. M., & T. R. R. Stebbing. 1886. On the Crustacea Isopoda of the Lightning, Porcupine, and Valorous Expeditions.—Transactions of the Zoological Society of London 12:77–141.

Sieg, J. 1986. Tanaidacea (Crustacea) von der Antarktis und Subantarktis. II. Tanaidacea gesammelt von Dr. J. W. Wägele während der Deutschen Antarktis Expedition 1983.—Mitteilungen aus dem Zoologischen Museum der Universität Kiel 2:1–80.

———, & R. W. Heard. 1989. Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico. VI. On the genus *Mesotanais* Dollfus, 1897 with descriptions of two new species, *M. longisetosus* and *M. vadicola.*—Gulf Research Report 8:73–95.

Viskup, B. A., & R. W. Heard. 1989. Tanaidacea (Crustacea: Peracarida) of the Gulf of Mexico. VIII. *Pseudosphyrapus siegi,* n.sp. (Sphyrapidae) from the continental slope of the northern Gulf of Mexico.—Gulf Research Reports 8: 107–115.

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A new cavernicole species of the genus *Anelpistina* (Insecta: Zygentoma: Nicoletiidae) from the Guánica subtropical dry forest, Puerto Rico

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Abstract.—A new species of genus Anelpistina (Insecta: Zygentoma: Nicoletiidae) from the Antillean island of Puerto Rico is described here. This is the first species of this genus to be described outside Continental America.

The sub-tropical dry forest reserve of Guánica, Puerto Rico, contains 4050 hectares of one of the best-preserved dry subtropical forests in the world and is also host to some of the island's greatest diversity of species (Wiley 1985). Since the arrival of European colonists in the 16th century, 90% of the island has been deforested, and almost all remaining forests are intensely disturbed. Puerto Rico's original forests now remain largely in Guánica and in the Luquillo Experimental Forest (Wiley 1985). In 1981, UNESCO declared the Guánica forest to be a biosphere reserve.

Guánica forest caves, from the middle Tertiary Ponce limestone (Peck 1981), harbor several uniquely adapted cave organisms (troglobites). La Cueva de los Murciélagos de Guánica (The Bat Cave), a cave with several sink and collapse entrances and a large section floored by a brackish lake containing vast quantities of liquefied guano, is home to several such species including three crustaceans, *Stygiomysis holthuisi, Metaniphargus bousfieldi,* and *Thyphlatya monae.* Another troglobite recorded from this cave is a thysanura insect of the family Nicoletiidae, which P. Wygodzinsky determined to be from the genus *Cubacubana* (Peck 1981).

In 1974, a single male thysanura of the genus *Anelpistina* (Insecta: Zygentoma: Nicoletiidae) was collected from Cueva Murciélagos by Dr. S. Peck and subsequently deposited in the American Museum of Natural History in New York, U.S.A. Acknowledging the expertise of P. Wygodzinsky on this group, we can probably exclude the possibility that this is the specimen studied by him as he would not have confused this specimen, clearly an *Anelpistina*, as belonging to the genus *Cubacubana*. Therefore, this cave locality most likely hosts two cave-adapted Nicoletiid species, the new *Anelpistina* species described here, and an undescribed *Cubacubana* species. Espinasa (2000) described a cave in Mexico in which two species of these genera coexist but with niche differentiation: *Anelpistina* in the surface and penumbra zone and *Cubacubana* in the dark zone. The situation appears to be different in Guánica. Since the new *Anelpistina* species of Guánica appears to be cave-adapted based on its long body and length of appendages, we assume that it inhabits the dark zone.

Materials and Methods

A single individual was in a vial with ethanol in the collection of the American Museum of Natural History. Dissections were made with the aid of a stereomicroscope. All illustrations were made with the aid of a camera lucida attached to a compound microscope.

Type was deposited in the American Museum of Natural History.

Anelpistina puertoricensis, new species
Figs. 1A–E, 2A–D, 3A–F

Type material.—Puerto Rico, Guánica State Forest, La Cueva de los Murciélagos de Guánica (the bat cave), about 9 km E of Guánica. 12–14 Jun 1974. Stewart B. Peck & J. Peck colls. Male holotype. Personal contact with S. B. Peck corroborated the collection locality.

Description.—Body length 13 mm. Antennae and caudal appendages broken. Maximum conserved length of antennae 10 mm and of caudal appendages 2 mm. Body proportions as in Fig. 1A. General color light yellow to white.

Antennae as shown in Fig. 1B–C. Basal article without projections. Pedicellus two thirds as long as the basal article, with unicellular glands on the ventral surface with a row of microchaetae bordering them in the form of a "U". The glands cluster into three groups, one very long and partially subdivided (Fig. 1B). Head with abundant and long macrochaetae, as shown in Fig. 1C, with approximately 8 + 8 macrochaetae on border of insertion of antennae. Microchaetae less abundant on back of the head.

Mouthpart appendages relatively long, maxilla as shown in Fig. 1D. Last articles of maxillary palp missing in individual. Apex of maxillary palp with two conules of similar width. Mandibles long, without very small pegs on bigger tooth and chaetotaxy as in Fig. 1E. Labial palp as in Fig. 2A, apical article barely longer than wide and barely longer than the next to last article. Penultimate article with bulge containing two macrochaetae. Labium and first article of the labial palp with macrochaetae.

Mesonotum with approximately 5 macrochaetae on lateral borders apart from several setae of varied sizes (Fig. 2D). Legs as shown in Fig. 2B–C. Hind tibia approximately 5× longer than wide and slightly shorter than tarsus. Inner face of trochanter with a projection like a talon (Fig. 2C). Trochanter in first and second legs normal. Claws of normal size.

Abdominal terga and sterna as in other members of genus. Abdominal sterna II–VII subdivided into coxites and sternite. Sterna VIII and IX of male entire. Appendages of urosternum IV relatively short, attaining slightly above 1/2 the length of stylets, and approximately 3× longer than wide (Fig. 3A). Outer border with a row of pegs (Fig. 3A–B). Apex of appendages with a small hook (Fig. 3B). Urosternum VIII of male long and shallowly emarginate on posterior margin, posterior projections slightly acute (Fig. 3C). Urosternum IX without a row of sensory cones, highly sclerotized submedian longitudinal macrochaetae, or a small group of short distinct setae behind insertion of parameres in center. Inner projection of insertion of stylets enlarged and protruding (Fig. 3C). Protuberance of internal face of coxal processes with spiniform macrochaetae highly sclerotized (Fig. 3C–D). Point of insertion of parameres in urosternum IX deep. Stylets II–VIII as usual for subfamily. Stylets IX larger than others, with 2 macrochaetae and an extra subapical pair, but otherwise without pegs or modifications (Fig. 3C). Terminal spine with small teeth. Urotergite X shallowly emarginate, posterior angles with several macrochaetae and a few relatively strong setae. Length of inner macrochaetae slightly longer than distance between them (Fig. 3E).

Penis and parameres as shown in Fig. 3C–D. Parameres attain slightly below ½ the length of stylets IX in adults. Surface of parameres with short setae.

Cerci of adult male with a wider than long basal article, then a very long one bearing numerous spines. Spines consist of a very small one, a strong, subacute one inserted in a tubercle, another very small one and a long, acute and slightly curved

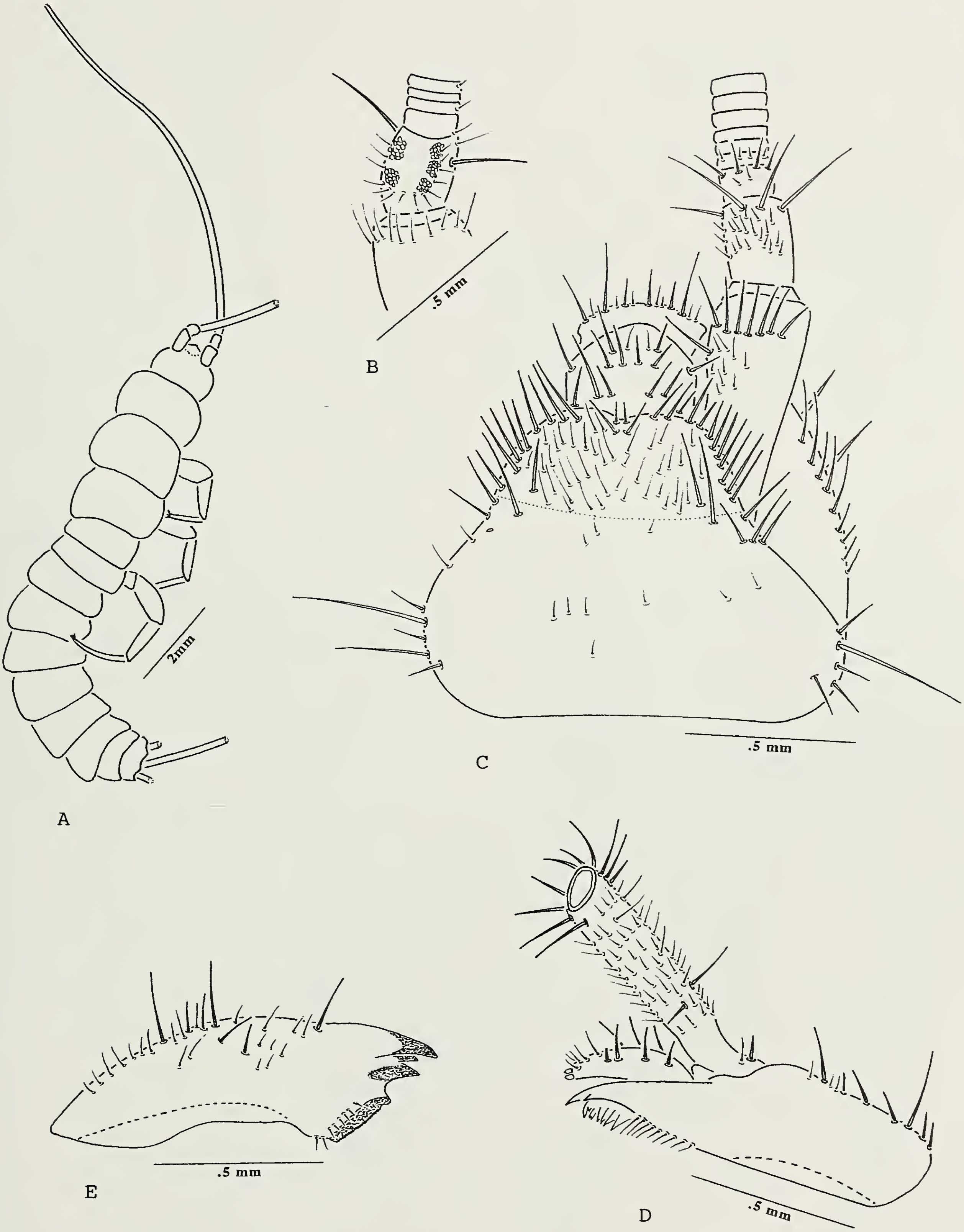

Fig. 1. *Anelpistina puertoricensis*, n. sp.: Adult male holotype; A, Body; B, Pedicellus; C, Head and basal portion of antenna; D, Maxilla; E, Mandible.

one also inserted in a tubercle. Below this group several long and highly sclerotized macrochaetae inserted in tubercles (Fig. 3F).

Females unknown. Postembryonic development unknown because only a single male examined. It is assumed that this individual is an adult based on its large size and the pedicellus already with unicellular glands. The number of pegs on appendages

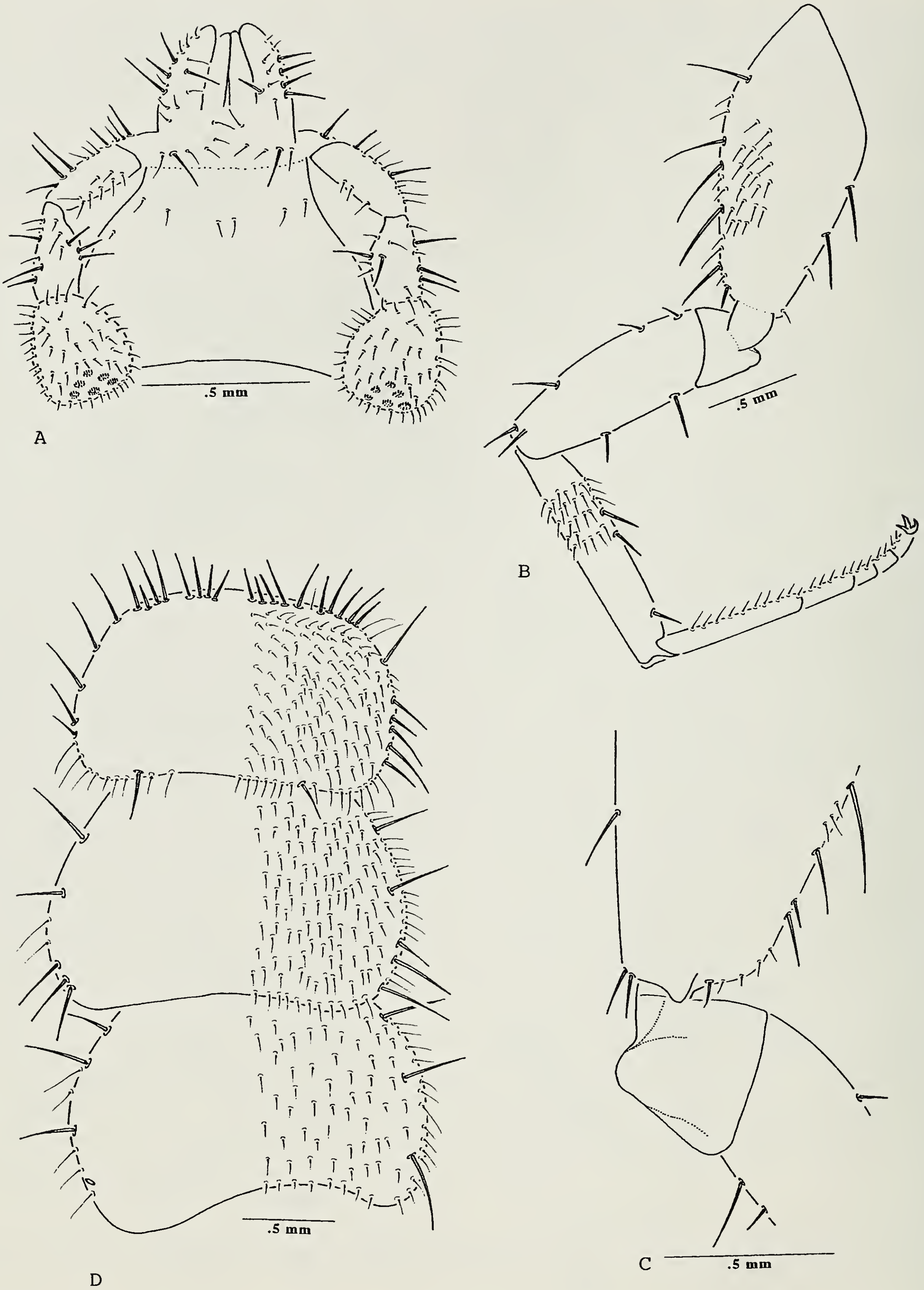

Fig. 2. *Anelpistina puertoricensis,* n. sp.: Adult male holotype; A, Labium; B, Hind leg; C, Hind trochanter; D, Thoracic terga.

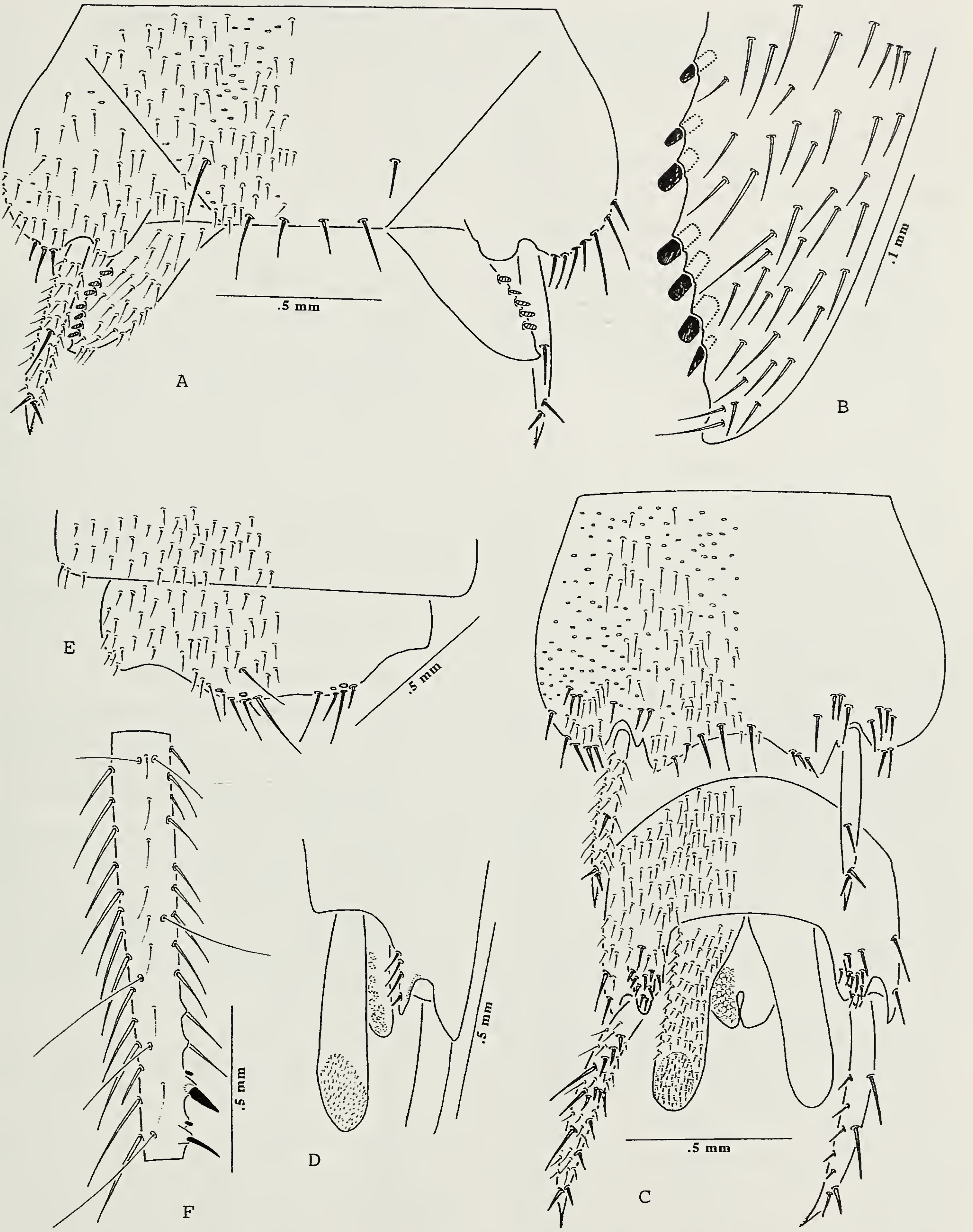

Fig. 3. *Anelpistina puertoricensis,* n. sp.: Adult male holotype; A, Urosternum IV; B, apex of articulated appendage of urosternum IV; C, Urosternum VIII and IX, ventral; D, Urosternum IX, lateral; E, Urosternite X; F, Cercus basal portion.

of urosternum IV are variable, seven on the right side and five on the left. This character may also be variable in the postembryonic development. We could expect a reduced number of pegs in younger instars or higher in older ones. Comparison to other species within the genus indicates that in younger instars, a reduction in or even the absence of secondary sexual characters such as the unicellular glands in the pedicellus, talon in legs, length of appendages of urosternum IV, length of parameres, and spines in cerci may be expected.

Known range.—Known only from the type locality.

Etymology.—In reference to the type locality, the Caribbean island of Puerto Rico.

Remarks.—Adult males of the genus *Anelpistina* can be easily subdivided by the morphology of the appendages of urosternum IV (Fig. 3A). *Anelpistina decui* (Wygodzinsky & Hollinger 1977) and *A. inappendicata* (Espinasa 1999) lack them. In *A. weyrauchi* (Wygodzinsky 1959), the medium-sized appendages have a small subapical projection on outer margin, and two projections on both sides of insertion of stylets. *A. ruckeri* (Silvestri 1905), *A. carrizalensis* (Wygodzinsky 1946), and *A. doradoi* (Espinasa and Baker Alpheis 2001) have simple appendages of very long size, their length being approximately equal to twice the length of urosternum IV and more than 6× longer than wide. Adults of *A. anophtalma* (Bilimek 1867), *A. wheeleri* (Silvestri 1905), *A. miranda* (Silvestri 1912), *A. boneti* (Wygodzinsky 1946), *A. bolivari* (Wygodzinsky 1946), and *A. cuaxilotla* (Espinasa 1999) have simple appendages of medium size, their length being similar to the length of urosternum IV and less than 5× longer than wide, with a small hook on the apex (Figures of Silvestri's description of *A. wheeleri* and *A. miranda* are not clear enough on the presence or absence of the hook). The new species belongs to this last group.

The new species can be differentiated from all congeners by the presence of pegs in appendages of urosternum IV (Fig. 3B), trochanter with a projection like a talon (Fig. 2C), and the coxal processes of urosternum IX, with the inner projection of the insertion of stylets enlarged and protruding (Fig. 3C).

Acknowledgments

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Literature Cited

Espinasa, L. 1999. Two new species of the genus *Anelpistina* (Insecta: Zygentoma: Nicoletiidae) from Mexican caves, with redescription of the genus.—Proceedings of the Biological Society of Washington 112(1):59–69.

Espinasa, L., & M. Baker Alpheis. 2001. A new species of the genus *Anelpistina* (Insecta: Zygentoma: Nicoletiidae) from the Biosphere Reserve Sierra de Huautla.—Proceedings of the Biological Society of Washington 114(2):489–496.

Peck, S. B. 1981. Zoogeography of invertebrate cave faunas in southwestern Puerto Rico.—NSS Bulletin 43:70–79.

Silvestri, F. 1905. Materiali per lo studio dei Tisanuri. VI. Tre nuove specie di *Nicoletia* appartenenti ad un nuovo sottogenero.—Redia (Firenze) 2: 111–120.

———. 1912. Tisanuri finora noti del Messico.—Bolletino del Laboratorio di Zoologia general e agraria di Portici 6:204–221.

Wygodzinsky, P. 1946. Sobre *Nicoletia* (*Anelpistina*) Silvestri 1905 e *Prosthecina* Silvestri, 1933.—Ciencia 7:15–25.

———. 1959. Contribution to the Knowledge of the "Thusanura" and "Machilidae"(Insecta).—Revista Brasileira de Biologia 19(4):441–457.

Wygodzinsky, P., & A. M. Hollinger. 1977. A study of Nicoletiidae from Cuba (Thysanura).—Resultats des Expéditions Biospéleologiques Cubano-Roumaines à Cuba 2:313–324.

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A second species of the rare milliped family Apterouridae (Diplopoda: Chordeumatida: Striarioidea)

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Abstract.—*Apterourus serratus,* sp. nov., is described from a single male collected in Monterey County, California, U.S.A. This is the fourth sexually mature specimen and second species in the family to be found since the original collection of *A. horizontalis* Loomis, in 1929. Features of the gonopods of the new species and second and ninth legs confirm the placement of the family in the suborder Striariidea, superfamily Striarioidea. New figures of the gonopods of *A. horizontalis* are provided.

A number of families of millipeds are not only monobasic (including a single genus) but are also based on monotypic genera (including a single species). For many of these families, their apparent distinctness is the result of our ignorance, i.e., we have not understood the real relationships of the species involved or have yet to find their relatives. In such cases, the system may be best served by eventually collapsing the monobasic families into larger units that more accurately reflect their phylogenetic position. For a few of them, however, their monobasic states may be the taxonomic consequence of the great age of the group, as the last remnants of phyletic lines isolated by extinction. In such cases, the maintenance of these taxa seems well justified, although such status can only be inferred by their evident distinctness from their nearest relatives. Such appears to be the case for the milliped family Apterouridae.

The family Apterouridae was established by Loomis in 1966 for the single species *Apterourus horizontalis,* described as new from specimens that had been collected in southern California by O. F. Cook in 1929. When I surveyed North American chordeumatids in 1972, the type specimens of *A. horizontalis* Loomis (the only known material) were unavailable for study, and the original description lacked information needed for an accurate systematic placement of the family. The specimens were finally located in the collections of the National Museum of Natural History (Smithsonian Institution), and in 1977 I redescribed *A. horizontalis,* correcting a number of crucial errors due to the failure of Loomis to completely dissect the male; these errors were the source of the taxonomic problems. Properly understood, apterourids find a place as members of the superfamily Striarioidea, a moderately diverse assemblage of chordeumatidans limited, except for one species, to North America, and with its center of diversity along the Pacific Coast.

Order Chordeumatida Koch, 1847
Suborder Striariidea Cook, 1896
Superfamily Striarioidea Cook, 1896
Family Apterouridae Loomis, 1966

Apterouridae Loomis 1966:221.—Shear, 1972:247; 1977:689.

Diagnosis.—Thirty segments in both sexes. Terga granulate, strongly arched, bearing prominent bilobed paranota. Gonopods with two colpocoxites, one of which sheaths a branch or branches of a flagellocoxite. Ninth legs strongly reduced, lacking telopodites, concealed beneath reflexed gonopods, wholly enclosed within seventh diplosegment. Coxae 10 and 11 with eversible glands. Openings of vas deferentia on posterior surfaces of second coxae, surrounded by short, membranous tubes. Monobasic.

Notes.—My earlier discussion of the family (Shear 1977) corrects the erroneous interpretations in the original description (Loomis 1966). However, in 1977 my understanding of chordeumatid gonopods and the relationships of the families was quite different than it is now (Shear 2000). Additional study of the gonopods of several striariidean families has led to a more accurate interpretation.

Chordeumatidan gonopods are primitively derived only from the modified eighth legpair. The ninth legpair should be called "posterior gonopods" only in members of the suborders Chordeumatidea and Heterochordeumatidea, where their modification suggests a possible role in spermatophore transfer. Indeed, in a few species of these groups, the anterior gonopods are completely suppressed and their function has been entirely assumed by the posterior gonopods, a development that has led to considerable confusion. In the suborder Striariidea, the ninth legs have coxites only in the superfamily Caseyoidea, and there they only serve to physically support the gonopods. In the superfamily Striarioidea, to which the Apterouridae undoubtedly belong, ninth leg coxites are absent. The ninth legs are very strongly reduced in both known species of apterourids, and completely concealed *in situ* by the gonopods; there is no evident division between sternum, coxa and telopodite.

Returning to the gonopods proper, I am now sure that all choreumatidan gonopods are derived entirely from the coxae, and the telopodite of the eighth leg plays no role. Vestigial telopodites are present in a few families of the superfamilies Brannerioidea and Antroleucosomatoidea (see, for example, Shear 2002), where they appear as small, articulated, rodlike structures bearing a few apical setae. What I persistently called "telopodites" prior to about 1995 are, in fact, colpocoxites, the sclerotized and sometimes elaborated homologs of the coxal glands of the eighth legpair. The rest of the elaborations of the gonopod are properly referred to as angiocoxites: derived from the body of the coxa and rim of the coxal gland opening.

The following general description of apterourid gonopods incorporates these new interpretations. There appears to be no distinct sternum, and the sternal apodeme arises directly from the coxal region (Fig. 3A), which therefore is best termed a coxosternite. The right and left gonopods are separate and linked only by lightly sclerotized membrane. As in other Striariidea, each angiocoxite is fundamentally bipartite. The mesal section in *Apterourus* consists of two flagelliform branches, the inner being the largest (mc1, mc2, Fig. 1E). The outer, or ectal, angiocoxite section (ec, Fig. 1D) forms a broad sheath, within which is nested a movable flagellocoxite (fc, Fig. 1E; term introduced by Gardner & Shelley [1989]). Although I referred to a low, mound-like colpocoxite in *A. horizontalis,* I could not detect one in the new species, nor could such a structure be found on reexamination of the types of *A. horizontalis.* Either the colpocoxite is completely lacking, or what I am referring to as the flagellocoxite is in fact a colpocoxite. Unfortunately, it is not possible at this point to decide between these two alternatives.

I remain confident in my placement of the family in the Striariidea, and now it seems clear that the apterourids are the adelphotaxon of Striariidae + Rhiscosomididae, based on the flagelliform mesal angiocoxite branches and the extreme reduction of the ninth legs. The gonopods are apomorphic in comparison to those of the other two families in lacking a distinct sternum. Striariids and rhiscosomidids share a more plesiomorphic form of the ninth legs, with separate telopodites not concealed by the gonopods, and the mesal angiocoxites are robust, flattened, and bear

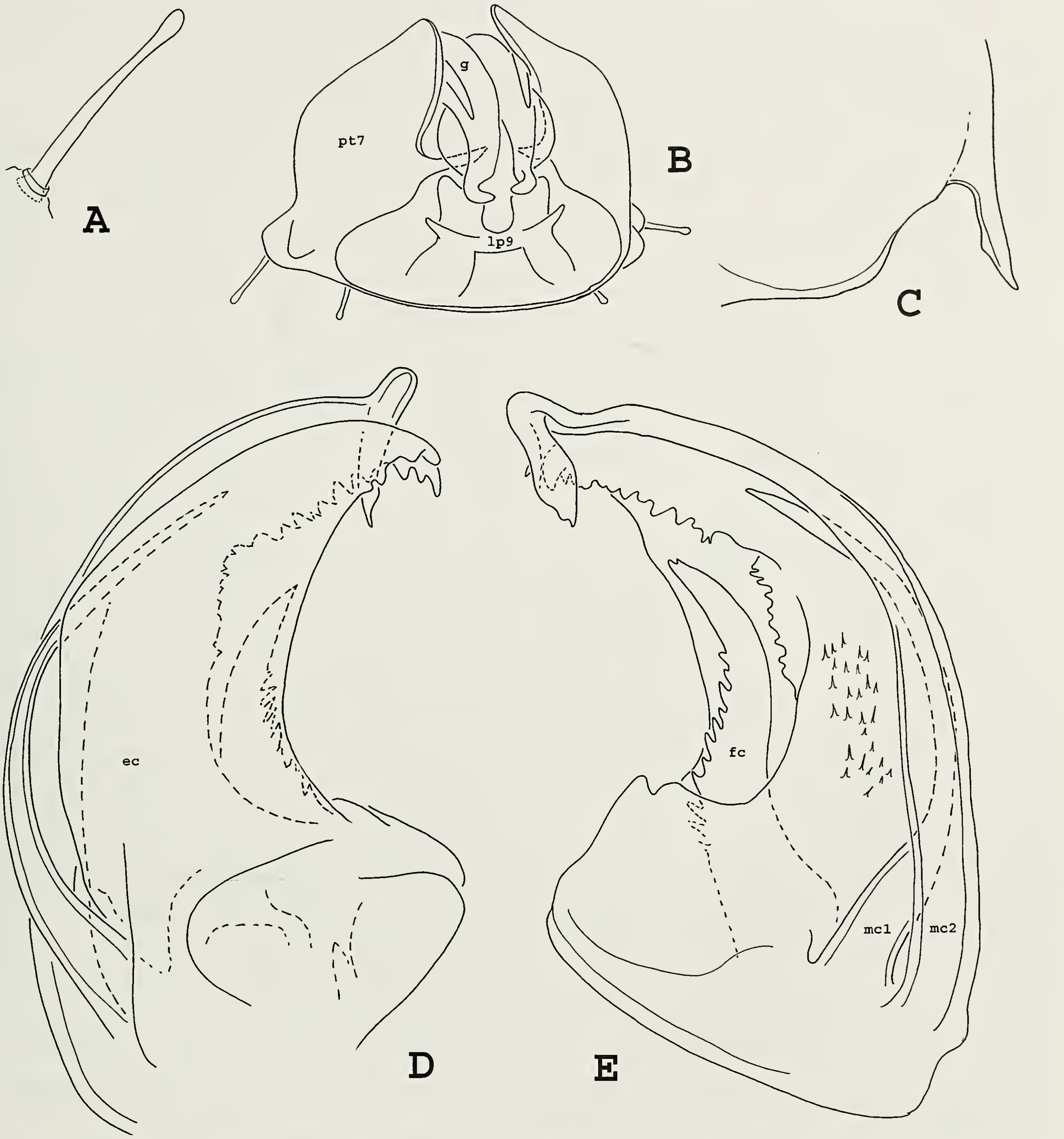

Fig. 1. *Apterourus serratus,* male. A. Typical segmental seta, 400×. B. Diagrammatic plan of segment 7, posterioventral view; pt7, paratergum 7; g, gonopod; lp9, legpair 9. C. Ventral margin of left pleurotergite, ventral view, 200×. D. Right gonopod, lateral view, 400×; ec, ectal coxite. E. Right gonopod, mesal view, 400×; fc, flagellocoxite; mc1, mc2, branches of mesal coxite.

apical elaborations. All three families are characterized by rather heavy sclerotization and the presence of paranota, though it is not clear that the paranota are homologous in all of them. Those of the rhiscosomidids and apterourids look similar, but paranota-like extensions in an undescribed genus of striariid (minute creatures recently recognized in collections from California and Oregon) appear to be exaggerated segmental crests set low on each segment. The smaller basal lobe of an apterourid paranotum is actually a distinct structure, set higher on the segment than the main part of the paranotum, raising the possibility that the two are developed from separate crests, the remainder of which have been entirely suppressed.

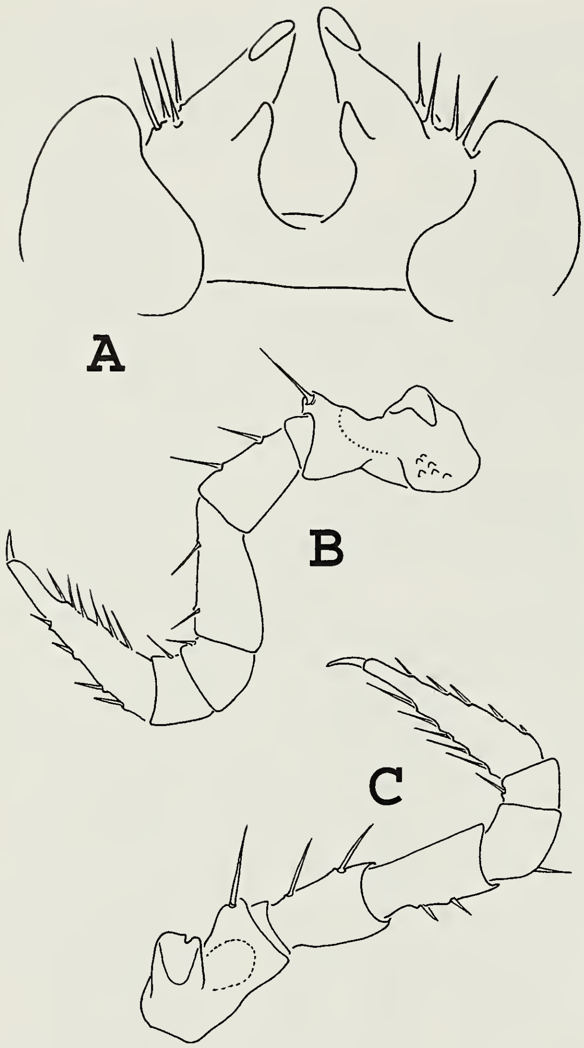

Fig. 2. *Apterourus serratus,* male. A. Ninth legs, anterior view, 200×. B. Right tenth leg, anterior view, 200×. C. Left eleventh leg, anterior view, 200×.

Apterourus Loomis, 1966

Apterourus Loomis 1966:221.—Shear, 1977:689.

Diagnosis.—As for family.

Contents and distribution.—*Apterourus horizontalis* Loomis, *A. serratus,* sp. nov. Known from two localities in southern California. The localities are separated by about 435 km, a rather remarkable distance. I strongly suspect that additional species of *Apterourus* await collection and description in the intervening region.

Notes.—The name of the genus is a Greek neologism roughly meaning "wingless tail," and refers to the absence of paranota posterior to segment 26 in *A. horizontalis* (Loomis 1966).

Apterourus serratus, new species

Figs. 1, 2

Type.—Male holotype (Essig Entomological Museum, University of California, Berkeley) from California, Monterrey County, 12 km SE of California Highway 1 on Palo Colorado Road, collected in a pitfall trap by A. Gilbert and B. Oliver, 23 Feb 1984.

Diagnosis.—Distinct from *A. horizontalis* in details of the gonopods, ninth legpair, and tenth coxae; the inner edge of the flagellocoxite of the gonopod of the present species is serrated, that of *A. horizontalis* smooth; the ninth leg coxae of *A. serratus* are much more reduced than in *A. horizontalis,* appearing as small hooks each with a single basal tooth, rather than as concave lamellae; the tenth coxae of *A. horizontalis* have a large apical knob that is absent in those of *A. serratus.* The modifications of the seventh segment of the male described below are not seen in *A. horizontalis.* Additionally, the males of *A. horizontalis* have 4–5 poorly developed, indistinct ocelli, while the single male of *A. serratus* has 15 uniform, well-defined ocelli in an oval group. The posterior lobes of the paranota are acute in *A. horizontalis,* rounded in *A. serratus.*

Etymology.—The species epithet refers to the serrate margins of the gonopod coxites.

Male holotype.—Length, about 5.8 mm; width, 0.8 mm across the paranota of segment 6. Structure generally as described for *A. horizontalis* (Loomis 1966, Shear 1977), but paranota smaller, thicker, with posterior lobe low and rounded; paranota growing smaller after segment 18, absent from segments posterior to 24. Metazonites coarsely granular, especially at bases of paranota. Segmental setae (Fig. 1A) blunt-tipped. Color dark brown. Pregonopodal legs (pairs 3–7) slightly more crassate than postgonopodal legs; legpair 3 not notably larger than others, lacking modifications to prefemora.

Segment 7 modified (Fig. 1B, C); pleu-

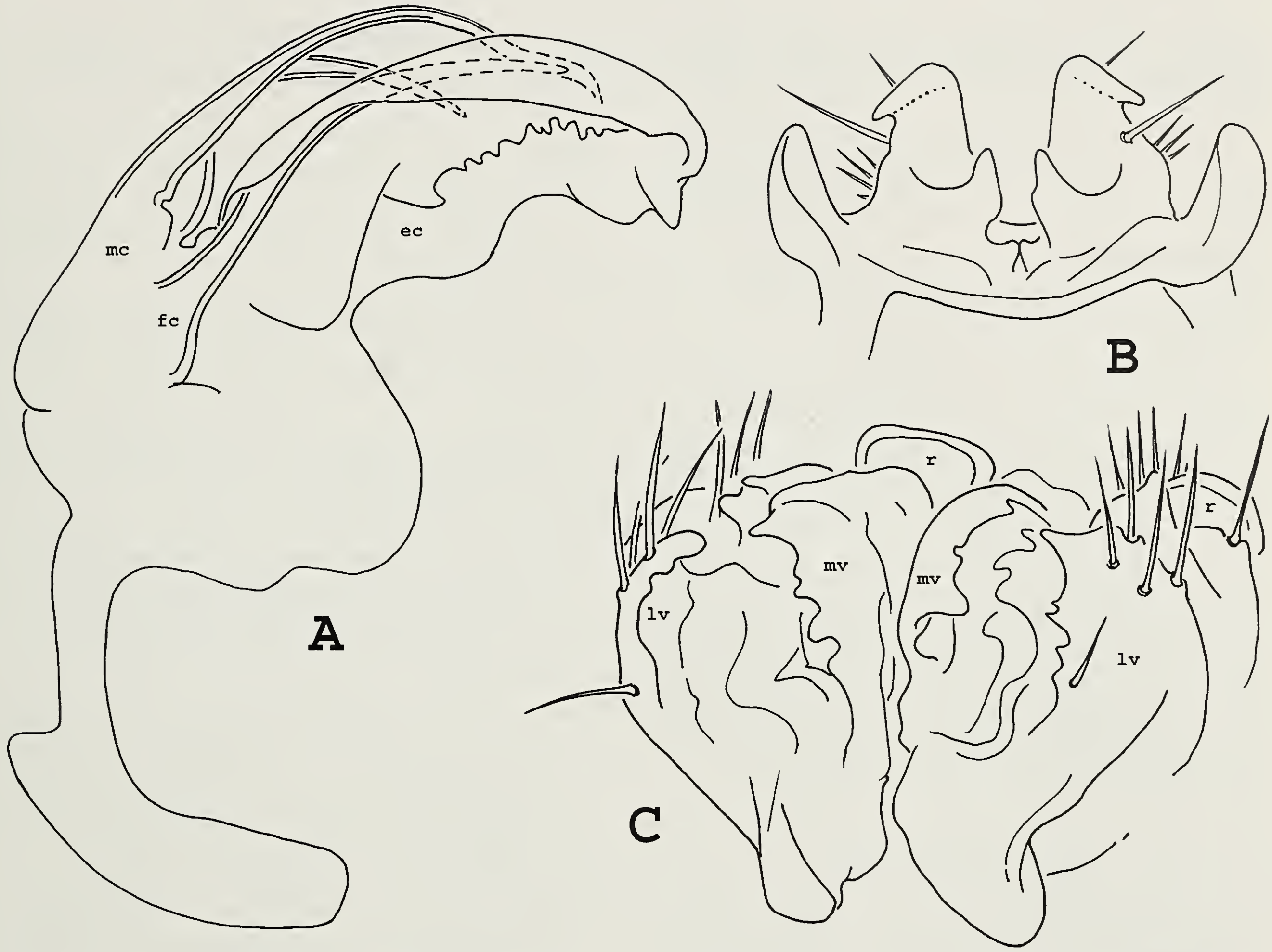

Fig. 3. *Apterourus horizontalis.* A. Left gonopod, mesal view, 200×; mc, mesal coxite; fc, flagellocoxite; ec, ectal coxite. B. Ninth legs of male, anterior view, 200×. C. Female genitalia, ventral view, 200×; lv, lateral valve; mv, mesal valve; r, receptacle.

rotergites meet in ventral midline, each bears long posterior extension fitting dorsal to gonopods.

Gonopods (Fig. 1D, E) with ectal coxite (ec) broadly based, apically acuminate, outer margin with few distal teeth, inner margin conspicuously serrate. Mesal coxite (mc1, mc2) bipartite; outer branch short, curved, acute; inner branch longer, heavier, sharply curved mesoventrally at tip. Flagellocoxite (fc) broad, with distinct, even, marginal serrations. Ninth legs (Fig. 2A) consisting of single, fused coxosternal unit, tapered, curved, with mesal teeth on each side, with lateral setal group. Legpairs 10 (Fig. 2B) and 11 (Fig. 2C) with coxal glands, coxae 10 without distal knobs.

Female unknown.

Distribution.—Known only from the type locality.

Notes.—The pitfall trap from which the type was taken was evidently in place all winter, having been set up in November and collected in February. No information is available on the nature of the habitat. *Apterourus horizontalis* was also collected in February, and this meager evidence points to surface activity by these millipeds in the cooler, rainier winter months.

Apterourus horizontalis Loomis, 1966
Fig. 3

Apterourus horizontalis Loomis, 1966:223, figs. 1–4.—Shear, 1977:689, figs. 1–8.

Types.—Male holotype, male, female and juvenile paratypes from Cajon Pass, 11.25 km W of Cajon on Big Pine Road, San Bernardino Co., California, collected 14 Feb 1929 by O. F. Cook, deposited in the National Museum of Natural History, Smithsonian Institution (myriapod collection, USNM 3159).

Notes.—I re-examined the types for this study. My earlier redescription is generally accurate, but in my 1977 fig. 1, the segmental setae are shown as acute; in fact they are blunt and slightly clavate as in *A. serratus* (Fig. 1A, this study).

For purposes of comparison with the new species, new figures of the gonopods (Fig. 3A) and ninth legs (Fig. 3B) are presented here. While I characterized the gonopod in 1977 as having a low, mound-like colpocoxite ("telopodite"), I cannot now, using better optical equipment, detect such a structure. Because of a growing awareness that the female genitalia of millipeds may be of taxonomic utility, those of *A. horizontalis* are illustrated here (Fig. 3C).

Acknowledgments

Thanks are due to C. Barr, curator of the Essig Entomological Museum, for the loan of material which contained the holotype specimen of *A. serratus,* and to J. Coddington, Smithsonian Institution, for the loan of the types of *A. horizontalis.*

Literature Cited

Cook, O. F. 1896. On recent diplopod names.—Brandtia 2:5–8.

Gardner, M., & R. Shelley. 1989. New records, species and genera of caseyid millipeds from the Pacific coast of North America (Diplopoda: Chordeumatida: Caseyidae).—Pan Pacific Entomologist 65:177–268.

Koch, C. L. 1847. System der Myriapoden. Pp. 61–119 *in* A. Herrich-Schäffer, ed., Kritische Revision der Insectenfauna Deutschlands, vol. 3.

Loomis, H. F. 1966. Two new families and other North American Diplopoda of the Suborder Chordeumida.—Proceedings of the Biological Society of Washington 79:221–230.

Shear, W. A. 1972. Studies in the milliped order Chordeumida (Diplopoda): a revision of the family Cleidogonidae and a reclassification of the order Chordeumida in the New World.—Bulletin of the Museum of Comparative Zoology 141:151–352.

———. 1977. The systematic position of the milliped family Apterouridae (Diplopoda, Chordeumida, Striarioidea) and a redescription of *Apterourus horizontalis* Loomis.—Proceedings of the Biological Society of Washington 89:689–694.

———. 2000. On the milliped family Heterochordeumatidae, with comments on the higher classification of the order Chordeumatida (Diplopoda).—Invertebrate Taxonomy 14:363–376.

———. 2002. Five new chordeumatid millipeds from China: New species of *Vieteuma* (Kashmireumatidae) and *Nepalella* (Megalotylidae).—Proceedings of the California Academy of Science 53:63–72.

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Sponges of the family Chondrillidae (Porifera: Demospongiae) from the Pacific coast of Mexico, with the description of three new species

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Abstract.—Two new species of *Chondrilla* from the Mexican Pacific coast are described, based mainly on the distribution of the spherasters throughout the body of the sponge and in the cortex. *Chondrilla montanusa,* n. sp. is mainly characterized by the presence of a minutely warty surface formed by the accumulation of the spherasters in the cortex which gives it a microtuberculate aspect. This feature clearly distinguishes the species from other known species of *Chondrilla. Chondrilla pacifica,* n. sp. is easily distinguished from the former by having a smooth surface and a thin layer of spherasters in the cortex and by a low proportion of spicules in the choanosome, which is clearly different from the related *C. verrucosa.* We also describe *Chondrosia tenochca,* n. sp., mainly characterized by having a cortex composed of two layers, a very dense choanosome, with hardly any canals, little or no foreign debris, and spherulous cells that are very irregularly formed. A key to all chondrillids from the East Pacific is also provided.

Chondrosida is a group of encrusting to massive, liver-like or gelatinous sponges (Lévi 1973) with only four valid genera: *Chondrosia* Nardo, 1847, *Chondrilla* Schmidt, 1862, *Thymosia* Topsent, 1895, and *Thymosiopsis* Vacelet & Perez, 1998. These genera had traditionally been included in two different families: Chondrillidae Gray, 1872 and Chondrosiidae Schulze, 1877. Even though Chondrosiidae has been used by many authors, the recent tendency is to include these genera in a single family Chondrillidae (Bergquist 1978, Hooper & Wiedenmayer 1994). It was difficult to assign these genera to ordinal level mainly because of the complete lack of spicules; the megascleres have been lost secondarily, and in some chondrillids, microscleres may or may not be present (such as *Chondrosia*) (Topsent 1895). Moreover, biochemical evidence showed the affinity of Chondrillidae with the order Hadromerida (Bergquist 1978). Due to these features the order Chondrosiida was proposed to harbor the family Chondrillidae (Boury-Esnault & Lopes 1985). Later, molecular data confirmed the validity and the monophyly of the order Chondrosiida (Boury-Esnault 2002).

The systematics of the group has been based almost entirely on the size and morphology of the spicules, which in *Chondrilla* are exclusively asters, mainly spherasters. However, the size and morphology of the spherasters can vary between populations of the same species and, thus, may be an unreliable character to discriminate between species (Bavestrello et al. 1993, Klautau et al. 1999). This lack of morphological taxonomic characters in many genera such as *Chondrilla* (Klautau et al. 1999), or the avoidance of proper techniques to study small microscleres in detail in genera such as *Guitarra* (Boury-Esnault et al. 1993), *Mycale* (Carballo & Hajdu 1998), etc., have led many morphologically similar but evolutionary distinct species to be lumped into artificially cosmopolitan morphospecies. A case in point is the sponge species *Chondrilla nucula,* which traditionally has been considered to have a very wide geographical distribution, but was recently separated into five distinct genetic forms in the Caribbean and the Southwestern Atlantic (Klautau et al. 1999). Currently, the sponge populations from the Mediterranean and the adjacent Atlantic (coasts of Spain, Portugal and Morocco) are the only ones considered to be *Chondrilla nucula* (Klautau et al. 1999). It has also been recently suggested that *Chondrosia reniformis* (as with *Chondrilla nucula*) may be a species complex, and that citations of this species in places such as the Indo-Pacific region are probably not correct (Lazoski et al. 2001).

Of the four genera included in the family, only *Chondrosia* and *Chondrilla* are represented in the East Pacific. In the Northeastern Pacific the only known *Chondrilla*-species is *Chondrilla nucula* [recorded by de Laubenfels 1935, by Green & Gómez (1986) from the west coast of Mexico, and by Hofknecht (1978) from the Gulf of California]. More recently *Chondrilla verrucosa* Desqueyroux-Faúndez & Van Soest, 1997 has been described in the Central Eastern Pacific (Galapagos Islands), which is actually the only record of the genus *Chondrilla* from the Southeast Pacific.

This study seeks to clarify the differences between the taxonomy of sponges of the family Chondrillidae in the Mexican Pacific. Three new species are recognized: *Chondrilla montanusa,* n. sp., *Chondrilla pacifica,* n. sp. and *Chondrosia tenochca,* n. sp.

Materials and Methods

Specimens were collected by scuba diving and snorkelling along the Mexican coast of the Pacific Ocean and preserved in 70% alcohol. Spicule preparation followed the techniques described by Rützler (1974) for light and scanning electron microscopy (SEM) using a JEOL JSM-35 and a gold-coated 300 Å layer. Twenty or more spicules randomly chosen were measured for each of the specimens studied.

Material, paratypes and spicule slides have been deposited in the sponge collection of the Laboratorio de Ecología del Bentos del Instituto de Ciencias del Mar y Limnología (ICMyL) in Mazatlán, México (LEB-ICML-UNAM), as well as in the Colección Nacional del Phylum Porifera Gerardo Green in México, D. F. (CNPGG). The type material has been deposited in the Museo Nacional de Ciencias Naturales in Madrid (Spain) (MNCN) and in the British Museum of Natural History (BMNH) (London).

Results

Order Chondrosida Boury-Esnault & López, 1985

Family Chondrillidae Gray, 1872

Synonymy.—see Boury-Esnault 2002.

Diagnosis.—Chondrosida, encrusting to massive, with a marked cortex enriched with fibrillar collagen, with inhalant apertures localized in pore-sieves or cribriporal chones and a skeleton often absent, composed, when present, of nodular sponging fibers or aster microscleres only (never megascleres). Collagen always very abundant. Oviparous (Boury-Esnault 2002).

Chondrosia Nardo, 1847

Synonymy.—See Boury-Esnault 2002.

Type species.—*Chondrosia reniformis* Nardo, 1847 (by monotypy).

Diagnosis.—Chondrillidae without skeleton and with a well developed cortex made of thick fascicles of collagen and with numerous spherulous cells (Boury-Esnault 2002).

Chondrosia tenochca, new species

Synonymy.—*Chondrilla nucula* De Laubenfels, 1935: 12.

Material examined.—Holotype: MNCN 1.01/236, Cerritos, (Mazatlán, Sinaloa), 23°18′51″N, 106°29′31″W, 18 Feb 2000, intertidal, on rocks. Paratypes: LEB-ICML-UNAM-59, Islas Isabeles (Nayarit), 21°50′33″N, 105°53′10″W, 20 Nov 1999, intertidal, on rocks. LEB-ICML-UNAM-120, Cerritos, (Mazatlán, Sinaloa), 23°18′51″N, 106°29′31″W, 18 Feb 2000, intertidal, on rocks. LEB-ICML-UNAM-474, Antiguo Corral del Risco (Punta Mita, Nayarit), 20°46′20″N, 105°32′49″, 7 Apr 2002, 4 m depth, on dead corals. CNPGG-0457, Bahía Santa Cruz (Oaxaca), 15°45′N, 96°07′W. 22 Nov 1985, 1–2 m depth.

Description.—Encrusting to semi-encrusting sponge, 2 to 10 mm thick, spreads out over rocky substrate, covering areas up to about 6.5 × 5 cm. The smallest specimens measure 1 by 1.4 cm. The sponge is firm, rubbery and variably compressible. Live specimens have conspicuous oscules, circular to oval, up to 2 mm in diameter, some with slightly elevated rims. The surface is smooth and shiny. The color is evenly dark brown or black on the top of the sponge, and dark gray on the sides. Choanosome and base are ivory-colored. The color is well preserved in spirit, but paler after several years. The choanosome is very dense, almost without canals (fleshy), with little or any foreign debris. It has a notorious undetachable cortex up to 300 μm thick, free of debris. The cortex seems composed of two layers: the most superficial with a very high density of spherulous cells, and the internal with less spherulous cells. The density of these cells in the choanosome decreases slightly from the zone near the cortex to the basal part. The spherulous cells contain 9 to 20 spherules 0.5 to 2.5 μm in diameter. They are very irregular in form; most frequently they are enlarged or oval.

Distribution.—The species has been found in Oaxaca, Nayarit and Sinaloa (México, eastern Pacific). De Laubenfels (1935) described an encrusting (2–3 mm thick) and aspiculous sponge from the West coast of the Peninsula of California as *Chondrilla nucula,* which should be considered a *Chondrosia tenochca.* Between 0 to 4 meters depth, typical of the intertidal zone, on rock or dead coral.

Etymology.—*Tenochca* means tribe that inhabited México. The term is derived from the Nahuatl word "Tenochtitlan", which was the largest city in America in its time.

Remarks.—De Laubenfels (1936) established *Chondrosia chucalla* from the Central Pacific as a nomen novum for *C. collectrix* Lendenfeld, 1888 from Australia, in order to correct a junior secondary homonym of *C. collectrix* Schmidt, 1870 from the Caribbean. Previously, *C. collectrix* Lendenfeld, 1888 was considered a synonym of *C. spurca* (Carter, 1887) by Topsent (1895). Later, Wiedenmayer (1989), and Hooper & Wiedenmayer (1994) considered *C. spurca* Carter, 1887 a synonym of *C. reticulata* (Carter, 1886, as *Halisarca reticulata*). Our specimens match the description of *C. chucalla* sensu de Laubenfels (1954) but do not agree with the description of *C. reticulata,* a deep purple sponge with foreign debris scattered or crowded throughout the choanosome (Wiedenmayer 1989). Desqueyroux-Faúndez & Van Soest (1997) assigned specimens from the Galapagos to *C. chucalla* with some hesitation, as well as Wiedenmayer (1989), who doubtfully considered the specific name *chucalla* from the Central Pacific (de Laubenfels 1951, 1954, 1955) as a synonym of *C. reticulata.* We think that the de Laubenfels (1954) specimens, and ours, are a new species, different from *C. reticulata,* and must be considered as *Chondrosia tenochca.*

Chondrilla Schmidt, 1862

Synonymy.—see Boury-Esnault, 2002.

Type species.—*Chondrilla nucula* Schmidt, 1862 (by subsequent designation).

Diagnosis.—Chondrillidae with a skeleton composed only of siliceous spicules of the aster type, mainly in the cortex and around the canals (Boury-Esnault 2002).

Chondrilla montanusa, new species

Figs. 1, 2, 4, Table 1

Synonymy.—*Chondrilla nucula* Green & Gómez, 1986:284.

Material examined.—Holotype: MNCN-1.01/176, Isla Lobos (Mazatlán, Sinaloa), 23°13′49″N, 106°27′43″W, 17 Feb 2000, intertidal, on rocks. Paratypes: BMNH-2002.9.10.1, Isla Lobos (Mazatlán, Sinaloa), 23°13′49″N, 106°27′43″W, 17 Feb 2000, intertidal, on rocks. LEB-ICML-UNAM-428, Isla Pájaros (Mazatlán, Sinaloa), 23°15′29″N, 106°28′25″W, 15 Feb 2002, 4 m depth, on rocks. LEB-ICML-UNAM-135, Cerritos (Mazatlán, Sinaloa), 23°18′51″N, 106°29′31″W, 02/02/2001, 1 m depth, on rocks. LEB-ICML-UNAM-136, Isla Lobos (Mazatlán, Sinaloa), 23°13′49″N, 106°27′43″W, 02/17/2000, intertidal, on rocks. CNPGG-0450, Hermano del Sur, (Mazatlán, Sinaloa), 23°11′N, 106°27′W, Mar 1982 on barnacle shells. LEB-ICML-UNAM-452, Cerritos (Mazatlán, Sinaloa), 23°18′51″N, 106°29′31″W, 10/30/01, intertidal on bivalve shell. CNPGG-0448, Calerita (La Paz, Baja California), 24°22′N, 110°17′W, on rock. CNPGG-0449, Hermano del Norte (Mazatlán Sinaloa), 23°11′N, 106°26′W, 03/1982. CNPGG-0458, Bahía Tangolunda (Oaxaca), 15°46′N, 96°05′30″W.

Description.—Thinly encrusting, 1–4 mm thick, covering rocky substrate up to about 2.5 by 7 cm. The surface is shiny and minutely warty, these warts are evenly scattered and conspicuous, 183–(226)–283μm in diameter, 50–265 μm apart (Fig. 1A). The thickest specimens (up to 45 mm in thickness) have a mostly smooth surface, with a few warts in some areas and on the edges. Oscules are slightly elevated in some specimens (up to 2 mm). The consistency is cartilaginous. The color alive is black, dark brown or gray (slightly mottled); it is light gray towards the border and in the choanosome; it conserves the same color in spirit.

Structure.—Cortex not detachable, up to about 400 μm thick (250–500 μm at the top of a wart), organized by accumulated spherasters in mounds, forming a very particular layer that gives the surface a warty appearance. In the choanosome the spherasters are scarce and wide apart, they are mainly at the base of the sponge and surrounding the canals. Canal diameters are 20–370 μm. The spiculation consists of spherasters 25.5 μm in average diameter (Table 1), which may appear in very different shapes in a single specimen: rays can be conical, short and blunt or reduced, in some cases mammiform. Others have only a centrum with very small rays or a granulose surface. The extremities of the rays are often smooth, seldom slightly rough, and sometimes exhibit several small spines at the tip. The number of rays varies between 10 to 26.

Distribution.—Sinaloa (Mazatlán) (Green & Gómez 1986 as *C. nucula*), present records in Baja California Sur and Oaxaca.

Etymology.—The specific epithet is derived from Latin *montanusa,* referring to the mountain aspect of the cortex.

Remarks.—See below

Chondrilla pacifica, new species

Figs. 1, 3, 4, Table 1

Synonymy.—*Chondrilla nucula* Hojknecht, 1978: 55.

Material examined.—Holotype: MNCN-1.01/233, Isla San José (La Paz, Baja California Sur), 21°01′41″N, 110°42′19″W, 26 Jan 2000, 1 m depth, on mangrove roots. Paratypes: BMNH-2002.9.10.2, Isla San José (La Paz, Baja California Sur), 21°01′41″N, 110°42′19″W, 26 Jan 2000, 1 m depth, on mangrove roots. LEB-ICML-UNAM-14, Isla Pájaros (Mazatlán, Sinaloa), 23°15′29″N, 106°28′25″W. LEB-ICML-UNAM-84, Peña de La Virgen (San Blas, Nayarit), 21°31′05″N, 105°20′05″W, 22 Nov 1999, 5 m depth, on rocks. LEB-ICML-UNAM-150, Cerritos (Mazatlán, Sinaloa), 23°18′51″N, 106°29′31″W, 2 Jan 2001, 0.5 m depth, on rocks. LEB-ICML-

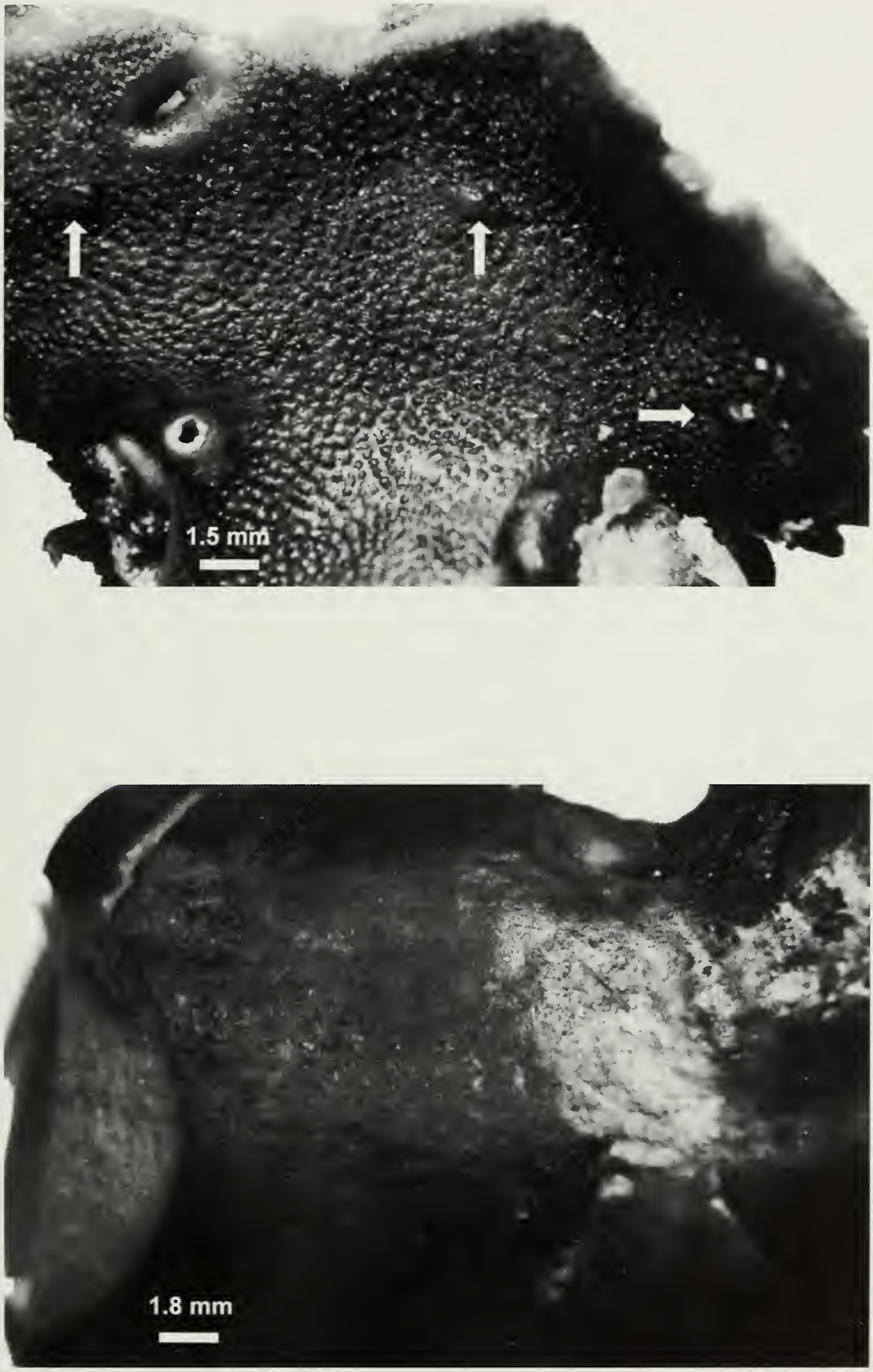

Fig. 1. A. Close up view of surface of *Chondrilla montanusa*, new species, showing the characteristic warty surface. Arrows indicate oscules. B. Close-up view of surface of *Chondrilla pacifica*, new species.

Table 1.—Characteristics of *Chondrilla montanusa* and *Chondrilla pacifica,* new species. (Numbers in brackets indicate averages).

	Asters (μm)	Shape & size (cm)	Thickness (mm)	Cortex (μm)	Color alive	Surface	Distribution
Chondrilla montanusa							
Holotype							
MNCN-1.01/176	7.5–(25.3)–38.5	Encrusting (5 by 2)	1–4	260–400	Evenly black	Evenly microtuberculate	Sinaloa
Paratypes							
BMNH-2002.9.10.1	7.5–(25.3)–38	Encrusting (3 by 1.5)	1–3	260–400	Evenly black	Evenly microtuberculate	Sinaloa
LEB-ICML-UNAM-135	10–(26.8)–40	Encrusting, with elevated oscules (3 by 2.4)	2–4	200–365	Evenly black	Evenly microtuberculate	Sinaloa
LEB-ICML-UNAM-428	13–(27.4)–37.5	Encrusting (3 by 1)	1–3	200–500	White pink	Microtuberculate	Sinaloa
CNPGG-0448	12–(28.7)–39	Encrusting (5 by 3) with elevated oscules	2–5	50–200	Evenly black outside, white inside	Microtuberculate/ Smooth	Baja California
CNPGG-0449	15.6–(27.6)–36.4	Encrusting	1–3	100–300	Light brown	Microtuberculate/ Smooth	Sinaloa
CNPGG-0450	15.6–(28.5)–39	Encrusting (3 by 4.5)	1–2	97–130	Dark brown	Evenly microtuberculate	Sinaloa
CNPGG-0458	14.5–(27.8)–37.5	Encrusting, with elevated oscules	1–3	100–240	Evenly black	Microtuberculate/ Smooth	Oaxaca
Chondrilla pacifica							
Holotype							
MNCN-1.01/233	8.8–(26.3)–37.5	Lobed (5.5 by 4.2)	5–15	130–350	Dark gray to light brown, mottled	Smooth	Baja California Sur
Paratypes							
BMNH-2002.9.10.2	8.8–(26.3)–37.5	Lobed (7 by 2)	8–14	130–350	Dark gray to light brown, mottled	Smooth	Baja California Sur
LEB-ICML-UNAM-14	17.5–(29.8)–38	Encrusting (10 by 8)	2–6	199–332	Black mottled	Smooth	Sinaloa
LEB-ICML-UNAM-84	15–(26.8)–40	Encrusting (3 by 1.5)	2.5–7	150–250	Light brown, mottled	Smooth	Sonora
LEB-ICML-UNAM-150	7.5–(23)–40	Lobed (5.1 by 3.6)	1–18	130–250	Dark brown	Smooth	Sonora

Table 1.—Continued.

	Asters (µm)	Shape & size (cm)	Thickness (mm)	Cortex (µm)	Color alive	Surface	Distribution
LEB-ICML-UNAM-264	15–(27.4)–32.5	Encrusting (3 by 1.6)	2	60–200	White (in cave)	Smooth	Sonora
LEB-ICML-UNAM-265	16.3–(23.8)–31.3	Encrusting	12–45	90–130	Dark brown	Smooth	Sinaloa
LEB-ICML-UNAM-287	15–(24.8)–35	Encrusting (9 by 6.5)	2–11	70–180	Dark gray to light brown, mottled	Smooth	Sonora
LEB-ICML-UNAM-301	8–(23.8)–35	Encrusting (18.2 by 11.5)	4–9	100–180	Dark brown to light brown	Smooth	Baja California Sur
LEB-ICML-UNAM-368	17.5–(30.5)–45	Encrusting (7.5 by 7.5)	2–10	250–650	Dark brown	Smooth	Sinaloa
CNPGG-0451	11.5–(26.6)–34	Encrusting lobed (11.2 by 4.5)	2–20	70–500	Dark gray to light brown, mottled	Smooth	Baja California Sur
CNPGG-0453	10.5–(21.7)–26	Encrusting lobed (5 by 6.5)	10–30	120–500	Pale pink (in spirit)	Smooth	Guerrero

UNAM-264, Paraje Viejo (Guaymas, Sonora), 27°52′20″N, 110°52′08″W, 4 Nov 2000, 12 m depth, on rocks in cave. LEB-ICML-UNAM-265, Paraje Viejo (Guaymas, Sonora), 27°52′20″N, 110°52′08″W, 11/04/2000, 12 m depth, on rocks. LEB-ICML-UNAM-287, Ensenada de Bacochibampo (Guaymas, Sonora), 27°54′37″N, 110°57′12″W, 6 Nov 2000, 6 m depth, on bivalve shell. LEB-ICML-UNAM-301, Punta Cazón (Kino, Sonora), 28°52′20″N, 112°02′01″W, 8 Nov 2000, 3 m depth, on rocks. LEB-ICML-UNAM-308, Isla San José (La Paz, Baja California Sur), 21°01′41″N, 110°42′19″W, 21 Mar 2001, 1 m depth, on mangrove roots. LEB-ICML-UNAM-368, 23°12′29″N, 106°25′40″, Punta Chile (Mazatlán, Sinaloa), intertidal, on dead bivalve shells. LEB-ICML-UNAM-550, Sayulita (Nayarit), 20°52′29″N, 105°26′43″, 5 m depth, on rocks. CNPGG-0447, Punta Gorda (Ensenada, Baja California), 31°47′N, 116°45′W, 6 Mar 1977. CNPGG-0451, Bahía Concepción (Baja California), 26°30′N, 111°45′W, 30 Oct 1998. CNPGG-0453, (Guerrero), 17°54′24″N, 101°53′42″W, 11 Feb 1982, 10 m depth.

Description.—Encrusting or thickly encrusting over rocky substrate from 1 to 30 mm thick, covering areas up to 6.1 by 3.6 cm. Some specimens have meandering lobes and rounded borders. In mangrove habitats it covers submerged mangrove roots like fleshy cushion-shaped or lobate clumps up to about 2 cm thick (extent of spread approximately 11.5 by 6.5 cm). The color alive is black, dark-brown to light brown or beige, often mottled on the upper surface, and light beige to buff at the base and choanosome. In spirit, whitish or the same color as when alive. Specimens growing in dark areas or under rocks may be pale. The consistency is cartilaginous, firm, slightly compressible, and tough. The surface is smooth and shiny (Fig. 1B). Oscules wide or evenly scattered all over the surface, mostly minute (<1 mm), and slightly elevated in some specimens.

Structure.—Cortex pigmented, not de-

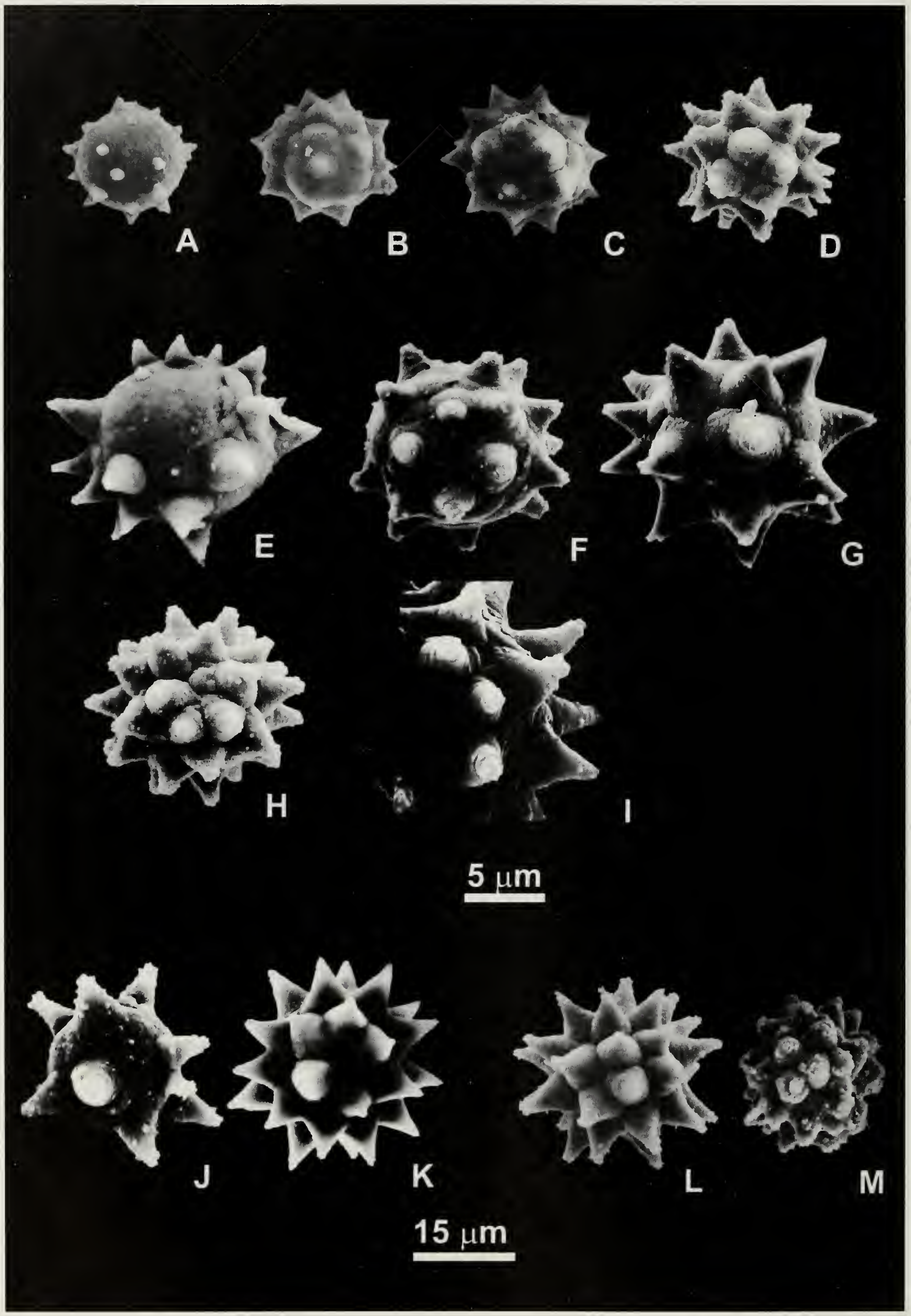

Fig. 2. SEM. Spherasters of *Chondrilla montanusa,* new species. A–D. Holotype MNCN-1.01/176. E–I. Paratype LEB-ICML-UNAM-135. J–K. Paratype CNPGG-0449. L–M. Paratype CNPGG-0458. Scale bars = 15 μm (except detail I = 5 μm).

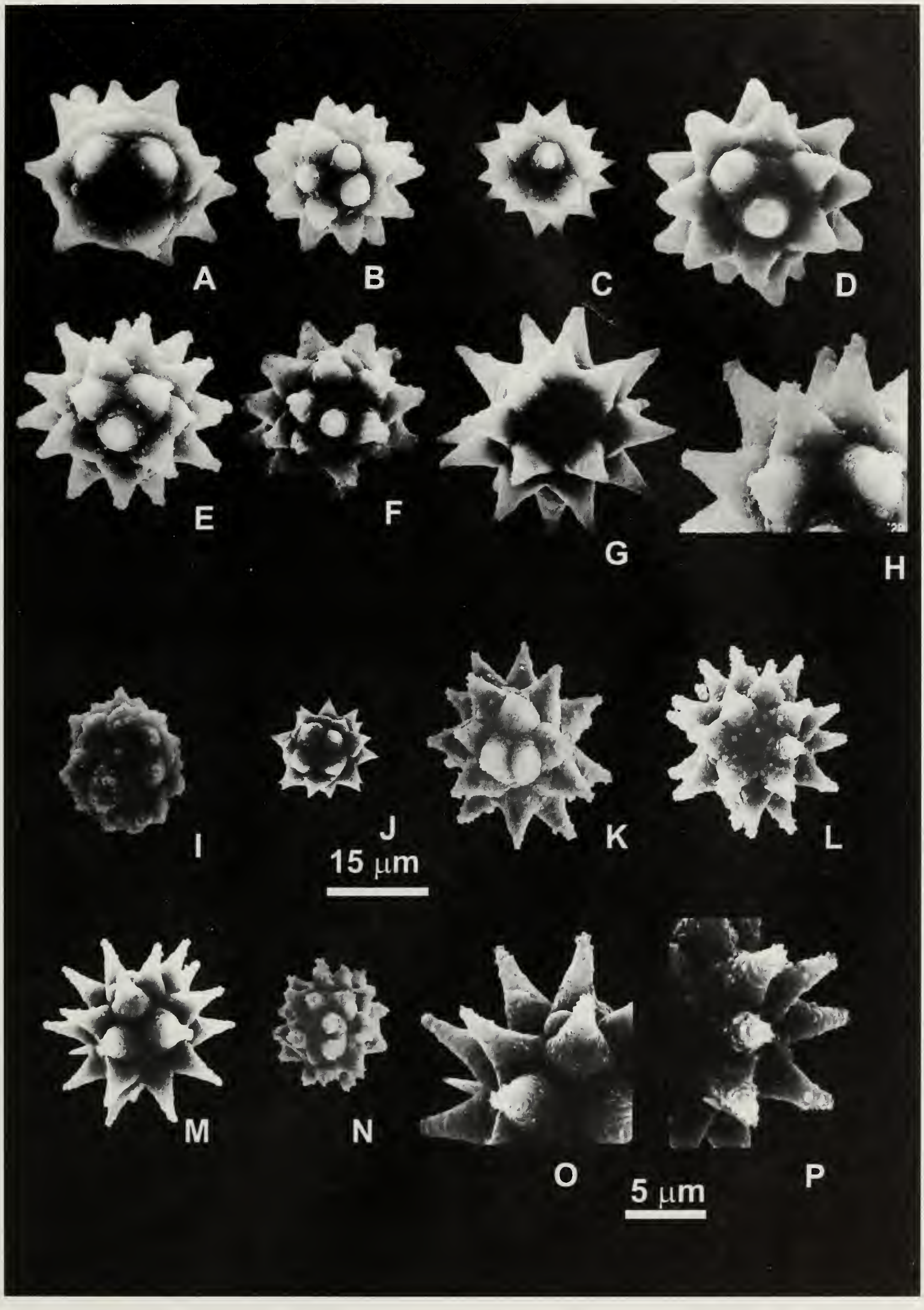

Fig. 3. SEM. Spherasters of *Chondrilla pacifica,* new species. A–H. Holotype MNCN-1.01/233. I–P. Paratype CNPGG-0451. Scale bars =15 μm (except details H, O, P = 5 μm).

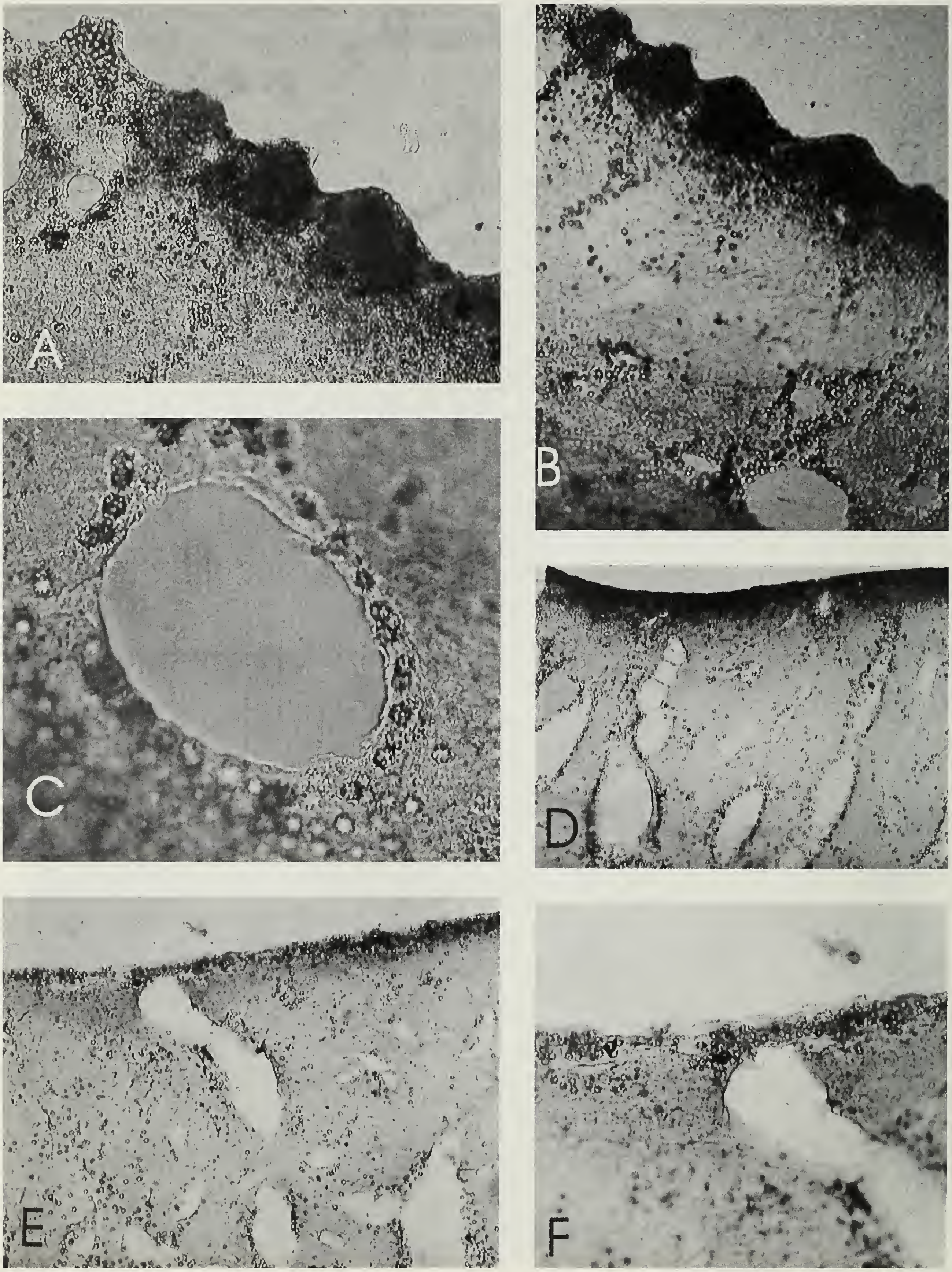

Fig. 4. Cross section of choanosome. A–B. *Chondrilla montanusa* holotype MNCN-1.01/176, detail of the elevations in the surface of the sponge due to high proportion of spherasters. C. Ample aquiferous space with spherasters organized in unispicular layer. D–E. *Chondrilla pacifica* holotype MNCN-1.01/233, surface and choanosome showing distribution of spherasters around canals and aquiferous spaces. F. Detail of the surface.

tachable, up to 650 μm in thickness, but slightly differentiated in most encrusting specimens (Table 1). The ostia (25–65 μm wide) are regularly distributed over most of the surface. The choanosome is dense, fleshy, with canals from 20 to 370 μm in diameter. The spiculation consists entirely of spherasters, 25.5 μm in average diameter (Table 1). The rays are conical, smooth, or slightly rough, but the extremities of the rays are often rough or slightly spiny. In the same specimens spherasters may appear with small irregular and mammiform rays. The number of rays varies between 20 and 30. The spherasters form a thin layer in the ectosome. In the choanosome they are not so abundant; they are scattered in the mesohyl, mainly surrounding the canals where they are organized in an uni/bispicular layer. In the basal part of the sponge they form a very dense layer.

Distribution.—Northeastern Pacific coast of Mexico. Nayarit (San Blas), Sinaloa (Mazatlán), Sonora (Guaymas, Kino), Baja California Sur (La Paz). Previously cited from Sonora (Puerto Peñasco) by Hofknecht (1978). On rocks, on bivalve shells, on mangrove roots, small caves, between 0 and 12 meters depth.

Etymology.—The specific epithet refers to the Pacific Ocean.

Remarks.—The two *Chondrilla* species that coexist in the Mexican Pacific are clearly separated by the type of surface and the organization of the choanosome. The surface in *Chondrilla montanusa* is microtuberculate and smooth in *C. pacifica. Chondrilla montanusa* is characterized by a minutely warty surface, visible to the naked eye, due to the high proportion of spherasters in the cortex. The proportion of spherasters in the choanosome in *C. montanusa* is higher than in *C. pacifica.*

Chondrilla pacifica is characterized by the presence of spherasters with reduced rays, a low proportion of spicules in the choanosome mainly surrounding the canals, and the presence of a smooth surface. A closely related species to *C. pacifica* is *C. verrucosa,* the only valid record of a *Chondrilla* species in the Central Eastern Pacific. *Chondrilla verrucosa* is characterized mainly by the warty surface of the spherasters (Desqueyroux-Faúndez & Van Soest 1997) which can also appear in some spherasters of *C. pacifica.* However, the low proportion of spicules in the choanosome of the two new species distinguish them from *C. verrucosa,* which has a clearly higher proportion of spherasters in the choanosome (Desqueyroux-Faúndez & Van Soest 1997).

The morphology and the size of the spherasters have been reported to vary between populations of the same species and may not be a good character to discriminate between the species of *Chondrilla* (Bavestrello et al. 1993, Klautau et al. 1999). However, the distribution and abundance of the spherasters in the cortex and in the choanosome appear to be better diagnostic characters (Klautau et al. 1999).

Key to the Chondrillidae from the East Pacific Coast

1\. With spherasters 2
1′. Without spherasters *Chodrosia tenochca*
2\. Surface completely or partly microtuberculate .... *Chondrilla montanusa*
2′. Surface always smooth 3
3\. Spherasters are mainly smooth and scarce in the choanosome .... *Chondrilla pacifica*
3′. Spherasters are mainly warty and abundant in the choanosome .... *Chondrilla verrucosa*

Acknowledgments

This study was financed in part by the project "Biodiversidad de esponjas del Mar de Cortés: bases para su conservación y valoración como recursos marinos" funded by the CONABIO (National Commission for Biodiversity Research), and by the Consejo Estatal de Ciencia y Tecnología (CECyT) of the Government of Sinaloa, through a grant to JACB. We thank N. Boury-Esnault and J. Vacelet for generous help with information and valuable comments, Ruth Desqueyroux-Faúndez for the loan of the SEM photograph of *Chondrilla verrucosa.* Martín Merino Ibarra for his support, Yolanda Hornelas and Silvia Antuna for the SEM photographs, Clara Ramírez Jáuregui (ICML-Mazatlán) for help with the literature, and German Ramírez Reséndiz and Carlos Suarez for their computer assistance.

Literature Cited

Bavestrello, G., M. Bonito, & M. Sarà. 1993. Silica content and spicular size variation during an annual cycle in *Chondrilla nucula* Schmidt (Porifera, Demospongiae) in the Ligurina Sea. Pp. 421–425 *in* M. J. Uriz & K. Rützler, eds., Recent advances in ecology and systematics of sponges. Instituto de Ciencias del Mar, C. S. I. C., Barcelona.

Bergquist, P. R. 1978. Sponges. Ed. Hutchinson, London, 268 p.

Boury-Esnault, N. 2002. Orden chondrosida. Pp. 299–305 *in* J. N. A. Hooper and R. W. M. Van Soest, eds., A guide to the supraespecific classification of the phylum Porifera. Kluwer Academic, Plenum Publishers, NY.

Boury-Esnault, N., & T. Lopes. 1985. Les démosponges littorales de l'Archipel des Açores.—Annales de l'Institut Océanographique 61:149–225.

———, M. Pansini, & M. J. Uriz. 1993. Cosmopolitanism in sponges: the "complex" *Guitarra fimbriata* with description of a new species of *Guitarra* from the northeast Atlantic. Pp. 367–373 *in* M. J. Uriz and K. Rützler, eds., Recent advances in ecology and systematics of sponges. Instituto de Ciencias del Mar, C. S. I. C., Barcelona.

Carballo, J. L., & E. Hajdu. 1998. Micromorphology in *Mycale* taxonomy (Mycalidae, Poecilosclerida, Demospongiae), with the description of two new micracanthoxea-bearing species.—Contribution of Zoology 67:187–195.

Carter, H. J. 1886. Supplement to the descriptions of Mr. J. Bracebridge Wilson's Australian sponges.—Annals and Magazine of Natural History (ser. 5)18:286–288.

———. 1887. Description of *Chondrosia spurca,* n. sp. from the south coast of Australia.—Annals and Magazine of Natural History (ser. 5)19: 271–290.

Desqueyroux-Faúndez, R., & R. W. M. Van Soest. 1997. Shallow water Demosponges of the Galápagos Islands.—Revue suisse de Zoologie 104(2):379–467.

Gray, J. E. 1872. Notes on the classification of the sponges.—Annals and Magazine of Natural History (ser. 4) 9:422–461.

Green, G., & P. Gómez. 1986. Estudio taxonómico de las esponjas de la Bahía de Mazatlán, Sin. México.—Anales del Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México 13:273–300.

Hofknecht, G. 1978. Descriptions and key to the intertidal sponges of the Puerto Peñasco area in the Gulf of California.—Journal of the Arizona Nevada Academy of Science 13:51–56.

Hooper, J. N. A., & F. Wiedenmayer. 1994. Porifera. Zoological Catalogue of Australia, vol. 12. CSIRO Australia, Melbourne, 624 pp.

Klautau, M., C. A. M. Russo, C. Lazoski, N. Boury-Esnault, J. P. Thorpe, & A. M. Solé-Cava. 1999. Does cosmopolitanism result from overconservative systematics? A case study using the marine sponge *Chondrilla nucula.*—Evolution 53: 1414–1422.

Lazoski, C., A. M. Solé-Cava, N. Boury-Esnault, M. Klautau, & C. A. M. Russo. 2001. Cryptic speciation in a high gene flow scenario in the oviparous marine sponge *Chondrosia reniformis.*—Marine Biology 139:421–429.

Laubenfels, M. W. de. 1935. Some sponges of lower California (México).—The American Museum of Natural History 779:1–14.

———. 1936. A discussion of the sponge fauna of the Dry Tortugas in particular, and the West Indies in general, with material for a revision of the families and orders of the Porifera.—Carnegie Institute of Washington Publication Number 467. Papers of the Tortugas Laboratory 30:1–225.

———. 1951. The sponges of the Island of Hawaii.—Pacific Science 5:256–271.

———. 1954. The sponges of the west-central Pacific. Oregon State College Press Monographs, Studies in Zoology, No. 7, 306 pp.

———. 1955. Sponges of Onotoa.—Pacific Science 9: 137–143.

Lendenfeld, R. L. R. 1888. Descriptive catalogue of the sponges in the Australian Museum, Sidney. London Australian Museum 16, 260 pp.

Lévi, C. 1973. Systématique de la Classe des Demospongiaria (Démosponges). Pp. 576–631 *in* P. Grassé, ed., Traité de Zoologie Spongiaires. Masson et Cie Editeurs, París 3(1):715.

Nardo, G. D. 1847. Osservazioni anatomiche sopra l'animale detto volgarmente rognone di mare.—Atti Istitute Veneto 6:267–268.

Rützler, K. 1974. The burrowing sponges of Bermuda.—Smithsonian Contributions to Zoology 165:1–32.

Schmidt, E. O. 1862. Die spongien des Adriatischen Meeres. Engelmann, Leipzig, vii, 88 pp.

———. 1870. Grundzüge einer spongien-fauna des Atlantischen Gebietes. Leipzig, Engelmann, pp. 1–88.

Schulze, F. E. 1877. Untersuchungen über den Bau und die Entwicklung der Spongien. Dritte Mittheilung. Die Familie der Chondrosidae.—Zeitschrift für wissenschaftliche zoologie 29:87–122.

Topsent, E. 1895. Etude monographique des Spongiaires de France. II. Carnosa.—Archives Zoologie expérimental et genérale 3° série: 493–590.

Vacelet, J., & T. Perez. 1998. Two new genera and species of sponges (Porifera, Demospongiae) without skeleton from a Mediterranean cave.—Zoosystema 20:5–22.

Wiedenmayer, F. 1989. Demospongiae (Porifera) from northern Bass Strait (Shelf of Southern Australia).—Memoirs Museum Victoria 50:1–242.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(2):528. 2003.

Errata

Fumio Iwata. 2001. *Nipponnemertes fernaldi,* a new species of swimming monostiliferous hoplonemertean from the San Juan Archipelago, Washington, U.S.A.—Proceedings of the Biological Society of Washington 114 (4): 833–857. Figure 4, page 842, due to author oversight figure captions were misplaced:

Image for Fig. 4f appears above the Fig. 4h legend.
Image for Fig. 4g appears above the Fig. 4f legend.
Image for Fig. 4h appears above the Fig. 4g legend.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(2):529–530. 2003.

BIOLOGICAL SOCIETY OF WASHINGTON

129th Annual Meeting, 23 May 2002

President-elect Roy W. McDiarmid called the meeting to order at 11:05 a.m. in the Waldo Schmitt Room, National Museum of Natural History. Council members present: W. Duane Hope, Michael Carleton (Elected Council), Richard Sternberg (Editor), Stephen Cairns and Frank D. Ferrari (Finance Committee), Storrs L. Olson (Custodian of Publications), Richard Banks, Bruce Collette, Kristian Fauchald, David Pawson, Janet Reid, Richard Vari (Past Presidents), T. Chad Walter (Treasurer), Carole C. Baldwin (Secretary). Council members absent: Susan L. Jewett, G. David Johnson, Rafael Lemaitre, Jon Norenburg.

McDiarmid announced that due to illness, President Kensley would not be presiding over the meeting. McDiarmid noted that the Society had dealt with a number of difficult issues during the past year, including the replacement of long-time *Proceedings* Editor Brian Robbins and mail problems related to anthrax contamination of a postal facility in Washington, D.C.

Minutes of the 128th Annual Meeting of the Society were approved, and McDiarmid then called on Chad Walter for the Treasurer's Report (Table 1). Society income for the period 1 January 2001 to 31 December 2001 was $126,129.06; expenses for the same period were $178,033.71. Total assets for the Society as of 15 April 2002 were $107,599.72, the Society's endowment account declining by $7,942.12 because of stock-market fluctuations. Additionally, because of disruption to mail service at the Smithsonian Institution following the closure of the Brentwood mail facility after anthrax contamination, $24,953.66 was withdrawn from the Society's endowment fund to cover costs of publishing the *Proceedings*. By the end of April, all of the borrowed funds had been returned to the endowment account. Stephen Cairns noted that the Audit Committee had found the Treasurer's records to be in good order.

The new Editor of the *Proceedings*, Richard Sternberg, reported that his tenure began 1 January 2002, and that outgoing Editor Brian Robbins had handled the publication of Volume 114 and the first issue of Volume 115. Sternberg reported that four issues of Volume 114 were published comprising 85 papers and 988 pages. In addition, 31 papers and 363 pages were published in Bulletin No. 10 (S. D. Cairns and C. G. Messing, Editors), and a new Guidelines for Manuscripts (C. B. Robbins and D. B. Lellinger) was published as a supplement to Volume 114(4). As of 22 May 2002, there were 42 submissions for the year, up from 33 in May 2001; however, Sternberg noted that many of those 42 submissions were postmarked in the Fall of 2001. There continues to be no backlog for papers accepted in the *Proceedings*.

McDiarmid announced that the Council had voted to adopt four recommendations of the Finance Committee: (1) Increase cost of reprints by approximately 20%; (2) increase cost of library subscriptions from $40 to $50 (which still keeps the price of the *Proceedings* in the lowest five percentile of scientific journals); (3) re-invest $55,000 of the Society's endowment funds into the American Funds Investment Company of America; and (4) establish gift-fund categories and list benefactors on a front page of the *Proceedings*. These measures are designed to help the Society reach a financial goal of $200,000 in the endowment fund. McDiarmid further noted that the Council had agreed to a vote at next year's annual meeting on a change suggested by the Finance Committee in By-Law No. 8, which establishes and describes the Society's endowment fund. The proposed change would remove "and surplus funds from operations" from the first sentence of By-Law 8, and the amended first sentence would read as follows:

> "Endowment Fund. There shall be an Endowment Fund which shall consist of gifts from members and miscellaneous gifts."

The Finance Committee (Stephen Cairns, Frank Ferrari, Oliver Flint, and Chad Walter, with assistance from Richard Banks) was thanked for its extended efforts on behalf of the Society.

In view of the very low attendance by members at the annual meeting of the Society, Bruce Collette suggested a single annual meeting in the future that combines the Council meeting and the annual meeting; a decision regarding a single meeting will be made after an Executive Committee examines the issue in more detail.

Results of the 2002 Election of Officers were then announced by President-elect McDiarmid: Rafael Lemaitre (President-elect), Carole Baldwin (Secretary), Chad Walter (Treasurer), Michael Carleton, G. David Johnson, Clyde Roper, Marilyn Schotte, Michael Vecchione, and Don Wilson (Elected Council). Assuming his new role as President, McDiarmid then thanked outgoing President Brian Kensley and adjourned the meeting.

Respectfully submitted,
Carole C. Baldwin
Secretary

Summary Financial Statement for 2001

	General Fund	Endowment Fund	Total Assets
Assets: January 1, 2001	29,028.46	83,732.79	112,761.25
Total Receipts for 2001	112,675.16	13,453.90[a]	126,129.06
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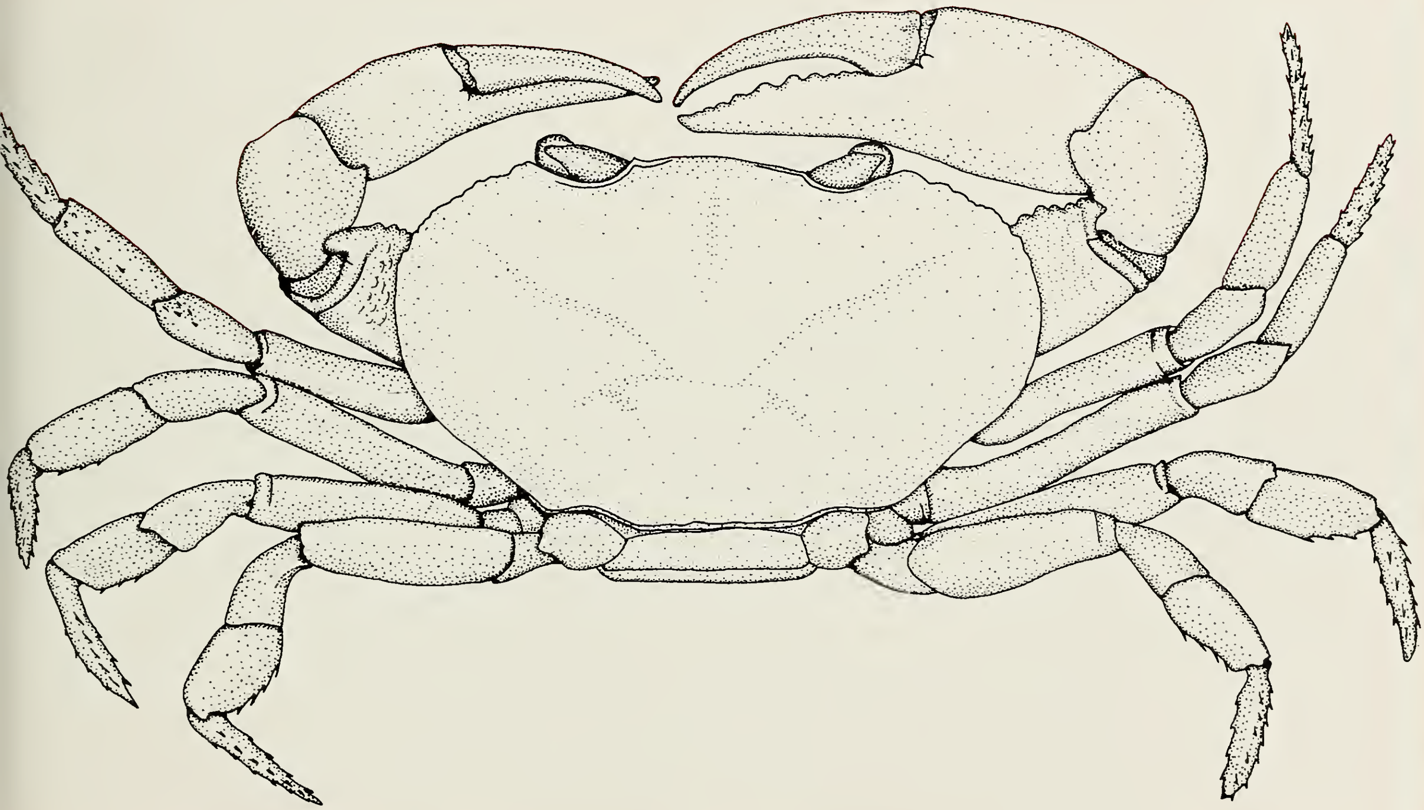

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Rediscovery, systematic position, and re-description of "*Leptoxis*" *melanoides* (Conrad, 1834) (Mollusca: Gastropoda: Cerithioidea: Pleuroceridae) from the Black Warrior River, Alabama, U.S.A.

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Abstract.—The rediscovery of *Leptoxis melanoides,* a pleurocerid snail from the Black Warrior River drainage of Alabama, previously considered to be extinct, is presented. The radula of *L. melanoides* more closely resembles that of *Elimia,* and an analysis of 16S rDNA sequences positions the species within a monophyletic clade of *Elimia.* Therefore, we re-describe the species as *E. melanoides,* designate a neotype, precise type locality, and illustrate the specimen and its radula.

The Mobile River basin, which drains much of Alabama and parts of Georgia, Mississippi, and Tennessee, is not only one of the largest drainage systems east of the Mississippi River (70,252 km^2; Lydeard et al. 1997), but was also home to more freshwater gastropod taxa than anywhere else in the world, accounting for 118 species in nine families (Bogan et al. 1995). Unfortunately, based on recent surveys and literature records, 38 (32%) of the gastropod species in the basin are now presumed extinct and many others have exhibited a marked decline in their distribution. One family that makes up a large component of the aquatic gastropod fauna in the basin is the Pleuroceridae.

Pleurocerids are freshwater, gill-breathing, operculate snails that reach their highest diversity in the southeastern United States (Burch & Tottenham 1980, Lydeard & Mayden 1995, Neves et al. 1997). Unfortunately, 25 pleurocerid species and one genus (*Gyrotoma*) are now presumed extinct due to the inundation of shoal areas by impoundment and habitat degradation from poor land use practices (Stein 1976, Bogan et al. 1995, Lydeard & Mayden 1995, Neves et al. 1997). Besides *Gyrotoma,* the genus *Leptoxis* has fared equally poorly in recent times, as 11 of 15 *Leptoxis* species in the Mobile River system are presumed extinct. Eight of the presumed 11 species were restricted to the main channel of the Coosa River of Alabama (Bogan et al. 1995), which is now a highly modified and regulated system (Hershler et al. 1990). Of the three other species, *L. compacta* was restricted to the middle portion of the Cahaba River, which, although lacking major dams, was and remains subject to high environmental stress from urban development and activity near the city of Birmingham. Another presumed extinct species, *L. melanoides,* was restricted to the Black Warrior River of Alabama. Recent surveys of the Coosa (Bogan & Pierson 1993a, J. Godwin, pers. comm.) and Cahaba (Bogan & Pierson 1993b) Rivers failed to find any of the presumed extinct *Leptoxis* species.

In 1996, the authors conducted a gastropod survey in one of the few remaining

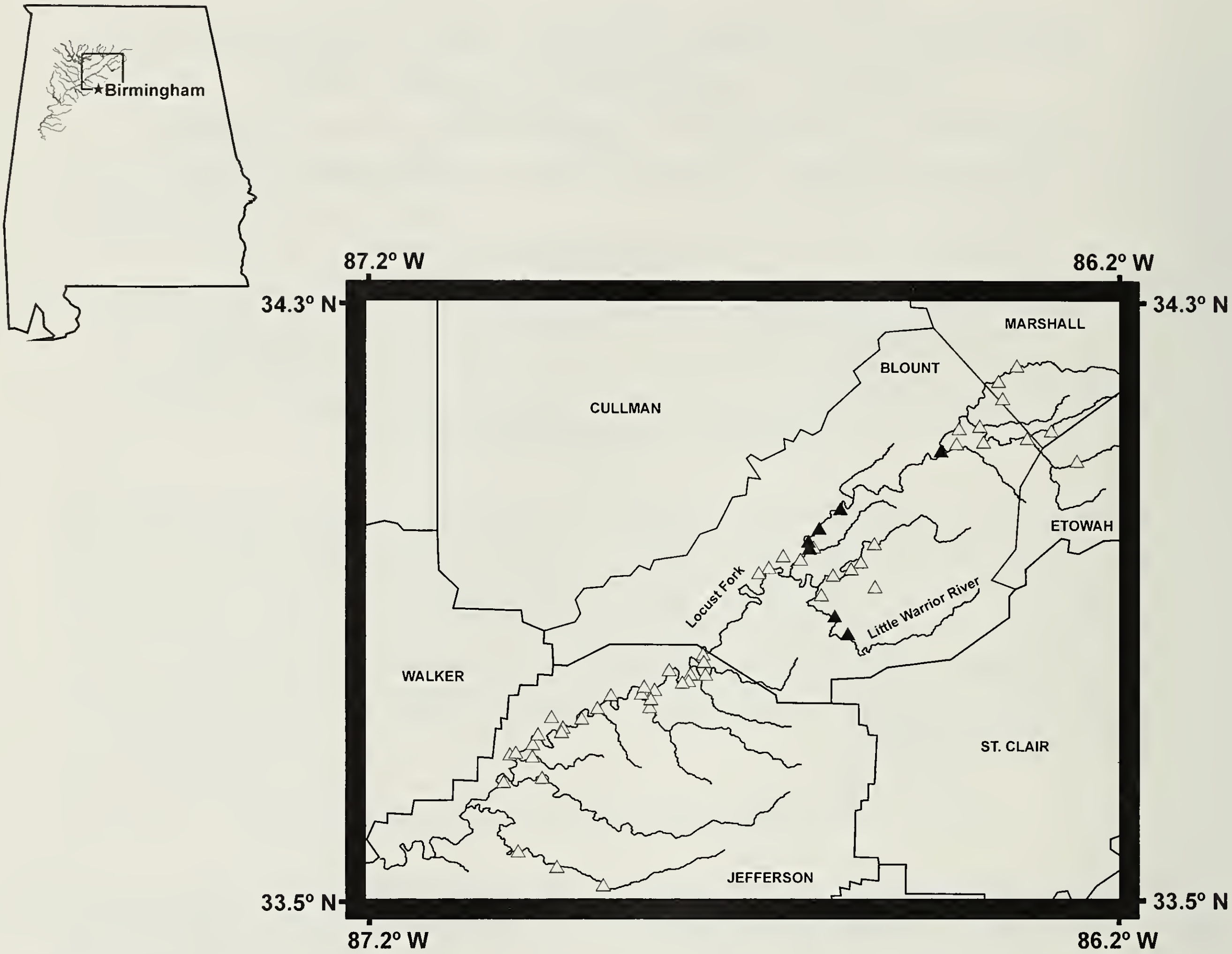

Fig. 1. Map of sites visited in this study. Upper map shows location of Black Warrior River drainage, lower map shows individual sites in Locust Fork portion. Closed triangles indicate those sites where *Leptoxis melanoides* was present.

free-flowing rivers in Alabama, the Locust Fork of the Black Warrior River. The main objective of the study was to determine the distribution of the third species, *L. plicata,* now restricted to the Locust Fork. During this survey, we rediscovered putative *L. melanoides.* This paper reviews the taxonomic and conservation history of *L. melanoides,* examines the historical and recent distribution of the species, and evaluates its phylogenetic position based on an analysis of mitochondrial 16S rDNA sequences. In addition, causes for the evident contraction of the distribution of the species are provided, along with a complete re-description of the species.

Methods

During the survey, 57 sites were visited in the Locust Fork drainage of the Black Warrior River in Blount, Etowah, Jefferson, and Marshall Counties (Fig. 1 & Appendix I). *Leptoxis melanoides* was found living in a total of seven localities in Blount County, five in the Locust Fork proper, and two in the Little Warrior River. Five individuals of *L. melanoides* from the Little Warrior River in Blount County, Alabama were collected in 2002 and used in this study. Radulae were prepared and visualized using the methods of Holznagel (1998) and compared to other pleurocerid radulae as figured in Holznagel (2000).

Genomic DNA was isolated from head tissues using standard phenol/chloroform methods. Sequences were obtained for an amplified segment of the mitochondrial large ribosomal subunit (16S) gene using the SR14231/SNL002 and H3080/L2510 primer pairs of Holznagel & Lydeard (2000) and Palumbi et al. (1991) respectively. The primers amplify an approximately 1 kb fragment of the gene and were used for amplification and sequencing. Double-stranded amplifications via PCR were generated using 50–500 ng of template genomic DNA in 25 μl volumes (10 mM Tris, 50 mM KCl, 2.5 mM $MgCl_2$, 1 μM each primer, 0.1 mM each dNTP, 1.5 units Taq DNA polymerase). The amplification regime consisted of 35 cycles of denaturation (92°C for 40 sec), annealing (52°C for 60 sec), and extension (72°C for 90 sec). Double-stranded products were purified using the Qiagen PCR Cleanup kit and provided the template for cycle sequencing using the ABI BigDye 2.0 kit following manufacturer's instructions. Reactions were purified using Qiagen DyeEx spin columns and sequenced on an ABI 3100 genetic analyzer.

Sequences of *L. melanoides* were entered in the software program BioEdit (version 5.0.9; Hall 1999), along with the 35 pleurocerid taxa used in Holznagel & Lydeard (2000), who provided the first phylogenetic survey of the Pleuroceridae (Appendix II). Sequences were aligned by eye to the secondary structure models suggested by Holznagel & Lydeard (2000) and Lydeard et al. (2002). Phylogenetic hypotheses were generated in PAUP* 4.0b10 (Swofford 2002) under maximum parsimony using 50 replicates of heuristic search with random addition. The following options were employed: uninformative characters were ignored, branches with a minimum zero length collapsed, and minimal length trees kept. To test the internal stability of the data, a jackknife analysis (Farris et al. 1996; 1000 replicates, 10 random additions per replicate) was performed using PAUP* and Bremer decay indices (Bremer 1994) were determined in SEPAL (Salisbury 2001). Holznagel & Lydeard (2000) showed significant phylogenetic signal and no evidence of base composition bias in their analysis. They also reported no TS/TV saturation up to near 20% genetic distance, so no weighting schemes were employed.

Specimens from the following museums were examined in this study: FMNH—Field Museum of Natural History, Chicago; FLMNH—Florida Museum of Natural History, Gainesville; NCSM—North Carolina State Museum of Natural Sciences, Raleigh; UMMZ—University of Michigan Museum of Zoology, Ann Arbor.

Results

Radulae taken from putative *Leptoxis melanoides* most resemble *Elimia* species, and not *Leptoxis* species (Fig. 2; see below and Fig. 4 for complete description). *Leptoxis melanoides* radulae have more rectangular laterals and more lateral cusps than other *Leptoxis* species, though the main lateral cusps are larger than those normally seen in *Elimia*. Also in *L. melanoides*, denticles are narrower and more numerous on the inner marginals.

Aligned sequences resulted in a matrix of 900 characters, including indels, of which 318 were parsimony informative. Maximum parsimony analysis yielded a single tree (1338 steps, CI = 0.52; Fig. 3). All five specimens of *L. melanoides* shared a single sequence and were resolved in a terminal clade of *Elimia* taxa and not in the polyphyletic groups of *Leptoxis* at the base of the tree. Jackknife values and Bremer indices strongly supported the resolution.

Systematics

Family Pleuroceridae Fischer, 1885

Genus *Elimia* Adams & Adams, 1854 (see Burch 2001)

Elimia melanoides (Conrad, 1834)

Fig. 4

Anculosa melanoides Conrad 1834:64, fig. 19.

Leptoxis melanoides Haldeman 1843–1853: 5, figs. 145–146.

Nitocris melanoides Adams & Adams 1858:308.

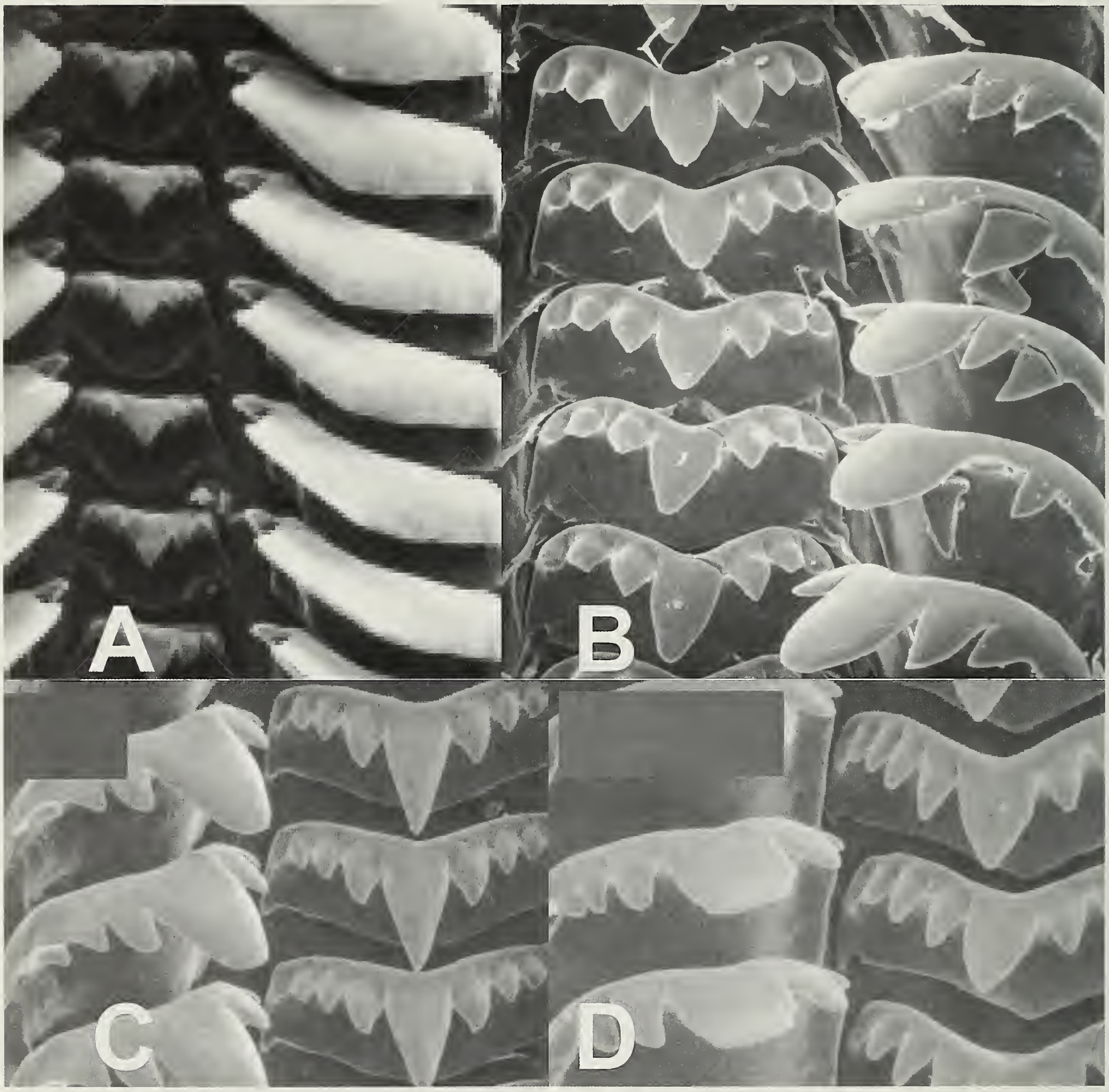

Fig. 2. Representative radulae from pleurocerids. A. *Leptoxis ampla*. B. *Elimia* sp. C. *Elimia alabamensis*. D. *Elimia showalteri*.

Anculosa turgida Haldeman 1840:2.
Leptoxis turgida Haldeman 1843–1853:5, fig. 151.

Type designation and locality.—Neotype FMNH 301993, Little Warrior River, dirt road bridge crossing off County Highway 15, R1E, T13S, sec. 30, Blount County, Alabama, U.S.A, here selected, in accordance with article 75.3.4 of the International Code of Zoological Nomenclature (I.C.Z.N. 1999). Neoparatypes FMNH 301889 (4 specimens).

Material examined (all in Alabama).—FMNH 33749, Black Warrior River; FMNH 57344, Black Warrior River; FMNH 76034, Black Warrior River; FMNH 80200, Warrior River, Jefferson County; FMNH 80243, Warrior River, Jefferson County; FLMNH 18219, Black Warrior River; FLMNH 81398, Locust Fork of Warrior River, Trafford, Jefferson County; FLMNH 81399, Black Warrior River, the forks; FLMNH 81400, forks of Warrior River, Walker County; FLMNH 81401;

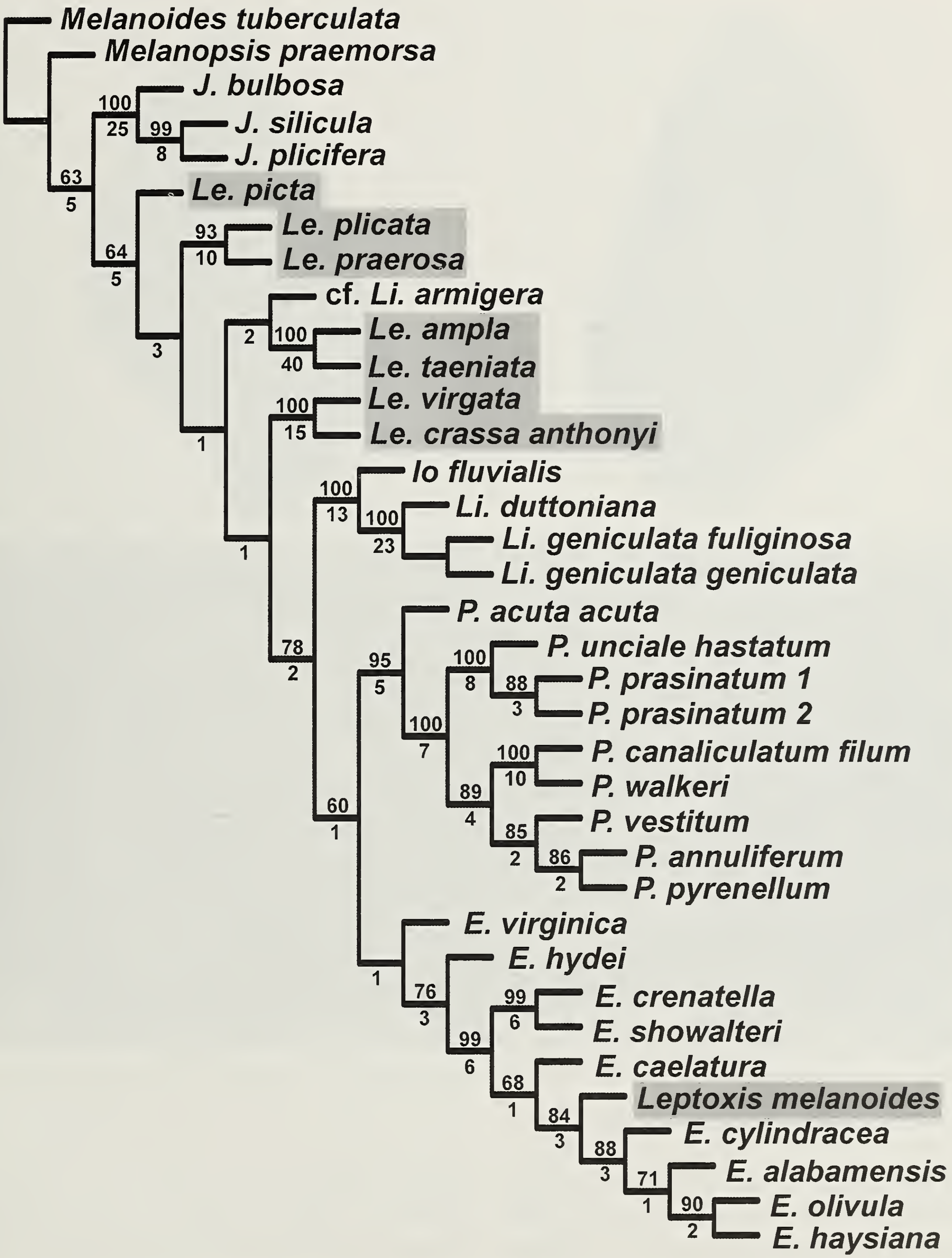

Fig. 3. The single most parsimonious tree generated using 16S rDNA sequences (1338 steps, CI = 0.52). Taxa historically considered *Leptoxis* are shaded. Values above branches are jackknife support, below are Bremer decay indices.

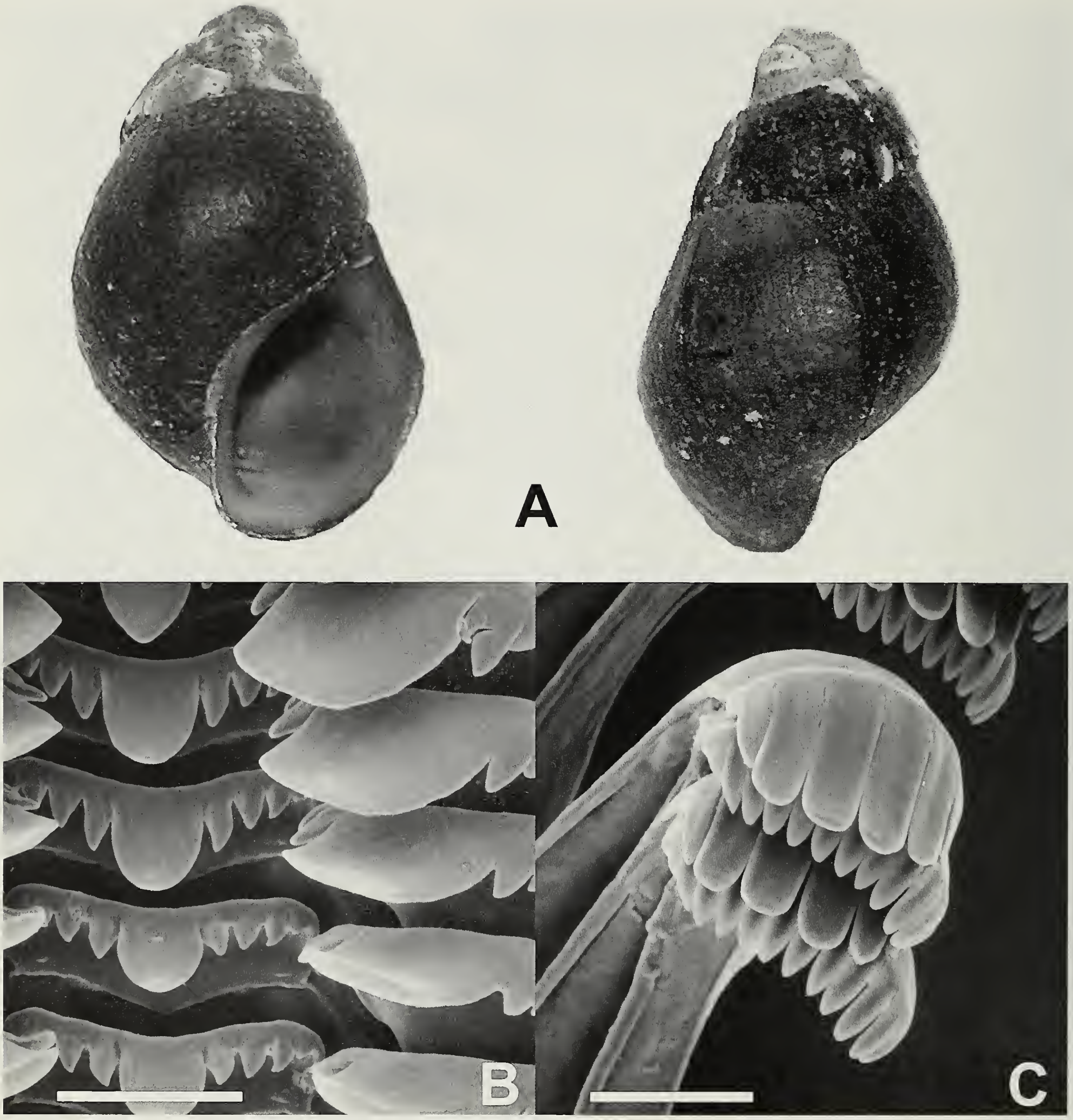

Fig. 4. *Elimia melanoides.* A. Neotype FMNH 301933, 10.8 mm. B. Rachidian and laterals. C. Inner and outer marginals. Scale bars: B, C = 50 μm.

FLMNH 82143, Locust Branch, Warrior River, Trafford; FLMNH 82144, Black Warrior River, Squaw Shoals, Jefferson County; FLMNH 82145, Warrior River; FLMNH 82146, Black Warrior River; FLMNH 82147, forks of Warrior River, Walker County; FLMNH 82148, Black Warrior River; FLMNH 82149, Warrior River, lock 15, Tuscaloosa County; FLMNH 82150, Black Warrior River, Tuscaloosa, Tuscaloosa County; FLMNH 82151, Valley Creek, Toadvine, Jefferson County; FLMNH 82152, Black Warrior River; FLMNH 82153, Black Warrior River, Squaw Shoals, Jefferson County; FLMNH 230087, Sipsey Fork, Bankhead National Forest N.F. 234, Winston County; FLMNH 230131, Sipsey Fork, Bankhead National Forest N.F. 234, Winston County; FLMNH 230766, Locust Fork, at Black Warrior River, Jefferson County; FLMNH 230803, Sipsey Fork, above Alabama Highway 33, Winston County; UMMZ 10169; UMMZ 37463, Alabama River; UMMZ 37464, Warrior River; UMMZ 37465, Locust Fork, Black Warrior River, Jefferson County; UMMZ 37466, forks of Black Warrior River, Walker County; UMMZ 49356, Black Warrior River, near mine, Jefferson County; UMMZ 55796 Locust (?) bridge of the Black Warrior River, Blount County; UMMZ 66275, Black Warrior River, Squaw Shoals, Tuscaloosa County; UMMZ 133928, Upper Black Warrior River; UMMZ 185760, Warrior River.

Diagnosis.—Shell small relative to sympatric pleurocerids, ovately conic and unsculptured, with even sutures. Shell more conic and aperture more ovate than typical *Leptoxis.* Columella white, frequently with pink to purple tinge. Distribution limited to Black Warrior River drainage, Blount County, Alabama.

Description.—Shell to 13 mm length, thin, ovately conic and smooth. Some early whorls and apex eroded. Fine transverse growth lines visible. Sutures flat to slightly impressed. Aperture oval, about one-half the length of the shell. Columella smooth and white, tinged with pink, red, or violet. Shell color green to brown, occasionally with brownish transverse bands. Operculum thin, dark, and oval, impressed at occasional growth lines (see Goodrich 1922, pl. 3, fig. 28). Radula rachidian tooth with nine triangular cusps, central cusp largest, slightly longer than wide. Lateral tooth broad, top edge straight with five cusps. Central cusp rectangular, broader and longer than others. Inner marginals with six to eight denticles, all equal size except for outer denticle on each side. Outer marginals with 12–14 denticles, all equal size except for outer denticle on each side.

Distribution.—Historically included the upper half of the Black Warrior River drainage, from Tuscaloosa and above. Currently restricted to stretches of the Locust Fork of the Black Warrior River and the Little Warrior River, Blount County, Alabama.

Remarks.—Conrad's (1834) original description of *Anculosa melanoides* was "Shell conical, with three entire volutions; apex eroded; whorls flattened, rounded only at the sutures; lines of growth prominent; body-whorl abruptly rounded; epidermis blackish, obscurely banded; aperture elliptical, about half the length of the shell" and the type locality, rivers of North Alabama, was ambiguous. Tryon (1873) reproduced Conrad's (1834) original description of *A. melanoides* and provided three figures of the species. Goodrich (1922) included an observation by H. H. Smith, who doubted that *A. melanoides* belonged in *Anculosa.* Goodrich (1941) later suggested that *A. melanoides* more closely resembled northern species in the genus and that its taxonomic position may change when its radula is obtained. A neotype designation was required, as the type specimen, once "in the possession of Mr. Anthony" (Tryon 1873: 400), was not available to Goodrich (1922), could not be located at the Museum of Comparative Zoology (Graf 2001) or the Academy of Natural Sciences in Philadelphia (Baker 1964), and has apparently been lost. The type locality has also been subsequently restricted to the drainage where the species is currently extant, following recommendation 76A of the code, as the original type locality could include the Tennessee River drainage, where the species does not occur.

Discussion

The rediscovery of putative *Leptoxis melanoides* was important and exciting, especially given the overall status of both many North American pleurocerid species and especially those in the Mobile River basin. This study helps to illustrate the need for thorough survey work combined with systematic analysis to rediscover and identify potentially "lost" or extinct taxa. Stein (1976:31) reviewed the conservation status of Alabama gastropods and stated ". . . it is doubtful whether living populations of this species still exist." In a subsequent report on rare and endangered invertebrates, Harris (1990) listed *L. melanoides* as endangered without evidence to suggest it still existed. Several formal and informal surveys had been conducted on various portions of the Black Warrior River and Locust Fork by U.S. Fish and Wildlife personnel and other investigators, but none documented the presence of *L. melanoides.* Given that the species had not been documented in over 50 years, Bogan et al. (1995) listed it as presumed extinct, a decision maintained by Turgeon et al. (1998). Comparisons of our material with museum specimens and cited illustrations support our notion of rediscovering *L. melanoides* in the Black Warrior River.

Of the 57 sites visited in the Locust Fork of the Black Warrior River drainage, *L. melanoides* was found at seven sites in two disjunct areas. Although it is possible the species may be more or less continuously distributed between the two areas, it still represents a small portion of the river system. It is evident, however, that based on historical distribution the species has declined drastically since the studies of Goodrich in the 1920's and 1940's. Blount County is home to poultry farms and coal mines which undoubtedly impact the surrounding water quality.

Analysis of mitochondrial 16S rDNA sequences suggests that *L. melanoides* should be placed in the genus *Elimia,* as it is resolved in a well-supported monophyletic clade of *Elimia* from the Mobile River basin. Such proposed generic reassignments are not uncommon in light of phylogenetic studies of freshwater mollusks (e.g., Lydeard et al. 2000, Minton & Lydeard 2003). The observed radulae are consistent with other species of *Elimia* (Holznagel 2000), and combined with shell morphology, make this species diagnosable in the upper reaches of the Locust Fork drainage. A redescription of what we are now considering *Elimia melanoides,* along with redesignation of type material, was needed given the presumed loss of the holotype and the phylogenetic placement resolved in this study.

Given its relative rarity and restricted distribution, and the overall decline of North American pleurocerids, remaining populations of *E. melanoides* should be monitored. Efforts are underway to list the species as endangered with the U.S. Fish and Wildlife Service. Until formally listed, the species should be treated as endangered and efforts made to preserve its remaining habitat.

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Literature Cited

Adams, H., & A. Adams. 1853–1858. Genera of recent mollusca arranged according to their organization. Three volumes. John van Voorst, Paternoster Row, London, 484 pp., 661 pp., 138 pl.

Baker, H. B. 1964. Type land snails in the Academy of Natural Sciences of Philadelphia. Part III. Limnophile and thalassophile Pulmonata, part IV. Land and fresh-water Prosobranchia.—Proceedings of the Academy of Natural Sciences of Philadelphia 116:149–193.

Bogan, A. E., & J. M. Pierson. 1993a. Survey of the aquatic gastropods of the Coosa River Basin, Alabama: 1992. Final Report. Submitted to Alabama Natural Heritage Program, Montgomery, Alabama, 13 pp.

———, & ———. 1993b. Survey of the aquatic gastropods of the Cahaba River Basin, Alabama: 1992. Final Report. Submitted to Alabama Natural Heritage Program, Montgomery, Alabama, 20 pp.

———, ———, & P. Hartfield. 1995. Decline in the freshwater gastropod fauna in the Mobile Basin. Pp. 249–252 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, & M. J. Mac, eds., Our living resources: a report to the Nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. U.S. Department of the Interior, National Biological Service, Washington D.C., 530 pp.

Bremer, K. 1994. Branch support and tree stability.—Cladistics 10:295–304.

Burch, J. B. 2001. On the genus name *Goniobasis* (*Elimia*: Gastropoda: Pleuroceridae) and other recent nomenclatural inconsistencies.—Walkerana 12:97–105.

———, & J. L. Tottenham. 1980. North American freshwater snails. Species list, ranges and illustrations.—Walkerana 1:81–215.

Conrad, T. A. 1834. New freshwater shells of the United States, with coloured illustrations, and a monograph of the genus *Anculotus* of Say; also a synopsis of the American naiades. Judah Dobson, Philadelphia, Pennsylvania, 76 pp.

Farris, J. S., V. A. Albert, M. Källersjö, D. Lipscomb, & A. G. Kluge. 1996. Parsimony jackknifing outperforms neighbor-joining.—Cladistics 12: 99–124.

Fischer, P. 1885. Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles (suivi dun appendice sur les Brachiopodes par D. P. Oehlert). F. Savy, Paris, pp. 689–784.

Goodrich, C. 1922. The *Anculosae* of the Alabama River drainage.—University of Michigan Museum of Zoology Miscellaneous Publications 7: 1–57, 3 plates.

———. 1941. Pleuroceridae of the small streams of the Alabama River system.—Occasional Papers of the Museum of Zoology, University of Michigan 427:1–10.

Graf, D. L. 2001. The cleansing of the Augean stables, or a lexicon of the nominal species of the Pleuroceridae (Gastropoda: Prosobranchia) of recent North America, north of Mexico.—Walkerana 12:1–124.

Haldeman, S. S. 1840. A monograph of the Limnaides and other freshwater univalve shells of North America. Supplement to No. 1. J. Dobson, Philadelphia.

———. 1843–1853. Monograph of *Leptoxis*. Pp. 1–6 *in* J. C. Chenu, Illustrations Conchyliologiques ou description et figues des toutes les coquilles connues vivantes et fossiles, classes suviant le systeme de Lamarck modifie d'apres les progres de la science, et comprenant les genres nouveaux et les especes recemment decouvertes. Four volumes.

Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT.—Nucleic Acids Symposium Series 41:95–98.

Harris, S. C. 1990. Preliminary considerations on rare and endangered invertebrates in Alabama.—Journal of the Alabama Academy of Science 61:64–92.

Hershler, R., J. M. Pierson, & R. S. Krotzer. 1990. Rediscovery of *Tulotoma magnifica* (Conrad) (Gastropoda: Viviparidae).—Proceedings of the Biological Society of Washington 103:815–824.

Holznagel, W. E. 1998. A nondestructive method for cleaning gastropod radulae from frozen, alcohol-fixed, or dried material.—American Malacological Bulletin 14:181–183.

———. 2000. A phylogenetic study of selected North American Pleuroceridae (Gastropoda: Cerithioidea) using molecular and radula data. Unpublished Ph.D. dissertation, University of Alabama, Tuscaloosa, 140 pp.

———, & C. Lydeard. 2000. A molecular phylogeny of North American Pleuroceridae (Gastropoda: Cerithioidea) based on mitochondrial 16S rDNA sequences.—Journal of Molluscan Studies 66:233–257.

International Commission on Zoological Nomenclature (I.C.Z.N.). 1999. International Code of Zoological Nomenclature, 4th edition. International Trust for Zoological Nomenclature, London, 306 pp.

Lydeard, C., & R. L. Mayden. 1995. A diverse and endangered aquatic ecosystem of the southeastern United States.—Conservation Biology 9: 800–805.

———, W. E. Holznagel, J. Garner, P. Hartfield, & M. Pierson. 1997. A molecular phylogeny of Mobile River drainage pleurocerid snails (Caenogastropoda: Cerithioidea).—Molecular Phylogenetics and Evolution 7:117–128.

———, R. L. Minton, & J. D. Williams. 2000. Prodigious polyphyly in imperiled freshwater pearly-mussels (Bivalvia: Unionidae): an examination of species and generic designations. Pp. 145–158 *in* E. Harper & J. Taylor, eds., The evolutionary biology of the Bivalvia, The Geological Society of London, Special Publications 177, 494 pp.

———, W. E. Holznagel, M. Glaubrecht, & W. F. Ponder. 2002. Molecular phylogeny of a circum-global, diverse gastropod superfamily (Cerithioidea: Mollusca: Caenogastropoda): pushing the deepest phylogenetic limits of mitochondrial LSU rDNA sequences.—Molecular Phylogenetics and Evolution 22:399–406.

Minton, R. L., & C. Lydeard. 2003. Phylogeny, taxonomy, genetics and global heritage ranks of an imperiled, freshwater snail genus *Lithasia* (Pleuroceridae).—Molecular Ecology 12:75–87.

Neves, R. J., A. E. Bogan, J. D. Williams, S. A. Ahlstedt & P. W. Hartfield. 1997. Status of aquatic mollusks in the Southeastern United States: a downward spiral of diversity. Pp. 46–85 *in* G. W. Benz & D. E. Collins, eds., Aquatic fauna in peril: the southeastern perspective. Lenz Design and Communications, Decatur, Georgia, 600 pp.

Palumbi, S., A. Martin, S. Romano, W. O. McMillan, L. Stice, & G. Grabowski. 1991. A simple fools guide to PCR. Privately distributed, Honolulu, Hawaii.

Salisbury, B. A. 2001. SEPAL: strongest evidence and parsimony analyzer. Version 1.4. Department of Ecology and Evolutionary Biology, Yale University, New Haven, Connecticut.

Stein, C. B. 1976. Gastropods. Pp. 1–41 *in* H. Boschung, ed., Endangered and threatened plants and animals of Alabama. Bulletin of the Alabama Museum of Natural History 2.

Swofford, D. 2002. PAUP*: Phylogenetic Analysis Using Parsimony, version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.

Tryon, G. W. 1873. Land and freshwater shells of North America, part IV. Strepomatidae.—Smithsonian Miscellaneous Collections 253:1–435.

Turgeon, D. D. et al. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks, 2nd edition. American Fisheries Society Special Publication 26, 526 pp.

Appendix I

Localities surveyed in 1996. Data include topographic coordinates; exact locality information is available from the authors. Localities where *E. melanoides* was found are indicated by an asterisk (*).

ALABAMA. Blount County: Berry Creek, T12S, R1E, sec. 33.—Calvert Creek, T13S, R1E, sec. 32.—Calvert Creek, T13S, R1E, sec. 6.—Calvert Prong of Little Warrior River, T12S, R1E, sec. 22.—Dry Creek, T12S, R1W, sec. 23.—*Little Warrior River, T13S, R1E, sec. 30.—*Little Warrior River, T13S, R1E, sec. 32.—Little Warrior River, T13S, R1W, sec. 13.—*Locust Fork, AL 160, T12S, R1W, sec. 23.—Locust Fork, T10S, R2E, sec. 25.—Locust Fork, T10S, R2E, sec. 27.—Locust Fork, T11S, R2E, sec. 1.—*Locust Fork, T11S, R2E, sec. 4.—*Locust Fork, T12S, R1E, sec. 6.—*Locust Fork, T12S, R1W, sec. 13.—*Locust Fork, T12S, R1W, sec. 23.—Locust Fork, T12S, R1W, sec. 27.—Locust Fork, T12S, R1W, sec. 32.—Mill Creek, T13S, R1E, sec. 10.—Sugar Creek, T13S, R1W, sec. 6.—Tucker Creek, T12S, R1W, sec. 28.—Whippoorwill Creek, T11S, R3E, sec. 3. *Etowah County*: Bristow Creek, 0.5 miles S of Pine Grove, T11S, R4E, sec. 7. *Jefferson County*: Campbell Creek, T15S, R4W, sec. 9.—Cane Creek, T15S, R4W, sec. 32.—Five Mile Creek, T16S, R4W, sec. 8.—Gurley Creek, T15S, R2W, sec. 21.—Locust Fork, 1.5 miles downstream of I-65, T14S, R3W, sec. 27.—Locust Fork, 5.5 miles downstream of I-65, T15S, R3W, sec. 32.—Locust Fork, 7 miles downstream of I-65.—Locust Fork, T14S, R2W, sec. 16.—Locust Fork, T14S, R2W, sec. 20.—Locust Fork, T14S, R2W, sec. 29.—Locust Fork, T14S, R2W, sec. 30.—Locust Fork, T14S, R3W, sec. 24.—Locust Fork, T14S, R3W, sec. 34.—Locust Fork, T14S, R3W, sec. 35.—Locust Fork, T14S, R3W, sec. 35.—Locust Fork, T15S, R2W, sec. 9.—Locust Fork, T15S, R4W, sec. 11.—Locust Fork, T15S, R4W, sec. 15.—Locust Fork, T15S, R4W, sec. 22.—Locust Fork, T15S, R4W, sec. 29.—Locust Fork, T15S, R4W, sec. 29.—Locust Fork, T15S, R5W, sec. 25.—Locust Fork, T15S, R5W, sec. 36.—Locust Fork, T15S, R6W, sec. 20.—Locust Fork, T16S, R5W, sec. 11.—Turkey Creek, T15S, R3W, sec. 2.—Village Creek, T16S, R5W, sec. 22.—Village Creek, T16S, R5W, sec. 36.—Village Creek, T17S, R4W, sec. 18. *Marshall County*: Clear Creek, T10S, R3E, sec. 35.—Drift Creek, T10S, R3E, sec. 17.—Locust Fork, T10S, R3E, sec. 34.—Slab Creek, T10S, R3E, sec. 6.—Slab Creek, T9S, R3E, sec. 33.

Appendix II

Systematic list of taxa used in this study. Taxon names (Burch & Tottenham 1980) are followed by museum voucher and GenBank accession numbers. FMNH—Field Museum of Natural History, Chicago. NCSM—North Carolina Museum of Natural Sciences, Raleigh.

PLEUROCERIDAE. *Elimia*: *E. alabamensis,* NCSM P4658, U73761; *E. caelatura,* NCSM P4659, AF100988; *E. crenatella,* NCSM P4660, U73762; *E. cylindracea,* NCSM P4661, U73765; *E. haysiana,* NCSM P4662, U73763; *E. hydei,* NCSM P4663, U73764; *E. interrupta,* NCSM 6595, AY010521; *E. melanoides,* FMNH 301889, AF540003; *E. olivula,* NCSM P4664, U73766; *E. showalteri,* NCSM P4665, U73767; *E. virginica,* NCSM P4666, AF100989. *Io*: *Io fluvialis,* NCSM P4667, AF100999. *Juga*: *J. bulbosa,* NCSM P4668, AF101005; *J. plicifera,* NCSM P4669, AF101004; *J. silicula,* NCSM P4670, AF101003. *Leptoxis*: *Le. ampla,* NCSM P4671, U73768; *Le. crassa anthonyi,* NCSM P4672, AF101001; *Le. picta,* NCSM P4673, U73769; *Le. plicata,* NCSM P4674, U73770; *Le. praerosa,* NCSM P4675, AF101002; *Le. taeniata,* NCSM P4676, U73771; *Le. virgata*; NCSM P4677, AF101000. *Lithasia*: cf. *Li. armigera,* NCSM P4678, AF100998; *Li. duttoniana,* NCSM P4679, AF100997; *Li. geniculata* *fuliginosa,* NCSM P4680, AF100995; *Li. geniculata geniculata,* NCSM P4681, AF100996. *Pleurocera*: *P. acuta acuta,* NCSM P4684, AF100994; *P. annuliferum,* NCSM P4685, U73772; *P. canaliculatum filum,* NCSM P4686, AF100991; *P. prasinatum* 1, NCSM P4689, U73774; *P. prasinatum* 2, NCSM P4688, U73773; *P. pyrenellum,* NCSM P4690, AF100990; *P. unciale hastatum,* NCSM P4687, AF100993; *P. vestitum,* NCSM P4691, U73775; *P. walkeri,* NCSM P4692, AF100992. THIARIDAE. *Melanoides tuberculata,* NCSM P4682, AF101006. MELANOPSIDAE. *Melanopsis praemorsa,* NCSM P4683, U73776.

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A new species of *Magelona* Müller, 1858 (Polychaeta: Magelonidae)

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Abstract.—*Magelona magnahamata,* new species, is described based on specimens found during a study of interstitial polychaetes carried out at Coiba National Park (Panamá). It differs from other species of *Magelona* with regard to features of chaetiger 9, hooded hooks on anterior abdominal segments, and coloration pattern. Specimens of this new species coincide widely with specimens from the Gulf of México reported and described previously as *Magelona* sp. C.

The family Magelonidae Cunningham & Ramage, 1888 currently includes three genera: *Magelona* Müller, 1858, with about 55 described species (Fiege et al. 2000) plus ten others identified and described, without specific names, by Uebelacker & Jones (1984); *Meredithia* Hernández-Alcántara & Solís-Weiss, 2000, with two species; and Octomagelona Aguirrezabala, Ceberio & Fiege, 2001, composed of a single known species.

The genus *Meredithia* is characterized by bearing large hooded curved spines in some abdominal chaetigers (Hernández-Alcántara et al. 2000), and the genus *Octomagelona* is distinguished by possessing eight thoracic segments instead of nine (Aguirrezabala et al. 2001).

Diagnostic characters of the genus *Magelona* are: presence and features of frontal horns, dimensions of the prostomium, presence of dorsal median lobes and lateral pouches, shape of chaetae on chaetiger 9, structure of the abdominal hooks and the various shapes of the lateral lamellae. These characters have been discussed by Jones (1963, 1977, 1978) and recently by Rouse (2001). The most recent review work for European magelonids is found in Fiege et al. (2000), who outlined the terminology frequently used for magelonids. Several authors agree that a high number of species are yet to be described (Uebelacker & Jones 1984, Hernández-Alcántara et al. 2000, Wilson 2000).

The new species belongs to the genus *Magelona,* and the specimens were found during a study carried out in the National Park of Coiba (Panamá), these specimens coincide widely with those described as *Magelona* sp. C found in the Gulf of México by Uebelacker & Jones (1984).

Only two species of this family have been reported in the Atlantic coast of Panamá (*Magelona pacifica* Monro, 1933 and *M. riojai* Jones, 1963); a single species both from the Atlantic and Pacific of Panamá (*Magelona papillicornis* Müller, 1858); and only one from the Pacific (*Magelona* sp., López et al. 2002, later identified as *M. sacculata* Hartman, 1961 after re-examination). Reports on Magelonidae from Panamá were made by Monro (1933), Fauchald & Reimer (1975) and Fauchald (1977).

Uebelacker & Jones (1984) described 12 species of *Magelona* from the Gulf of México, without giving specific names (*Magelona* sp. A to L) and found specimens of *M. pettiboneae* Jones, 1963. In Mexican Pacific waters, Hernández-Alcántara & Solís-Weiss (2000) reported four species of *Magelona*: *M. pacifica, M. sacculata, M. pitelkai* Hartman, 1944a, and *M. californica* Hartman, 1944b. Other reports from nearby regions were made by Jones (1963) (Caribbean Sea) and Hartman (1969), Jones (1978), and Blake (1996) (California).

Scientific expeditions dedicated to the knowledge of the flora and fauna of Coiba National Park (Pacific, Panamá) became regular from 1996. Characteristics of this area and previous results of the study of polychaetes from these expeditions are detailed in López et al. (1997, 2002), San Martín et al., (1997) and Capa et al. (2001a, 2001b, 2001c).

Materials and Methods

Material from the National Park of Coiba occurs in two samples from soft substrates taken at sampling stations of Mali Rock (7°39′N, 81°41′40″W) and Granito de Oro (7°35′30″N, 81°42′30″W). Sediment is composed of coarse sand, coming from coral destruction, sampled at depths to 0.5 m and 10 m. Samples were obtained using 1-liter capacity PVC tubes (core). Samples were filtered through a 0.1-mm gauge mesh sieve and retained material was fixed in formalin and preserved in ethanol (70%).

Material from the Gulf of México was loaned by the Smithsonian Institution and belongs to the collection examined by Uebelacker & Jones (1984). The samples were taken along the northeastern Gulf of Mexico (from Alabama to Florida); 10–117 m; coarse to fine-very fine sand, silty fine to very fine sand, and sandy silt containing clay.

Specimens were examined using a compound microscope equipped with an interference Nomarsky system, and drawings were made using a camera lucida drawing tube. Pictures from scanning electron microscopy (SEM) were taken at the SIDI (Servicio Interdepartamental de Investigación), Universidad Autonóma de Madrid.

Holotype, paratypes and additional material from Coiba National Park are deposited at the Museo Nacional de Ciencias Naturales (MNCN) de Madrid. Material from the Gulf of México is deposited in the Smithsonian Institution, National Museum of Natural History, Washington, D.C.

Results

Genus *Magelona* Müller, 1858

Magelona magnahamata, new species

Figs. 1, 2

Material examined.—Coiba National Park, Pacific of Panamá; Granito de Oro, holotype (MNCN 16.01/8736a), paratypes (4 spec. MNCN 16.01/8736b) and 3 specimens. Mali Rock (1 spec. MNCN 16.01/8737). Additional material: Gulf of México (1 spec., USNM 86713); (1 spec., USNM 86715); (1 spec., USNM 86716); (2 spec., USNM 86717); (2 spec., USNM 86718); (1 spec., USNM 867119); (2 spec., 86720); (1 spec., USNM 86722); (1 spec., USNM 86723); (1 spec., USNM 86725); (5 spec., USNM 86725); (3 spec., USNM 86721).

Description.—Holotype complete specimen with 82 chaetigers, 19 mm long and 0.39 mm wide at chaetiger 5, dark pigment on several specimens at anterior dorsal part of thorax and on each side of anterior abdominal chaetigers in some specimens. Prostomium triangular to semicircular, rounded anteriorly, almost as long as wide, frontal horns absent. Palps longer than thorax, reaching to about chaetiger 23 (paratype), with 2 rows of papillae, becoming smaller toward bases of palps. Dorsolateral margins of first segment covering posterior part of prostomium and ventrally surrounding bases of palps (Figs. 1A, 2A). Thoracic chaetigers bearing, both on notopodia and neuropodia, a pair of lanceolate, wide lateral lamellae; dorso-medial and neuropodial lobes absent (Figs. 1G, 2B). Abdominal chaetigers each with pair of lateral, foliaceous lamellae, smaller than thoracic ones (Fig. 1H). Lamellae gradually decreasing in size posteriorly, becoming digitiform (Fig. 1I). Dorsal medial and neuropodial lobes small, papilliform on anterior and posterior abdominal chaetigers (Fig. 1H, I). Thoracic capillary chaetae slender, long and limbate (Fig. 2B). Chaetiger 9 lacking specialized

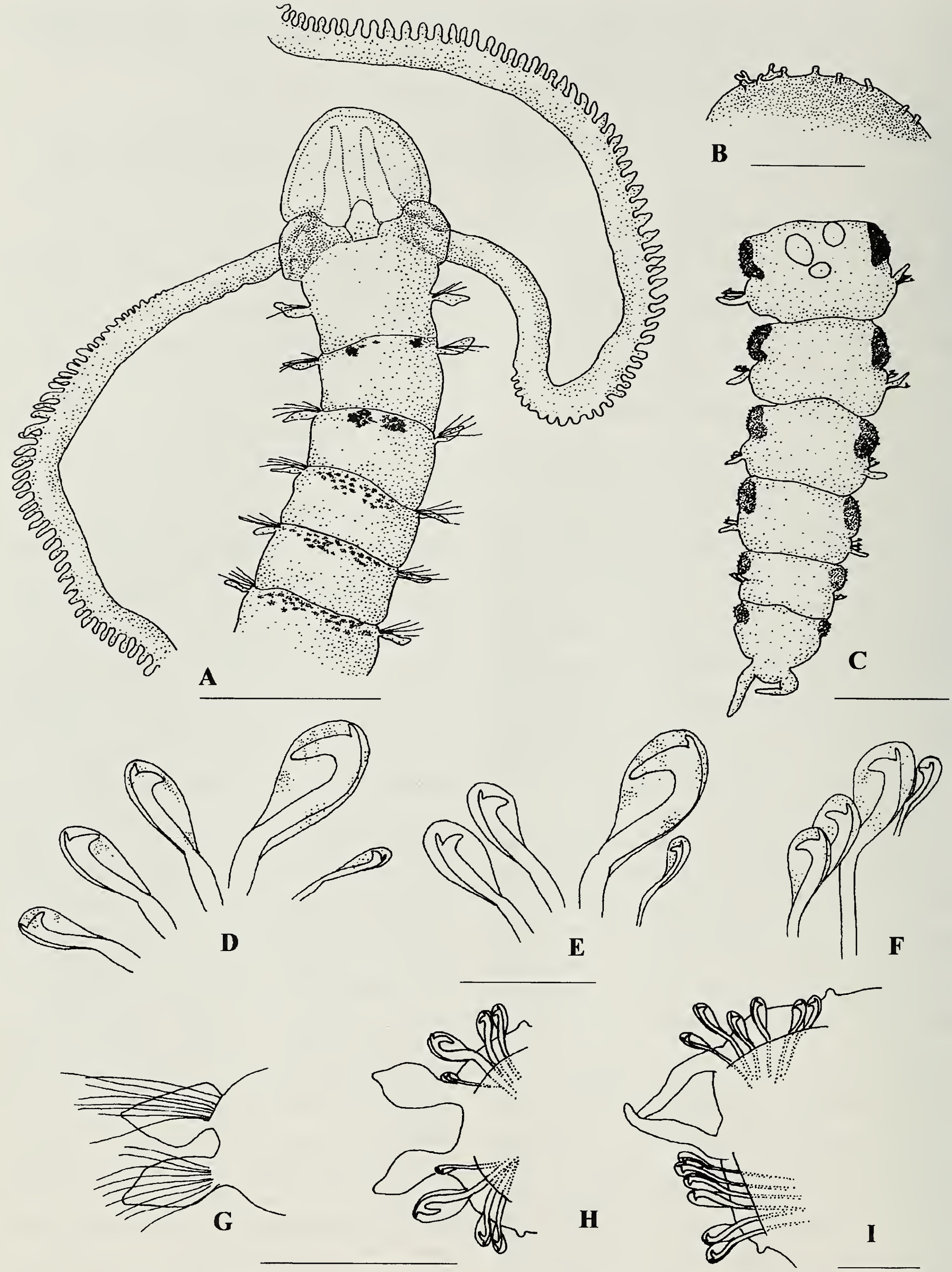

Fig. 1. *Magelona magnahamata,* n. sp. A: Anterior end, dorsal view; B: lateral papillae, posterior chaetiger; C: Posterior end, dorsal view; D: Hooks, anterior abdominal chaetiger; E: Hooks, abdominal chaetiger, segment 13; F: Hooks, posterior abdominal chaetiger; G: Parapodium, posterior view, anterior chaetiger; H: Parapodium, posterior view, median chaetiger; I: Parapodium, posterior view, posterior chaetiger. Scale A: 375 μm; B: 35 μm; C: 200 μm; D–F: 35 μm; G, H: 200 μm; I: 50 μm.

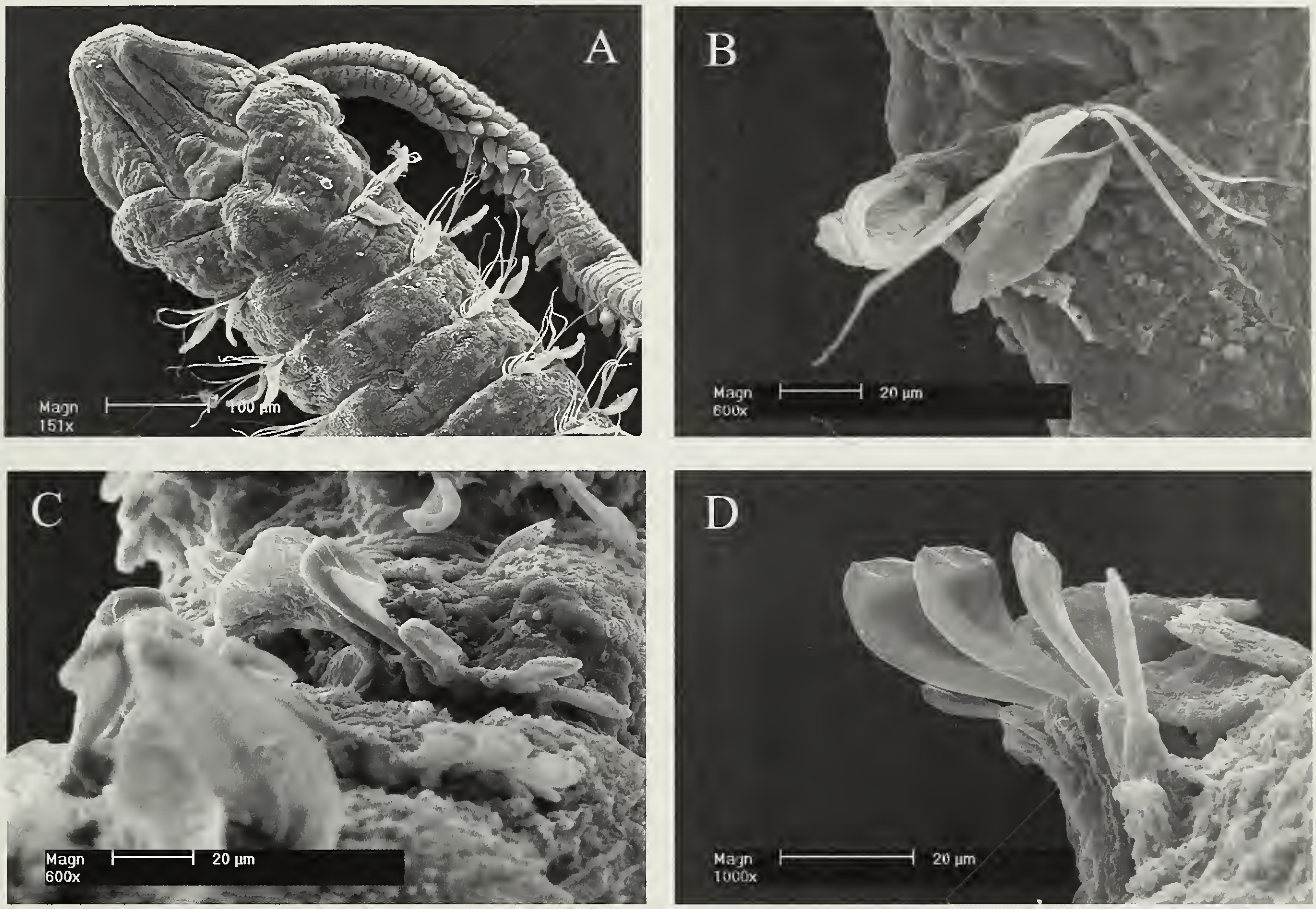

Fig. 2. *Magelona magnahamata,* n. sp. Scanning electron micrographs (SEM). A: Anterior end, dorsal view; B: Lamellae and capillary chaetae, thoracic segment; C: Hooded hooks on anterior abdominal chaetigers; D: Hooded hooks on posterior abdominal chaetiger.

chaetae. Abdominal hooded hooks bidentate, arranged in two groups on each ramus facing vis-à-vis. Hooded hooks of anterior abdominal chaetigers in three abruptly different sizes; each ramus with a very small hook originating at base of lateral lamella, a single large and strongly curved hook, and three intermediate-sized hooks (Figs. 1D, 2C). From abdominal chaetiger 2-5 on (depending upon specimens), intermediate hooks numbering two (Fig. 1E). On notopodium, smallest and largest hooks face dorsally, and intermediate sized ones face ventrally (vice versa at neuropodium) (Fig. 1H). On posterior chaetigers, hooded hooks in two sizes, a single small hook nearest to lamellae, and several larger hooks (Fig. 1F); on most posterior chaetigers all hooks of one size, all similar (Figs. 1I, 2D). The hooks, on posterior chaetigers, more numerous (5–6) than those on anterior abdominal chaetigers, oriented 4 to 2 in notopodium, 4 hooks face dorsally and 2 ventrally, and vice versa in neuropodium (Fig. 1I); and in others combinations (3 to 2, 4 to 1, 5 to 1). No lateral pouches. Conical pygidium with two short digitiform cirri (Fig. 1C). Abdominal chaetigers of some specimens (from chaetiger 40 in holotype, from the first abdominal chaetiger in others) with pronounced, rounded, lateral, glandular areas anterior to parapodia, also pronounced, dark to red, and covered with small papillae (Fig. 1B, C).

Remarks.—*Magelona magnahamata* is characterized by having a large, strongly curved, hooded hook on each anterior abdominal parapodial ramus and by lacking modified chaetae on chaetiger 9. Some lesser differences have been found between the Atlantic and Pacific material. For instance, the apical tooth of the large hooks is very small in some specimens from the Gulf of México, while in other specimens from this area and in those of Coiba it is long, but this condition probably can be attributed to intra-specific variation. In some specimens of the Gulf of México, the large hooks seem to be slightly more robust than those from Coiba. Finally, the size is also somewhat different: specimens from the Gulf of México are smaller than those Coiba, the largest being 10 mm long and 0.14 mm wide (at level of chaetiger 5), whereas in Coiba, the holotype is 19 mm long and 0.39 mm wide. However, these differences are not sufficient to consider the populations as belonging to two different species.

The closest species known from the Pacific Ocean is *Magelona pettiboneae* Jones, 1963. Both seem similar in the capillary chaetae, bidentate hooks, and the absence of modified chaetae in chaetiger 9; however, the hooks of *M. pettiboneae* are not so curved in anterior abdominal chaetigers, its lateral lamellae are shorter and rounded, and the hooks are more numerous.

Magelona magnahamata is also related to three other species from the Atlantic coast of North America (*M. papillicornis* Müller, 1858, *M. californica* Hartman, 1944b, and *M. minuta* Eliason, 1962) for which Jones (1977) established common characteristics. In this way, all four species would share a subtriangular prostomium with rounded anterolateral margins, absence of dorsal medial and neuropodial lobes at the anterior region, abdominal chaetigers with subtriangular or sublanceolate lateral lamellae, dorsal medial and neuropodial lobes papilliform, and bidentate hooded hooks, one of them, the nearest to lamellae, smaller than the remaining. However, the presence of very bidentate and strongly curved hooks separates *M. magnahamata* from the others.

Some specimens of *M. magnahamata* also possess modified posterior abdominal chaetigers with dark colored areas covered with papillae. These papillae have never been cited for any described species in the genus.

Etymology.—The specific name comes from Latin *magna* = large and *hamulus*, diminutive of *hamus* = hook, referring to the large strongly curved hooded hooks.

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Literature Cited

Aguirrezabala, F., A. Caberio, & D. Fiege. 2001. *Octomagelona bizkaiensis* (Polychaeta: Magelonidae) a new genus and species from the Cape Breton Canyon (Bay of Biscay, north-east Atlantic).—Journal of the Marine Biological Association of the United Kingdom 81:221–224.

Blake, J. A. 1996. Family Magelonidae Cunningham and Ramage, 1888. Pp. 253–260 *in* J. A. Blake, B. Hilbig, & P. H. Scott, eds., The Annelida, part 3. Polychaeta: Orbiniidae to Cossuridae, vol. 6. Santa Barbara Museum of Natural History: Santa Barbara, California.

Capa, M., G. San Martín, & E. López. 2001a. Syllinae (Syllidae: Polychaeta) del Parque Nacional de Coiba (Panamá).—Revista de Biología Tropical 48:101–113.

———, ———, & ———. 2001b. Description of a new species of *Parasphaerosyllis* (Polychaeta: Syllidae: Syllinae).—Proceedings of the Biological Society of Washington 114:280–284.

———, ———, & ———. 2001c. Autolitynae, Eusyllinae y Exogoninae (Syllidae: Polychaeta) con comentarios sobre la ecología y biogeografía de la familia Syllidae del Parque Nacional de Coiba, Panamá.—Revista de Biología Tropical 49:621–628.

Cunningham, J. T. & Ramage, G. A. 1888. The Polychaeta sedentaria of the Firth of Forth.—Transactions Royal Society of Edinburg 33:635–684.

Eliason, A. 1962. Undersökningar över Öresund. XXXXI. Weitere Untersuchungen über die Polychaetenfauna des Öresunds.—Lunds Universitets Arsskrift, N. F. Avd. 2, 58:1–98.

Fauchald, K. 1977. Polychaetes from intertidal areas in Panama, with a review of previous shallow-waters records.—Smithsonian Contributions to Zoology 221:1–81.

———, & A. A. Reimer. 1975. Clave de poliquetos panameños con la inclusión de una clave para todas las familias del mundo.—Boletín del Instituto Oceanográfico Universidad Oriente 14: 71–94.

Fiege, D., F. Licher, & A. S. Y. Mackie. 2000. A partial review of the European Magelonidae (Annelida: Polychaeta): *Magelona mirabilis* redefined and *M. johnstoni* sp. nov. distinguished.—Journal of the Marine Biology Association of the United Kingdom 80:215–234.

Hartman, O. 1944a. Polychaetous annelids from California, including the description of two new genera and nine new species.—Allan Hancock Pacific Expeditions 10:239–307.

———. 1944b. Polychaetous annelids, 6. Paraonidae, Magelonidae, Longosomidae, Ctenodrilidae and Sabellariidae.—Allan Hancock Pacific Expeditions 10:311–389.

———. 1961. Polychaetous annelids from California.—Allan Hancock Pacific Expeditions 25:1–226.

———. 1969. Atlas of the Sedentariate Polychaetous Annelids from California. Allan Hancock Foundation, University of Southern California, Los Angeles, 494 pp.

Hernández-Alcántara, P., & V. Solís-Weiss. 2000. Magelonidae from the Mexican Pacific and Northern Gulf of Mexico, with the description of a new genus (*Meredithia*) and four new species.—Bulletin of Marine Science 67:625–644.

Jones, M. L. 1963. Four New Species of *Magelona* (Annelida, Polychaeta) and a Redescription of *Magelona longicornis*.—American Museum Novitates 2164:1–31.

———. 1977. A Redescription of *Magelona papillicornis* F. Müller. Pp. 247–266 *in* D. J. Reish, & K. Fauchald, eds., Essays on Polychaetous Annelids in memory of Dr. Olga Hartman. Allan Hancock Press, Los Angeles, 604 pp.

———. 1978. Three new species of *Magelona* (Annelida, Polychaeta) and a redescription of *Magelona pitelkai* Hartman.—Proceedings of the Biological Society of Washington 91:336–363.

López, E., G. San Martín, P. Cladera, & M. Capa. 1997. La fauna de anélidos poliquetos del Parque Nacional de Coiba (Panamá) Pp. 57–73 *in* S. Castroviejo, ed., Flora y Fauna del Parque Nacional de Coiba (Panamá), 534 pp.

———, P. Cladera, G. San Martín, A. Laborda, & M. T. Aguado. 2002. Polychaete assemblages inhabiting intertidal soft bottons associates to mangrove systems from Coiba National Park (East Pacific, Panama).—Wetlands Ecology and Management 10:233–242.

Monro, C. C. A. 1933. The Polychaeta Errantia collected by Dr. C. Crossland at Colón in the Panama region and the Galapagos Islands during the expedition of the "St. George".—Proceedings of Zoological Society of London 1–96.

Müller, F. 1858. Einiges über die Anneliden Fauna der Insel St. Catharina an der Brazilianischen Küste.—Archiv für Naturgeschichte Berlin 24:211–220.

Rouse, G. W. 2001. *Magelona* Müller, 1858. Pp. 261–263 *in* G. Rouse, & F. Pleijel, eds., Polychaetes. Oxford University Press, New York, 354 pp.

San Martín, G., E. López, M. S. Redondo, M. Capa, P. Cladera, & A. J. Laborda. 1997. El bentos marino del Parque Nacional de Coiba (Panamá). Pp. 45–67 *in* S. Castroviejo, ed., Flora y Fauna del Parque Nacional de Coiba (Panamá), 534 pp.

Uebelacker, J. M., & M. L. Jones. 1984. Family Magelonidae Cunningham and Ramage, 1888. Pp. 7.1–7.29 *in* J. M. Uebelacker, & P. G. Johnson, eds., Taxonomic Guide to the Polychaetes of the Northern Gulf of Mexico, vol. 2. Barry A. Vittor & Associates, Inc., Mobile, Alabama.

Wilson, R. S. 2000. Family Magelonidae Pp. 194–195 *in* P. L. Beesley, G. J. B. Ross, & C. J. Glasby, eds., Polychaetes & allies. The southern synthesis. Fauna of Australia, vol. 4. Polychaeta, Myzostomida, Pogonophora, Echiura, Sipuncula. CSIRO Publishing, Melbourne, 465 pp.

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Allonais inaequalis (Annelida: Oligochaeta: Tubificidae) in North America

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Abstract.—The oligochaete *Allonais inaequalis* (Stephenson, 1911), previously thought to be unknown in North America, was found in the effluent of a sewage treatment plant in New Jersey and recently in the Greater Miami River in Ohio. It is redescribed from this material and compared to the other two species, *A. paraguayensis* (Michaelsen, 1905) and *A. pectinata* (Stephenson, 1910) reported from North America. Identifications of specimens collected from North America, previously thought to be *A. paraguayensis,* were determined to be incorrect; thus, this species is not yet known to occur in North America. *Nais magnaseta* Harman, 1973, which closely resembles *A. pectinata,* also is discussed.

The naidid oligochaete[1] *Allonais inaequalis* (Stephenson, 1911) was first described as *Nais pectinata* var. *inaequalis* Stephenson, 1911. Sperber (1948) erected the genus *Allonais,* using *A. inaequalis* as the generic type. She distinguished *Allonais* from *Nais* by the absence of eyes, by the anterior and posterior ventral chaetae being of similar size and shape, by no discernable stomachal dilatation, by a vascular plexus in the anterior segments, by no prostate gland cells, and by no formation of budding zones. She also indicated that *Allonais,* unlike *Nais,* was confined to the tropics. She included five species (all formerly found in *Nais*) in this new genus, including two, *A. pectinata* (Stephenson, 1910) and *A. paraguayensis,* (Michaelsen, 1905), subsequently reported from North America (Brinkhurst & Jamieson 1971, Brinkhurst 1986). Brinkhurst (1986) included *A. inaequalis* in his North American key, suggesting that it probably occurred in North America due to its worldwide distribution and because drawings of the chaetae of *A. paraguayensis* closely resembled the chaetae of *A. inaequalis* (e.g., Hiltunen & Klemm 1980). New material collected and identified by the authors, or sent to the authors for identification or verification, encouraged us to reassess the status of this genus in North America.

Materials and Methods

Oligochaetes were observed swimming in the effluent of the Linden-Roselle Sewage Authority wastewater treatment plant in New Jersey, U.S.A., in October 1999. The facility is a typical tertiary treatment plant,

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[1] Based on sequences of 18S rDNA and other molecular and morphological data, Erséus et al. (2002) concluded that the family Naididae is polyphyletic and that the species of naidids are more correctly placed within a subfamily of the Tubificidae. Therefore, Naididae has become a junior synonym of the family Tubificidae. As the name Naididae is older than Tubificidae, the authors are requesting that Tubificidae take precedence because of the large number of species in the family compared to those within the naidids and await a ruling by the International Commission on Zoological Nomenclature (C. Erséus, pers. comm.; Erséus & Gustavsson 2002).

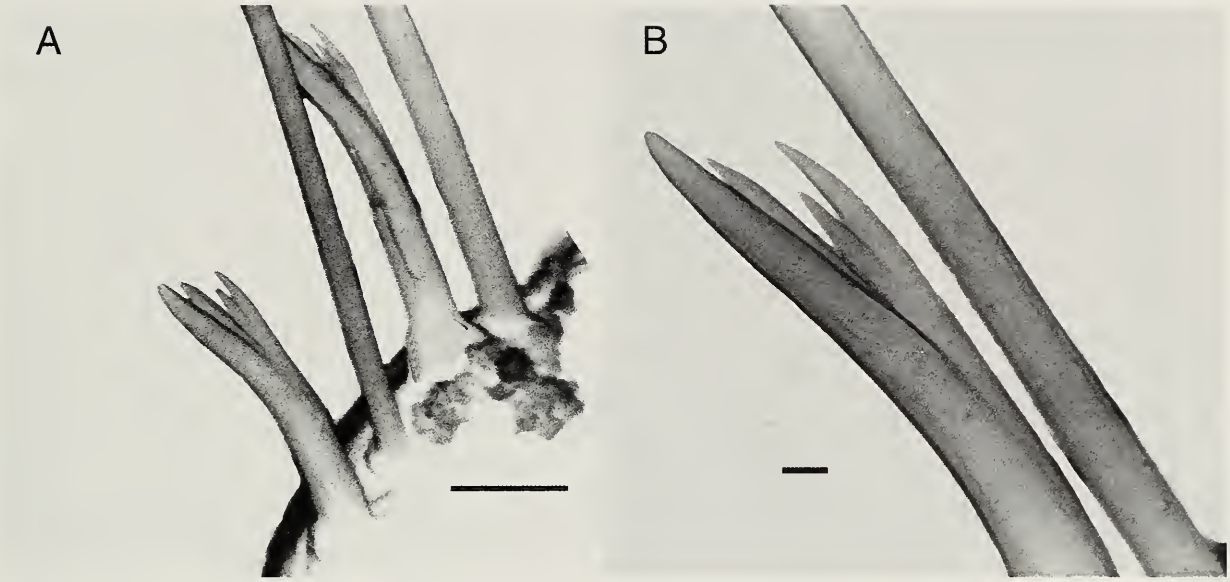

Fig. 1. *Allonais inaequalis* (SEM). A, dorsal chaetal bundle; B, same as A, enlarged. Scale bars: A = 5 μm, B = 1 μm.

treating approximately 80% residential and 20% municipal waste. Specimens were collected using a small bucket in the uptake valve in the aeration ponds immediately prior to chlorination. Half of the worms were fixed in 10% formalin; the remainder were fixed in 70% ethanol. One oligochaete specimen collected in July 2001 from the Greater Miami River, Ohio, U.S.A., tentatively identified as *A. paraguayensis,* was sent to the senior author for verification.

The description of *A. inaequalis* below is based on 10 specimens from the New Jersey material, preserved in ethanol, and mounted on slides using CMCP mounting medium for observations using light microscopy. Measurements were made using a calibrated ocular scale on a Leitz Laborlux-12 compound microscope, and drawings were made using a camera lucida drawing tube with the same microscope. Oligochaetes fixed in formalin from New Jersey material were prepared for scanning electron microscopy (SEM). Specimens were mounted on aluminum stubs by placing one to two specimens in a drop of water on each stub that had been prepared with transparent double-coated sticky tape (No. 666, 3M Corp.). Stubs were immersed in liquid nitrogen to instantly freeze the specimens, then placed in an Edwards-Pearse Model EPD3 tissue dryer (temperature −64°C; vacuum 0.0002 torr) for subsequent sublimation of liquid associated with the specimens. After sublimation was complete (4–6 hr), stubs were placed in an SPI Module Sputter Coater, where a thin (10–30 nm) film of gold-palladium was evaporated onto the specimens. After sputter-coating, specimens were examined using an Amray 1830 scanning electron microscope and photographed on positive-negative film and paper.

Allonais inaequalis (Stephenson, 1911)
Figs. 1, 2

Material examined.—Allonais paraguayensis: Louisiana, 1963, and Florida, 1975, W. J. Harman collection from the National Museum of Natural History-Smithsonian Institution (USNM), Washington, D.C.; Nevis, Lesser Antilles, 1997, Illinois Natural History Survey (INHS) Annelida Collection, Champaign, identified by the authors; Sudan, Africa, 1975 and 1984, R. Grimm collection, Zoologisches Institüt und Zoologisches Museum (ZMUH), Hamburg. *Allonais inaequalis*: Puerto Rico, 1994, INHS Annelida Collection, identified by the authors. *Allonais pectinata*: South Africa, 1968, Louisiana, 1974, 1975, Georgia,

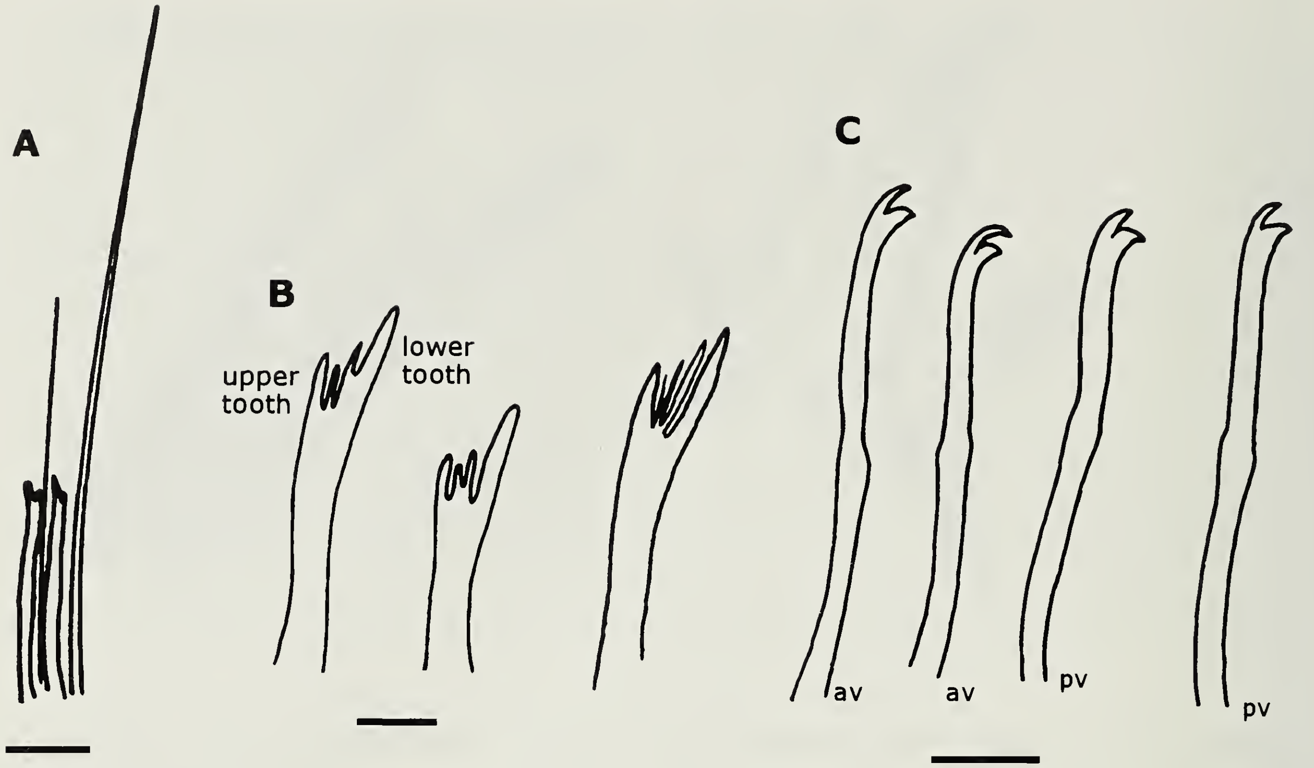

Fig. 2. Chaetae of *Allonais inaequalis*. A, dorsals; B, needles; C, ventrals. av, anterior ventral; pv, posterior ventral. Scale bars: A = 40 μm, B = 6.25 μm, C = 16 μm.

1967, and Florida, 1978, W. J. Harman collection from USNM. *Nais magnaseta* (holotype): Texas, 1973, USNM (45510).

Some specimens of *Allonais inaequalis* from New Jersey were deposited in the Annelida collection of Aquatic Resources Center, Thompsons Station, Tennessee, and the remainder were placed in the INHS Annelida Collection. The one specimen from Ohio was deposited in the collection at SoBran, Inc., Cincinnati, Ohio.

Redescription.—Body 3–9 mm long, consisting of 37–85 segments, no pigmentation. Prostomium rounded, without proboscis. No eyes. Dorsal chaetae begin in segment VI: 1–2 smooth hairs per bundle; if 2 hairs, then generally one longer (212–288 μm) and one shorter (75–160 μm); 1–2 needles per bundle, each usually with 2 intermediate teeth (but some with 1, 3, or 4), intermediate tooth next to upper is shortest of all teeth and intermediate tooth next to lower is second longest; needle length 64–96 μm, lower tooth (8–14 μm) almost twice as long as upper (5–8 μm). Ventral chaetae usually 5–7 per bundle (but as few as 3 or as many as 9) in II–V, 55–75 μm long and 1–3 μm wide, nodulus slightly proximal, upper tooth slightly longer and thinner than the lower; from VI posteriorad usually 5–7 per bundle (but ranging from 3–9), 60–93 μm long and 1.5–3 μm wide (Puerto Rico specimens up to 5 μm wide), nodulus median to slightly distal, upper tooth thinner and subequal or slightly shorter than the lower; number of ventral chaetae decreases to 2 per bundle near the tail. No mature individuals were collected.

Discussion

It can be difficult to distinguish *Allonais inaequalis* from *A. paraguayensis* based on external morphological characters. Although Sperber (1948) stated that the sexual organs of these two species of *Allonais* are similar, there appear to be several characters that can be used to identify them as being different, as shown in Tables 1 and 2. The most obvious character is the number of intermediate teeth found in the needle chaetae. While the needle chaetae of *A. inae-*

Table 1.—Descriptions of the North American species of *Allonais* Sperber (1948) and Brinkhurst & Jamieson (1971) and of *Nais magnaseta* by Harman (1973). All measurements in μm unless otherwise indicated.

Character	*Allonais paraguayensis*	*Allonais inaequalis*	*Allonais pectinata*	*Nais magnaseta*
Anterior ventral chaetae:				
no./bundle	2–8[a]; 2–6[b]	4–8[a]; 4–6[b]	3–5	3–4
length	55–123	60–105	56–65	54
width		1.5	2	<2
teeth (upper vs. lower)	longer	longer	longer	slightly longer
Posterior ventral chaetae:				
no./bundle	2–8[a]; 2–6[b]	4–8[a]; 4–6[b]	2–7	2–5
length	55–123	60–105	51–58	57-67
width		1.5	2	3
teeth (upper vs. lower)	equal	equal	equal	thinner; slightly shorter
Dorsal chaetae:				
no. of hairs/bundle	1–2	1–2	1–2	1–2
length of hairs	200–500	100–332	70–220	114–180
no. of needles/bundle	1–2	1–2	1–2	1–2
length of needles	60–192	67–112	42–68	50–60
length, outer needle teeth			3.5	5–6
no. of intermediate teeth	1–2	1–4	1–5	1–3
Total length of worm, mm	4–60	8–18	1.5–8	2
No. of segments	15–200	40–95	15–65	31+
No. of penial chaetae	3–11	4–6	3–5	immature
No. of specimens				1

[a] Brinkhurst & Jamieson (1971); [b] Sperber (1948).

qualis generally have two intermediate teeth (range 1–4; Figs. 1A, B, 2B), none of the specimens of *A. paraguayensis* examined had needle chaetae with intermediate teeth (Fig. 3). Sperber (1948) stated, however, that the upper tooth of *A. paraguayensis* can be bifid in some specimens. The posterior ventral chaetae generally are shorter and thinner in *A. inaequalis* (Fig. 2C) compared with those of *A. paraguayensis*; the upper teeth are always distinctly shorter than the lower teeth in *A. paraguayensis,* whereas in *A. inaequalis* the upper and lower teeth are generally subequal. The hair and needle chaetae are almost always shorter in *A. inaequalis* compared with *A. paraguayensis.* The needle chaetae of *A. pectinata* are distinct from those of its congeners, having both the upper and lower teeth subequal in length, and the intermediates recessed between the two.

Although most of the individuals examined from the USNM were in very poor condition, all of the specimens examined appear to be *A. inaequalis,* not *A. paraguayensis,* so it is very likely that the remaining specimens also are *A. inaequalis.* This means that *A. inaequalis* had already been found in North America (as early as 1963), but previously had been misidentified, and that *A. paraguayensis* has not yet been found in North America. Thus *A. inaequalis* can now be recorded from Florida, Louisiana, New Jersey, and Ohio, which suggests that it may be widespread but uncommon, at least in the eastern USA.

The specimens of *A. inaequalis* from North America fit the original description of Stephenson (1911) very well. All of his measurements fall within the ranges of ours, and he also noted the differences in length when two hair chaetae were present

Table 2.—Comparison of *Allonais paraguayensis* and *A. inaequalis* from specimens examined during this study. All measurements in μm unless otherwise indicated. If 2 hair chaetae present, then 1 is long and 1 is short. This agrees with the description of Stephenson (1911, 1920). First set of numbers for length of hairs reflects short hair; second set reflects long hair.

	Allonais paraguayensis		*Allonais inaequalis*			
Character	Sudan	Nevis	Florida, Louisiana[a]	New Jersey	Ohio	Puerto Rico
Anterior ventral chaetae:						
no./bundle	2 (3)	3–4 (5)	3–5	3–6	4	4–5
length	56–96	78–105	65–72	55–75	56–64	74–100
width	2–3	1.5–3 (4)	1–1.5	2–2.5	2–2.5	2–3
teeth (upper vs. lower)	thinner; subequal	thinner; subequal	thinner; slightly longer	thinner; slightly longer	thinner; slightly longer or subequal	thinner; slightly longer
Posteior ventral chaetae:						
no./bundle	(3) 5–6	4–6 (7)	3–5 (7)	5–9	5–7	(3) 4–6
length	80–118	88–105	64–75	60–70	64–72	75–93
width	3–4	3–5 (6)	1.5–3	2–3	3	3–5
teeth (upper vs. lower)	thinner; shorter	thinner; shorter	thinner; subequal or slightly shorter	thinner; subequal or slightly shorter	thinner; subequal or slightly shorter	thinner; subequal or slightly shorter
Dorsal chaetae:						
no. of hairs/bundle	1–2	1–2	1–2	1–2	1–2	1 (2)
length of hairs	110–198/225–353	150–200/205–325	95–125/212–250	88–160/213–275	75–112/238–262	75–80/224–288
no. of needles/bundle	1–2	1 (2)	1–2	1–2	1–2	1–2
length of needles	80–125	112–131	64–80	64–86	75–83	75–96
no. of intermediate teeth	0	0	(1) 2–3	(1) 2 (3)	2 (3)	(1) 2–3 (4)
Total length of worm, mm	ca. 3–4	ca. 5–8.5	ca. 2.6–4.5	ca. 3–9	posterior end missing	ca. 3–6
No. of segments	35–90	60–118	42–61	37–85	posterior end missing	42–60
No. of specimens	6	4	4	6	1	5

[a] Originally identified as *Allonais paraguayensis*.

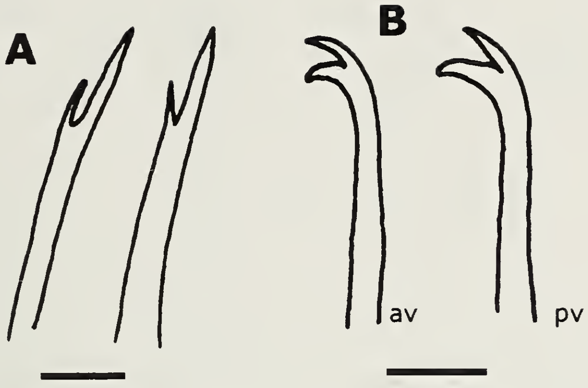

Fig. 3. Chaetae of *Allonais paraguayensis*. A, needles; B, ventrals. Abbreviations as in Fig. 2. Scale bars = 6.25 μm.

("one of the hair-setae is much shorter than the other"; Fig. 2A). Sperber (1948), in erecting the genus *Allonais* and describing the species she ascribed to it, made no mention of the differences in length of the hair chaetae, so we do not know if it applies to all *Allonais* species or only to those that we examined. She stated, however, that she felt that *A. pectinata* belonged in a different, but new, genus.

Allonais pectinata, the third species in this genus reported to occur in North America, is reported to be widespread in the eastern USA (Illinois, Ohio, New York, Pennsylvania, and Georgia) and Ontario, Canada (Hiltunen & Klemm 1980, Brinkhurst 1986), yet neither of the present authors has ever seen a specimen in our many collections, and neither Klemm nor Brinkhurst (pers. comm.) was able to provide any specimens to corroborate its published distribution. Because of the difficulty in distinguishing *A. pectinata* and *Nais magnaseta* Harman, 1973 from one another using the descriptions provided in the literature (Table 1), specimens of each species were obtained from the USNM for study.

Examination of the specimens from the USNM caused additional confusion. Two specimens from Lake Louisa at Clermont, Florida, previously identified as *A. pectinata*, were in fact *N. magnaseta* (see Table 3; Fig. 5), making this a new state record for the latter species, since it had previously only been reported from Bee County, Texas (Harman 1973). Another specimen from the USNM, collected from west of the Peach County line in Georgia and initially identified as *A. pectinata*, is actually *Nais variabilis* Piguet, 1906 with pectinate dorsal needle chaetae. The possible confusion of some specimens of *N. variabilis* (those with pectinate needle chaetae), and subsequent misidentification of them as *A. pectinata*, was noted previously by Brinkhurst (1986). The distinct difference in size and shape of the ventral chaetae in II–V compared with the rest of the ventrals in *N. variabilis* should easily separate those with pectinate needles from specimens of *A. pectinata*. Five specimens from Louisiana and three specimens from South Africa were examined and appear to be *A. pectinata*, although there are some differences between the two sets (see Fig. 4).

It is now clear that *A. pectinata* and *N.*

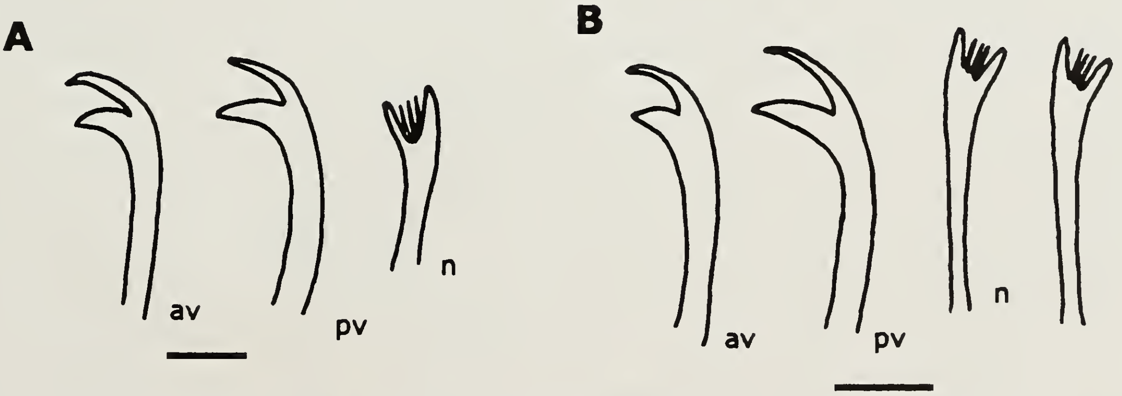

Fig. 4. Chaetae of *Allonais pectinata*. A, Louisiana specimen; B, South African specimen. av, pv as in Fig. 2; n, needle. Scale bars = 6.25 μm.

Table 3.—Comparison of *Allonais pectinata* and *Nais magnaseta* specimens examined during this study. All measurements in µm unless otherwise indicated.

	Allonais pectinata		*Nais magnaseta*	
Character	Louisiana	South Africa	Texas	Florida[a]
Anterior ventral chaetae:				
no./bundle	(3) 4–5	2–4	3–4	3–4
length	35–62	48–64	48–56	45–48
width	1–1.25	1–1.5	1.25–1.5	1.25
teeth (upper vs. lower)	slightly thinner; slightly longer	slightly thinner; equal or slightly longer	slightly thinner; equal or slightly longer	thinner; equal
Posterior ventral chaetae:				
no./bundle	4–6	3–5	(2) 3–5	3–5
length	48–64	54–83	53–64	48–56
width	1.5–1.8	1.6–3	1.9–2.1	1.5–1.7
teeth (upper vs. lower)	thinner; equal or slightly shorter	thinner; equal or slightly shorter	thinner; slightly shorter	thinner; shorter
Dorsal chaetae:				
no. of hairs	1 (2)	1 (2)[b]	1	1
length of hairs	93–112/128–176	112/168–256	128–160[c]	192–216
no. of needles/bundle	1–2	1–2	1	1–2
length of needles	35–53	45–70	48–56	45–53
no. of intermediate teeth	(2) 3	(2) 3	2–3 (?)[c]	2–4
length, outer needle teeth	3–4.3	3–4.5	5–6.3	4–6.4
No. of penial chaetae	4	immature	immature	immature
Total length of worm, mm	1.4–2.1	1.7–2.3	1.5	1.5
No. of segments	21+ to 36+	23+ to 37+	31+	36+
No. of specimens	5	3	1	1[d]

[a] Originally idenified as *Allonais pectinata*; [b] if 2 hair chaetae present, then 1 is long and 1 is short; first set of numbers for length of hairs reflects short hair, second set reflects long hair; [c] very difficult to determine the actual number or measure length; [d] there were 2 specimens in this collection, but the second was partially obscured by the ringing material and therefore a definite identification could not be made.

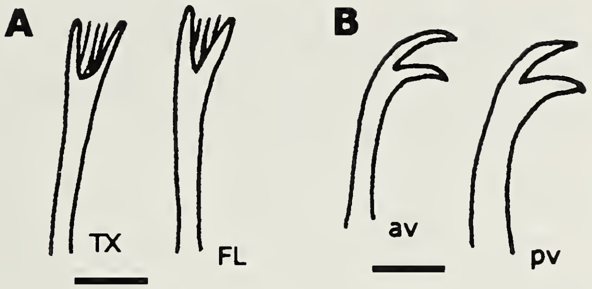

Fig. 5. Chaetae of *Nais magnaseta*. A, needles from Texas (TX) and Florida (FL) specimens; B, anterior ventral (av) and posterior ventral (pv), from Texas specimen. Scale bars = 6.25 μm.

magnaseta are recognized as two distinct species (Table 3; Figs. 4, 5). The main differences between the two species are the length of the needle chaetae teeth, with those of *N. magnaseta* almost twice as long as those of *A. pectinata,* and the distinct difference in the length and width of the anterior ventral chaetae compared to the posterior ventral chaetae in *N. magnaseta,* while there is only a slight difference between the anterior and posterior ventral chaetae in *A. pectinata.*

Apparently most of the confusion associated with the identification of *A. inaequalis* and *A. paraguayensis* results from the original misidentification of the specimens from Louisiana and Florida. Although identified as *A. paraguayensis,* these obviously are *A. inaequalis* (Table 2). Brinkhurst (1986), followed by Kathman & Brinkhurst (1998), hinted at this possibility when they stated that the needle chaetae of *A. paraguayensis* from Louisiana seemed to resemble the needle chaetae of *A. inaequalis.* Hiltunen & Klemm (1980), assuming the identifications of *A. paraguayensis* to be correct, illustrated the needle chaetae of *A. inaequalis* but listed the species as *A. paraguayensis.* Adding to the confusion, the drawings of the needle chaetae of *A. inaequalis* by Sperber (1948) do not agree with the original drawing of Stephenson (1911) but resemble those of *A. pectinata.* Sperber referred to this as a form of *A. inaequalis,* but it is unclear if it really belongs with *A. inaequalis.* Kathman & Brinkhurst (1998) added Florida, Illinois, and Colorado to the distribution list for *A. paraguayensis.* Examination of the Florida worms indicated that they were *A. inaequalis,* while those from Illinois and Colorado do not belong in *Allonais.* Brinkhurst (1986) and Brinkhurst & Marchese (1989) suggested that *A. inaequalis* had been synonymized with *A. paraguayensis* and *A. pectinata* but gave no references. In contradiction, Harman et al. (1988) stated that *A. inaequalis* clearly is distinct from *A. paraguayensis.* We do not know of any publications that have discussed possible synonymies of these two species, and Brinkhurst (pers. comm.) was unable to provide information about these comments.

Summary

Allonais inaequalis is herein reported for the first time in North America, although we believe that this species was found as early as 1963 but erroneously identified as *A. paraguayensis.* Its current distribution includes New Jersey, Ohio, Florida, and Louisiana. This means that *A. paraguayensis* has not yet been reported from North America. Although previously reported as fairly widespread, *A. pectinata* could only be confirmed as found in Louisiana. *Nais magnaseta,* known previously only from Bee County, Texas, has been identified from Florida.

Based on external morphological characters, it appears that the three *Allonais* species previously reported from North America can be easily differentiated, although *A. inaequalis* and *A. paraguayensis* seem to be more closely related to one another than to *A. pectinata,* as suggested by Sperber (1948). We know of no current phylogenetic analysis using either morphological characters or gene sequencing for this genus that would provide a more definitive approach to recognizing the species.

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Literature Cited

Brinkhurst, R. O. 1986. Guide to the freshwater aquatic microdrile oligochaetes of North America.—Canadian Special Publication of Fisheries and Aquatic Sciences 84, 259 pp.

———, & B. G. M. Jamieson. 1971. Aquatic Oligochaeta of the world. University of Toronto Press, Toronto, Ontario, Canada, 860 pp.

———, & M. R. Marchese. 1989. Guide to the freshwater aquatic Oligochaeta of South and Central America.—Colección CLIMAX 6:1–179.

Erséus, C., & L. Gustavsson. 2002. A proposal to regard the former family Naididae as a subfamily within Tubificidae (Annelida, Clitellata).—Hydrobiologia 485:253–256.

———, M. Källersjö, M. Ekman, & R. Hovmöller. 2002. 18S rDNA phylogeny of the Tubificidae (Clitellata) and its constituent taxa: dismissal of the Naididae.—Molecular Phylogenetics and Evolution 22:414–422.

Harman, W. J. 1973. New species of Oligochaeta (Naididae) with additional distributional records from Oklahoma and Texas.—Southwestern Naturalist 18:151–164.

———, R. O. Brinkhurst, & M. Marchese. 1988. A contribution to the taxonomy of the aquatic Oligochaeta (Naididae) of South America.—Canadian Journal of Zoology 66:2233–2242.

Hiltunen, J. K., & D. J. Klemm. 1980. A guide to the Naididae (Annelida: Clitellata: Oligochaeta) of North America.—U.S. Environmental Protection Agency, Cincinnati, Ohio, EPA-600/4-80-031, 48 pp.

Kathman, R. D., & R. O. Brinkhurst. 1998. Guide to the freshwater oligochaetes of North America. Aquatic Resources Center, College Grove, Tennessee, 264 pp.

Michaelsen, W. 1905. Zur Kenntnis der Naididen.—Zoologica 44:350–361.

Piguet, É. 1906. Observations sur les Naididées et revision systématique de quelques espèces de cette famille.—Revue Suisse de Zoologie 14:185–315.

Sperber, C. 1948. A taxonomical study of the Naididae.—Zoologiska Bidrag från Uppsala 28:1–296.

Stephenson, J. 1910. On some aquatic oligochaete worms commensal in *Sporgilla carteri.*—Records of the Indian Museum V:233–240.

———, 1911. On some aquatic Oligochaeta in the collection of the Indian Museum.—Records of the Indian Museum 6:203–214.

———, 1920. On a collection of Oligochaeta from the lesser known parts of India and from eastern Persia.—Memoirs of the Indian Museum 7:191–261.

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A systematic review of *Planaltina* (Teleostei: Characiformes: Characidae: Glandulocaudinae: Diapomini) with a description of two new species from the upper rio Paraná, Brazil*

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Abstract.—Two new species, *Planaltina glandipedis* and *Planaltina britskii,* glandulocaudine fishes of the family Characidae, tribe Diapomini, are described herein. They were collected from tributaries of the rio Grande and or the rio Tietê, both tributaries of the upper rio Paraná in the State of São Paulo, Brazil. The previously described species, *Planaltina myersi,* until now known almost exclusively from the holotype, is here redescribed from 47 specimens taken from tributaries of the rio Corumbá, a tributary of the upper rio Paraná. The two new species differ most prominently from the previously known species by possession of three somewhat elongate scales along the dorsal border of the male's caudal pouch opening. There is only one elongate scale in *P. myersi. Planaltina glandipedis* differs from *P. britskii* in having six or seven horizontal scale rows between the dorsal-fin origin and the lateral line versus five in the later species. The possible phylogenetic relationships among the three inseminating species within the tribe Diapomini, subfamily Glandulocaudinae, are discussed along with the putative phylogenetic relationships of the Diapomini to the newly recognized glandulocaudine outgroup containing the characid genera *Knodus* and a new genus related to *Attonitus.* Brief comments are presented concerning the geographical distribution and ecology of the species of *Planaltina.*

Resumo.—Duas novas espécies, *Planaltina glandipedis* e *Planaltina britskii,* peixes glandulocaudineos da família Characidae, tribo Diapomini, são aqui descritas. Elas foram coletadas em afluentes do rio Grande e/ou do rio Tietê, ambos tributários do rio Paraná no Estado de São Paulo, Brasil. A espécie apenas descrita, *Planaltina myersi,* conhecida até o presente apenas a partir do holótipo, é aqui redescrita com base em 47 exemplares originários do rio Corumbá, também tributário do rio Paraná. As duas espécies novas diferem marcadamente da espécie previamente conhecida pela presença de três escamas algo alongadas ao longo da margem dorsal da abertura da bolsa glandular dos machos. Há apenas uma escama alongada em *P. myersi. Planaltina glandipedis* difere de *P. britskii* pela presença de seis ou sete séries horizontais de escamas entre a

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origem da nadadeira dorsal e a linha lateral ao invés de cinco na última espécie. As possíveis relações filogenéticas entre as três espécies, todas inseminadoras dentro da tribo Diapomini, subfamília Glandulocaudinae, são discutidas juntamente com as relações filogenéticas tentativas de Diapomini com o grupo externo recentemente reconhecido de Glandulocaudinae constituído pelos gêneros *Knodus, Attonitus* e um novo gênero relacionado a *Attonitus* da família Characidae. Breves comentários são feitos sobre a distribuição geográfica e ecologia das espécies de *Planaltina.*

Relatively little is known about *Planaltina* Böhlke (1954:265) except from its original description based on *Planaltina myersi* described from a single damaged specimen collected through the use of dynamite. This specimen, the holotype, was collected from "Sarandi brook, Planaltina, Goyaz, Brazil," 21 September 1923 by Dr. Carl Ternetz. Böhlke (1954:265–267) was uncertain of the relationships of *Planaltina,* but considered it to possibly be among the " 'borderline' genera (between the Tetragonopterinae and Glandulocaudinae of Eigenmann) . . ." Böhlke referred to these genera as *Landonia, Argopleura, Acrobrycon,* and *Phenacobrycon.* Böhlke (1954) doubted the monophyly of the Glandulocaudinae and considered that these genera and the divergent members of the Glandulocaudinae may have arisen "at different times from different members of such generalized tetragonopterines as *Bryconamericus.*" No additional specimens were examined until Weitzman & Fink (1985:106) listed additional specimens with locality data. Weitzman et al. in Weitzman & Fink (1985:113) published a critique of the concept of the monophyly of the Glandulocaudinae and concluded that there was insufficient evidence to confirm or reject the monophyly of the subfamily. Burns et al. (1995:135–143) provided information that *P. myersi* is an inseminating species with aquasperm. Weitzman & Menezes (1998: 184) assigned this species to the Diapomini, which also included species of the characid genera *Acrobrycon* Eigenmann and *Diapoma* Cope, and, based on additional gross anatomical, histological, and sperm ultrastructural evidence, concluded that the Glandulocaudinae are probably monophyletic. Weitzman & Menezes (1998) also illustrated the osteology of the caudal region and associated caudal organ of *P. myersi.*

We provide a new definition of *Planaltina,* redescribe *P. myersi* based on 47 specimens and discuss its putative relationships with the two new species described herein. We also briefly discuss the possible phylogenetic relationships of the Diapomini to the Glandulocaudinae and to some of the characid species currently in the genera *Attonitus* Vari & Ortega, *Knodus* Eigenmann and a species of a new genus Weitzman et al. (2004). Species of *Attonitus,* the new genus and *Knodus* lack caudal organs as described for adult glandulocaudine males, but some species of *Knodus* and the three species of *Attonitus,* and the species of the new genus were recently found to be inseminating, Weitzman et al. (2004), and at least some of these have one or more of the synapomorphies of the primary and/or secondary sexual systems of glandulocaudines that were used by Weitzman & Menezes (1998) to diagnose that subfamily. Furthermore, sexually active males of one of the new species described here, *P. glandipedis,* has numerous club cells at or near the surface of the skin of the pelvic fins and the anterior part of the anal fin whereas the species of *Attonitus* and the new genus possibly related to *Attonitus* are found to have club cells at or near the surface of the skin in the anterior part of the anal fin. These cells have been shown to secrete in a holocrine manner in the species of the new genus. See Weitzman et al. (2004) for a more detailed discussion of the taxonomic distribution of these apparent glandulocaudine and glandulocaudine outgroup synapomorphies. Those authors also discuss the possible phylogenetic relationships of species of the glandulocaudine tribes with the outgroup characid species currently in *Knodus,* the new genus, and *Attonitus* as well as their apparent relatives not belonging to the Glandulocaudinae. The putative monophyletic relationships among the glandulocaudine tribes recognized by Weitzman & Menezes (1998) must again come into question and be reinvestigated in light of the newly recognized outgroup species for the putative glandulocaudine genera and tribes.

Methods and Materials

Counts and measurements and methods of taking and presenting data follow Menezes & Weitzman (1990:382–383) unless otherwise stated. For the most part, statistical comparisons were calculated using SigmaStat 2.0 for Windows 95. Meristic and morphometric data of males and females were treated separately in order to probe possible differences between the sexes, but secondary sexual differences were detected only in morphometric data. Morphometric data were transformed into ratios of standard length, or head length when they were subunits of that length, and are presented separately for males and females in the tables and regression graphs.

Although we summarize the statistical procedures used herein, see Weitzman & Malabarba (1999:2–4) and Weitzman & Palmer (1997:213–214) for more complete comments about their use. In making pairwise statistical comparisons of counts, all population samples except those few with non-variable counts were found to be at least somewhat skewed about the mean. In running simple *t*-tests, all paired samples failed to pass the normality test and some failed to pass an equal variance test. Thus all pairwise comparisons of counts were made using Mann-Whitney rank sum tests, but also in all cases the results of simple *t*-tests were compared and although not testing the same statistical parameters, both were used to evaluate differences among the species. In most cases both kinds of tests were found to indicate the same overall statistical results regarding a statistical test of null hypotheses of character similarities. However, in a few cases the *t*-test and the Mann-Whitney rank sum test provided opposing results. In these cases the statistical results were of marginal significance for both kinds of tests, and we opted to disregard the resulting hypotheses of differences, especially considering the population sample size limitations.

We utilized Tukey box plots for visual comparison of count distributions of the three species. In these plots the mean is represented by a thick vertical bar, the median by a thin vertical line that is often the same as one of the vertical lateral borders of the boxes. Therefore, the numerical value of the median is given in the legend. The 25th and 75th percentiles are represented by the lateral borders of the boxes and indicate the respective values at which 25% of the samples fall below and 25% fall above the lateral borders of the boxes. Error bars represent the 10th and 90th percentile points, and the circles represent the 5th and 95th percentiles. Extremes, not shown in the plots, are given in the text.

Regarding analyses for differences in sexual dimorphism in body ratios we executed a series of tests and present a few graphs using regression analyses. We used linear regression analysis, even though the statistics derived from it may rarely be a fully accurate representation of the more or less curvilinear mean growth lines expressed by the data. Nevertheless linear regression graphs provide useful comparative visual presentations of the relative morphological parameters of the population samples being compared as well as reasonable population growth patterns. In using the linear regression model for comparing body ratios of population samples, statistical tests of a null hypothesis of character similarities for ratios of body measurements follow Weitzman & Palmer (1997:213–214) and employed linear multiple regression analyses using dummy (indicator) variables. See Glantz & Slinker (1990:69–72) for an explanation. Also, analyses of covariance (ANCOVA) using BIOM-PC, version 2, Exeter Publishing Ltd. were performed. Such tests were done using base 10 log transformed data. However, it was found that in the cases discussed here the results of such tests did not need publication because in those cases used to search for population sample differences, the regression graphs, the mean regression lines, and 95% confidence intervals demonstrated clear statistical differences in ratios of body measurements. Even though statistical tests were done using base 10 log transformed data, neither the regression graphs, their accompanying regression equations, nor the r^2 values presented here are derived from base 10 log transformed data because presentation of non-transformed data in graphs is more visually accessible to the reader. In regression analyses a series of diagnostic tests using SigmaStat Version 2.0 were run to determine the suitability of the data for the linear regression model. In all cases the normality tests and the constant variance tests were passed.

For histological analyses, tissues were removed from specimens initially fixed in 10% formalin and subsequently transferred to 70% ethanol. Tissues containing bony elements were first decalcified. Some tissues were then dehydrated in an ethanol series, embedded in paraffin, sectioned at 5–10 μm, and stained with modified Masson's trichrome (Schreibman 1964:219). Other tissues were dehydrated in an ethanol series to 95% ethanol and infiltrated with and embedded in glycol methacrylate. Sections were cut at 2.0–3.5 μm and stained with toluidine blue and periodic acid-Schiff reagent (PAS)/hematoxylin (Quintero-Hunter et al. 1991:170). Measurements of testis areas were taken from mid sagittal sections as described by Burns et al. (1995:132).

For counts recorded in the descriptions, those of the holotype are provided first followed in parentheses by the mean of the population sample, (or median when the data are nonparametric), range, and the total number of specimens counted.

The terminations of the dorsal and anal fins are morphologically different and are treated as follows. The posterior branched ray of the dorsal fin has a single pterygiophore at its base, i.e., the ray is not split to its base and is counted as 1, but when it is rarely split to its base, then its last two rays are counted as 1 because there is only 1 pterygiophore at the base of these rays. In the anal fin the most posterior pterygiophore has its ray almost invariably split to its base and these two rays are counted as one.

The word pouch is used for that sac-like area internal to the modified caudal-fin scale or scales, called pouch scales, of the usually adult, sexually active males of glandulocaudine characids. The pouch opening to the surrounding water occurs along the posteroventral border of the scale or scales. In almost all case in males the pouch opening is provided with modified secretory cells presumably producing a pheromone. In diapomins both sexes have pouch scales. See Weitzman & Fink (1985) and Weitzman & Menezes (1998) for further explanation.

Specimens examined for this research are deposited in the Museu de Zoologia, Universidade de São Paulo (MZUSP); Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ); Laboratório de Ictiologia de Ribeirão Preto, Faculdade de Filosofia Ciências e Letras de Ribeirão Preto, Universidade de São Paulo (LIRP); Departamento de Zoologia, Universidade Estadual Paulista, Campus de São José do Rio Preto, São Paulo (DZSJRP); and the Smithsonian Institution, National Museum of Natural History (USNM). Comparative glandulocaudine and other characid specimens used in this report are listed in Weitzman & Fink (1985: Appendix 1), Weitzman et al. (1994), Burns et al. (1995, 1997), Weitzman & Menezes (1998:176), and Weitzman et al. (2004).

Planaltina Böhlke

Planaltina Böhlke, 1954:265 (type species: *P. myersi* Böhlke, 1954:267 by monotypy and original designation).

Definition.—1) There are fewer scales forming the dorsal border of the caudal pouch in *Planaltina* (1–2) than in *Acrobrycon* (4–7 or 8) and *Diapoma* (3–6). 2) In *Planaltina* one of the scales forming the dorsal border of the pouch opening is elongate and forms most of that border, whereas in *Acrobrycon* and *Diapoma,* even when one of the dorsal border scales of the pouch opening is somewhat elongate or larger, its actual contribution to the length of the dorsal pouch border is little more than that of the other dorsal border scales of the pouch opening. 3) The three species of *Planaltina* produce aquasperm, the nuclei of which vary in shape from spherical to slightly elliptical, whereas both *Acrobrycon* and *Diapoma* have elongate sperm cell nuclei.

Key to the species of *Planaltina*

The characters used in this key, except those in couplet 1a, are not necessarily synapomorphies and the key is not intended to reflect phylogenetic relationships, only information for species identification. The key assumes that at least adult male specimens are available and have a caudal organ consisting of hypertrophied scales enclosing a pouch that is in part open to the surrounding water and that the specimens do not fit the diagnosis of the Cheirodontinae proposed by Malabarba (1998:199–205).

1a. Male and female caudal organs as indicated by caudal squamation nearly equivalent in size and morphological development; three or more scales immediately ventral to lateral-line series extend posteriorly to form dorsal border of pouch opening . . . . Diapomini (2)

1b. Female caudal organs as expressed by caudal squamation never as hypertrophied as that of males; arrangement of scales bordering pouch opening not as above . . . . other Glandulocaudinae

2a. Dorsal border of pouch opening formed by one or two enlarged and elongate dorsal scales; sperm cell nuclei spherical to slightly elliptical (aquasperm) . . . . *Planaltina* (3)

2b. Dorsal border of pouch opening without especially enlarged scales or one somewhat enlarged scale present, but its perimeter entering pouch border not especially large; sperm-cell nucleus somewhat elongate . . . . *Acrobrycon* and *Diapoma*

3a. One much enlarged and elongate scale along dorsal border of pouch opening; adipose fin present . . . . *Planaltina myersi*

3b. Three enlarged and somewhat elongate scales along dorsal border of pouch opening; adipose fin present or absent (4)

4a. Six or seven scale rows between dorsal-fin origin and lateral line; 5 scale rows between anal-fin origin and lateral line; 16–17 scale rows around caudal peduncle (X = 16.2); 17–20 predorsal scales (X = 18.0); adipose fin absent . . . . *Planaltina glandipedis*

4b. Five scale rows between dorsal-fin origin and lateral line; 4 scale rows between anal-fin origin and lateral line; 12–14 scale rows around caudal peduncle (X = 13.1); 14–16 predorsal scales (X = 15.2); adipose fin present . . . . *Planaltina britskii*

Planaltina myersi Böhlke

Figs. 1–3, Table 1

Planaltina myersi Böhlke, 1954:267, original description, Brazil, "Goyaz, Sarandi brook, Planaltina," now in Distrito Federal.—Weitzman & Fink, 1985:106–107, listed specimens from several localities.—Burns et al. (1995:135–143) presented evidence that species is inseminating with aquasperm.—Weitzman &

Fig. 1. *Planaltina myersi,* USNM 221202, adult male above, SL 35.9 mm and adult female, below, SL 32.0 mm; córrego Pipiripau near Planaltina, Distrito Federal, Brazil, about 15°40′S, 47°39′W.

Table 1.—Morphometrics of *Planaltina myersi.* Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Minimum, maximum, *n, X,* and *SD* are based on the holotype, SU 18636 (now at CAS) and the following specimen lots: MNRJ 10634, MNRJ 10635, USNM 363088, USNM 2210202, USNM 236416, USNM 258458, USNM 278966, USNM 278986, USNM 278987, USNM 278989, and MUSP 63588.

	Holo-type	Males				Females			
		n	Range	*X*	*SD*	*n*	Range	*X*	*SD*
Standard length (mm)	36.8	14	22.3–38.0	33.7		33	19.0–43.0	30.7	
Body depth at dorsal fin origin	24.7	14	22.2–26.2	24.0	1.0	33	21.1–28.3	24.9	1.8
Snout to dorsal-fin origin	54.3	14	54.3–61.6	59.2	1.8	33	53.7–61.1	59.1	1.5
Snout to pectoral-fin origin	25.5	14	24.5–26.2	25.3	0.6	33	22.2–28.6	25.0	1.4
Snout to pelvic-fin origin	46.2	14	45.1–47.1	45.8	0.6	33	46.7–50.0	46.4	1.4
Snout to anal-fin origin	58.4	14	57.3–61.0	59.2	1.0	33	57.1–64.9	60.9	2.0
Caudal peduncle depth	10.9	14	09.3–11.1	10.0	0.5	33	0.84–10.6	09.8	0.5
Caudal peduncle length	12.8	14	10.8–14.2	12.7	1.0	33	11.1–17.1	13.1	1.0
Pectoral-fin length	20.9	14	20.1–24.2	22.1	1.0	33	18.8–25.3	21.7	1.2
Pelvic-fin length	14.4	14	12.5–16.1	15.1	1.1	33	12.0–15.6	14.1	0.7
Dorsal-fin base length	10.9	14	08.9–12.5	10.5	0.8	33	0.93–12.9	10.4	0.8
Dorsal-fin height	19.8	14	18.7–21.4	20.2	0.8	33	18.2–21.3	19.8	0.8
Anal-fin base length	29.9	14	27.6–33.3	30.6	1.4	33	26.0–32.0	28.6	1.5
Anal-fin lobe length	17.7	14	16.8–18.8	17.9	0.7	33	16.1–19.6	18.1	1.0
Eye to dorsal-fin origin	46.5	14	44.6–47.9	46.1	1.0	33	41.7–48.6	45.7	1.5
Dorsal-fin origin to caudal-fin base	43.5	14	40.1–43.9	42.2	1.1	33	38.7–47.7	42.2	1.6
Bony head length	23.4	14	22.6–25.4	23.7	0.8	33	20.5–26.4	24.1	1.1
Horizontal eye diameter	35.4	14	35.0–37.7	36.2	0.7	33	33.7–42.6	36.7	1.8
Snout length	22.1	14	18.8–23.7	21.2	1.6	33	17.8–23.4	21.2	1.2
Least interorbital width	31.4	14	31.4–36.1	33.8	1.4	33	31.1–38.3	33.5	1.5
Upper jaw length	43.0	14	40.0–45.9	43.1	1.4	33	40.3–47.7	43.8	1.5

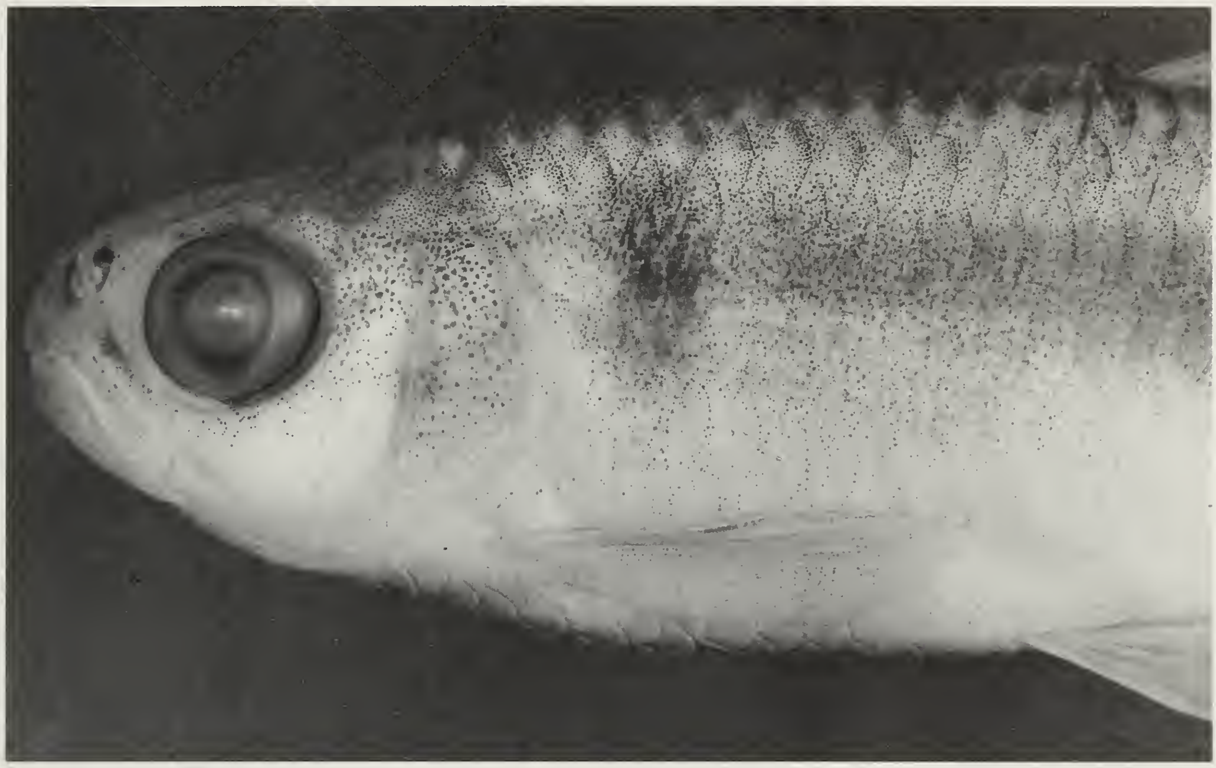

Fig. 2. *Planaltina myersi,* USNM 221202, adult male, SL 35.9 mm; córrego Pipiripau near Planaltina, Distrito Federal, Brazil, about 15°40′S, 47°39′W. Displays pigment pattern of head and anterior part of body.

Menezes (1998:184) discussed relationships and assigned it to Diapomini.

Specimens examined.—All specimens are from Brazil, Distrito Federal, drainage basin of rio Corumbá, tributary of upper rio Paraná.

Holotype.—SU 18636 (now at CAS), 1 male, 36.8 mm SL. Type locality: Brazil: "Goyaz, Sarandi brook, Planaltina" (approximately 15°40′S, 47°45′W). Now in Distrito Federal, see discussion below regarding type locality.

Additional specimens.—Brazil: Distrito Federal. MNRJ 10634, 24 (2 mature males, from 30.5 to 31.5 mm SL; 22 immatures of either sex to mature females, from 22.3 to 36.6 mm SL), córrego Fumal, where crosses road between Brasília and Planaltina, near Planaltina, about 15°20′S, 47°50′W, 11 Apr. 1982, L.E. de Macedo Cordoso. MNRJ 10635, 13 (including 1 c&s male, 33.3 mm SL; 1 c&s female, 36.4 mm SL), córrego Fumal, where it crosses road between Brasília and Planaltina, near Planaltina, about 15°20′S, 47°50′W, 5 Aug. 1981, L. E. de Macedo Cordoso. USNM 363088, 1 (mature male, 46.0 mm SL), rio Pipiripau near Planaltina, about 15°40′S, 47°39′W, 30 Sept. 1977, N. Menezes & party. USNM 221202, 6 (1 mature male, 35.9 mm; 5 mature females, 32.0–43.1 mm SL), rio Pipiripau near Planaltina, about 15°40′S, 47°39′W, 30 Sept. 1977. N. Menezes & party. USNM 236416, 3 (immatures to 1 mature female, 19.0–39.7 mm SL), córrego Vargem de Trás, rio Pipiripau, near Planaltina, about 15°40′S, 47°39′W, 1 Jun. 1979, N. Menezes & E. Bastos. USNM 258458, 1 (mature female, c&s, 41.0 mm SL), rio Pipiripau near Planaltina, about 15°40′S, 47°39′W, 19 Jan. 1976, E.C. Calaf. USNM 278966, 8 (7 mature sexually active males, 35.5–38.3 mm SL; 1 mature female, 37.8 mm SL), córrego Papuda, tributary of rio São Bartolomeu, about 40 km south east of Brasília, 1 Feb. 1985, M. Ribeiro & party. USNM 278985, 1 (mature male, 36.4 mm SL), rio Pipiripau near Planaltina, about 15°40′S, 47°39′W, 1985, M. Ribeiro. USNM 278986, 1 (mature female, 39.6 mm SL), córrego Papuda, tributary to rio São Bartolomeu, 28 Aug. 1985, M. Ribeiro &

R.C. Mendonça. USNM 278987, 1 (mature male, 37.1 mm SL), córrego Forquilha, tributary to rio São Bartolomeu, Sept. 1985, M. Ribeiro. USNM 278989, 3 (mature females, 28.7–37.4 mm SL), rio Taboca, tributary to rio São Bartolomeu, Sept. 1985, M. Ribeiro & J. Dalmaco. MZUSP 63588, 3 (mature females, 34.3–41.3 mm SL), córrego Vargem de Trás, rio Pipiripau, near Planaltina, 1 Jun. 1979, N. Menezes & E. Bastos.

Note.—Böhlke (1954:267) with the aid of other Dr. Carl Ternetz localities of about the same date discussed the type locality "as a small brook somewhere along the Chapadão do Sarandy, lying between the headwaters of the Rio Maranhão (which empties into the Tocantins) and those of the Rio São Bartholomeo [= rio São Bartolomeu] (which empties into the [rio] Corumbá and then into the [rio] Paranahyba [= rio Paranaíba]." Böhlke continued: "Thus the particular brook which Ternetz collected may drain into the Amazon system to the north or into the Paraná to the south, but more likely the latter . . ." Subsequent to the original description, several collections were made in this region as listed above and in Weitzman & Fink (1985:106). *Planaltina myersi* so far has been found only in the upper rio Paraná system.

Definition.—Following features distinguish *Planaltina myersi* from *P. glandipedis* and *P. britskii*: One much enlarged and elongate scale along dorsal border of pouch opening; adipose fin present. In addition, anterior teeth of inner tooth row of premaxilla of *P. myersi* pentacuspid, and dentary with its anterior large teeth pentacuspid or quadricuspid. Lower jaw not extending beyond upper. *Planaltina glandipedis* with tri-

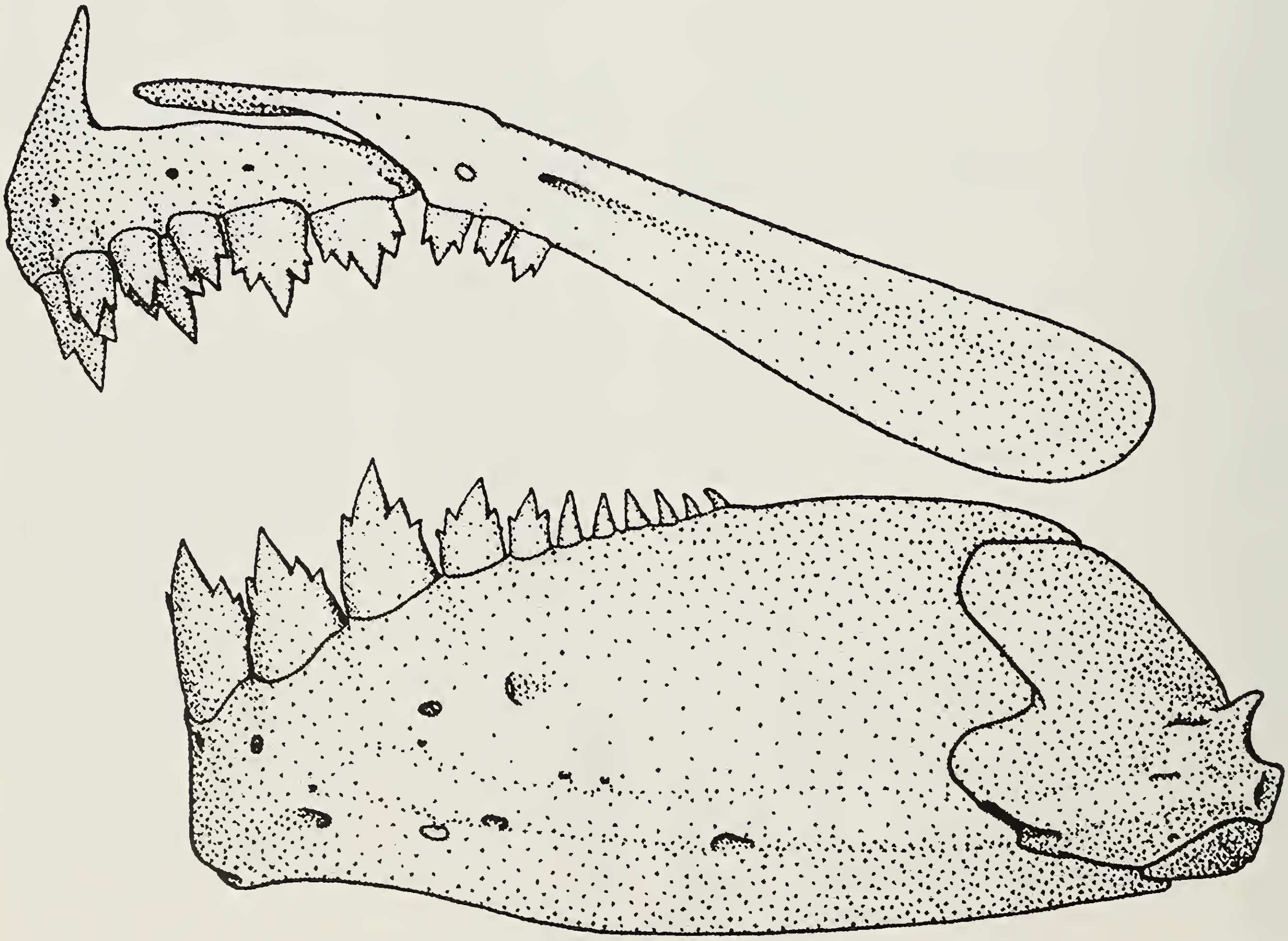

Fig. 3. *Planaltina myersi*, MNRJ 10635, c&s, sexually active male, SL 33.3 mm. Premaxilla, maxilla and mandible, left side, external view. Note relative positions of maxilla and premaxilla with dentary not normal so that all jaw teeth can be illustrated.

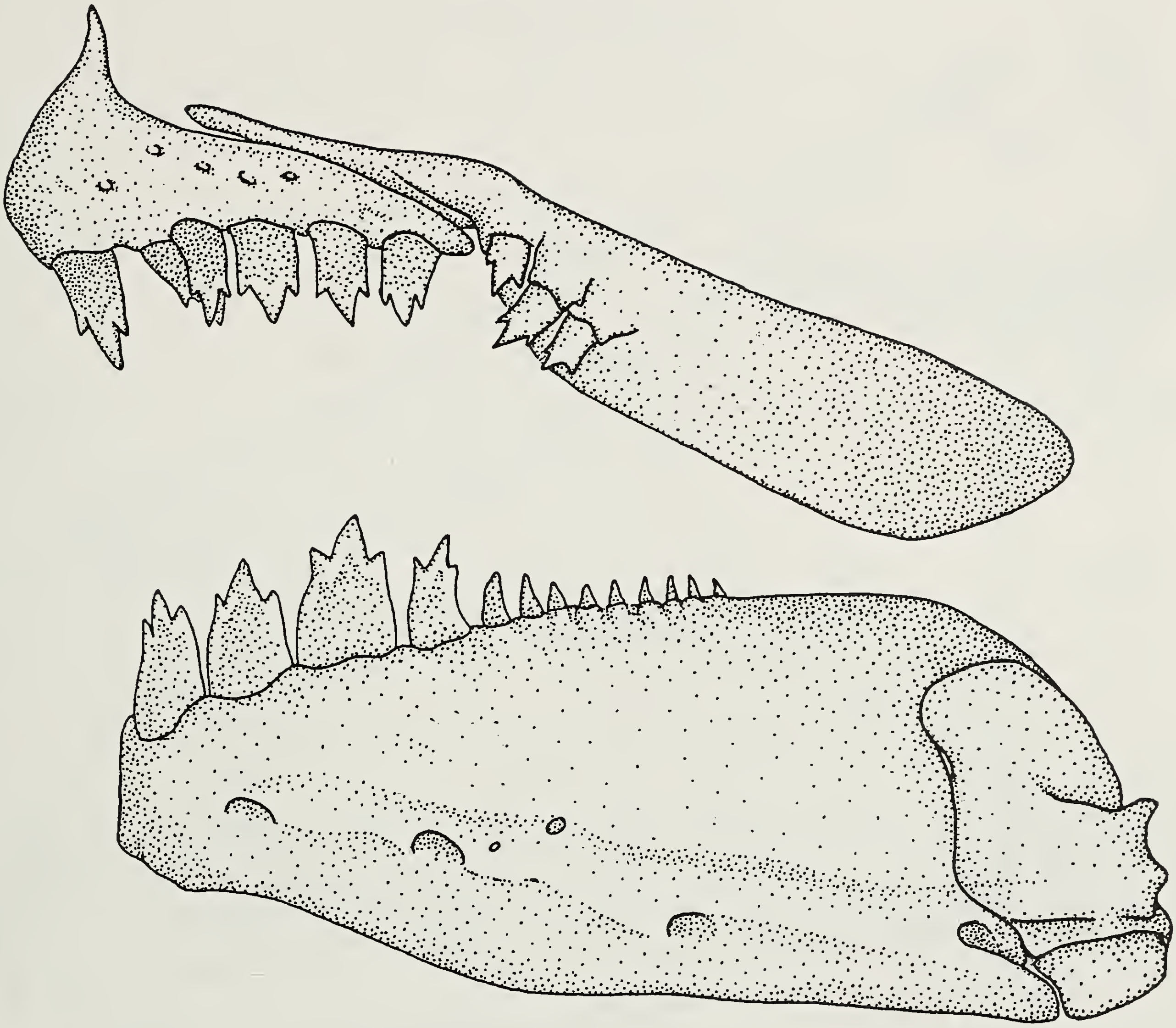

Fig. 4. *Planaltina glandipedis,* new species, paratype, USNM 362135, sexually active male, c&s, SL 24.3 mm. Premaxilla, maxilla and mandible, left side, external view. Note relative positions and premaxilla with dentary not normal so that all jaw teeth can be illustrated.

cuspid teeth in inner row of premaxilla; dentary with tricuspid anterior large teeth, lower jaw protrudes somewhat beyond upper jaw. *Planaltina britskii* with teeth of inner row of premaxilla and large anterior teeth of dentary pentacuspid and lower jaw included by upper (Figs. 3–5, but note: in drawings upper and lower jaws reproduced from independent drawings and not in a natural position in relation to one another, thus some dentary teeth not hidden by upper jaw teeth).

Figures 6–13 illustrate Tukey Box Plot distributions of population sample data for species of *Planaltina.* Captions of these figures provide results of Mann-Whitney rank sum tests regarding differences and similarities among *P. myersi, P. britskii,* and *P. glandipedis* in number of lateral-series scales, Fig. 6; number of predorsal scales, Fig. 7; number of branched anal-fin rays, Fig. 8; total number of vertebrae including those of Weberian apparatus, Fig. 9; least number of scale rows around caudal peduncle, Fig. 10; number of lower-limb gill rakers, Fig. 11; number of scale rows between dorsal-fin origin and lateral line, Fig. 12; and number of scale rows between anal-fin origin and lateral line, Fig. 13.

Description.—Morphometrics of the holotype and additional specimens presented in Table 1. Tables, graphs, and descriptions

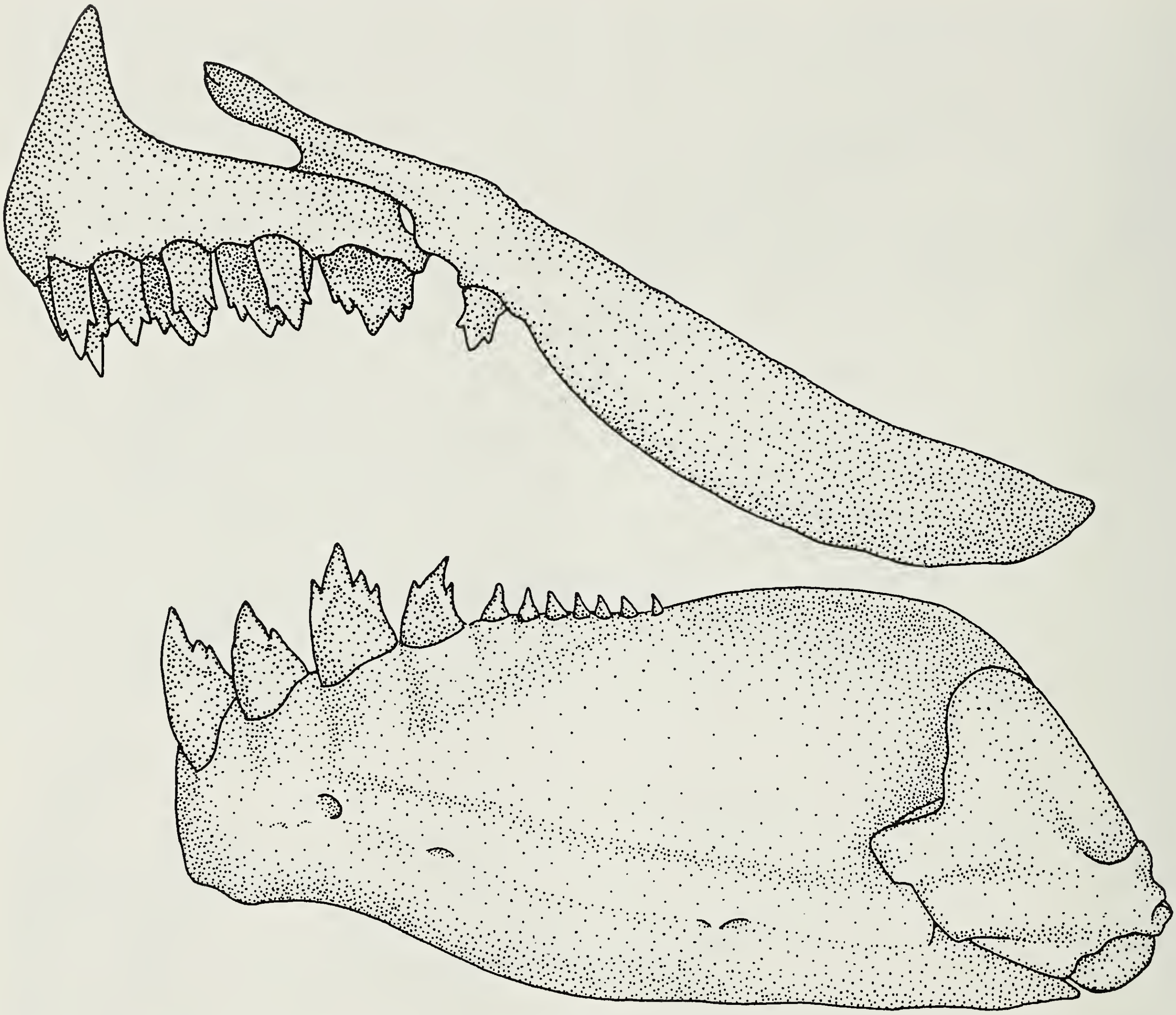

Fig. 5. *Planaltina britskii,* new species, paratype, MZUSP 62758, c&s, sexually active male, SL 35.6 mm. Premaxilla, maxilla and mandible, left side, external view. Note relative positions of maxilla and premaxilla with dentary not normal so that all jaw teeth can be illustrated.

provided below based on combined lots of this species because no statistical differences were found among examined same-sex population samples. All collection localities geographically close and in one drainage system, rio Corumbá, upper rio Paraná.

Body large, compressed and moderately elongate; greatest body depth between snout tip and dorsal-fin origin, near origin of pelvic fin. Dorsal body profile somewhat convex between nape and just anterior to dorsal-fin origin, only slightly elevated at dorsal-fin origin. Head profile to snout tip slightly convex. Snout rounded. Body profile nearly straight along dorsal-fin base and slightly concave in region of caudal peduncle. Dorsal-fin origin nearer to caudal-fin base than snout tip. Ventral body profile convex from tip of lower jaw to anal-fin origin, nearly straight along anal-fin base and slightly concave from end of anal fin to origin of procurrent caudal-fin rays.

Lower jaw terminal or only slightly protruding anterior to upper jaw. Mouth gape somewhat inclined posteroventrally towards mandibular joint. Maxilla extending posteriorly beyond vertical line passing through anterior border of orbit, but falling short of reaching a vertical line passing through anterior border of pupil of eye (see Fig. 2).

Dorsal-fin rays ii, 8 in 44 of 45 specimens including holotype, I, 7 in one spec-

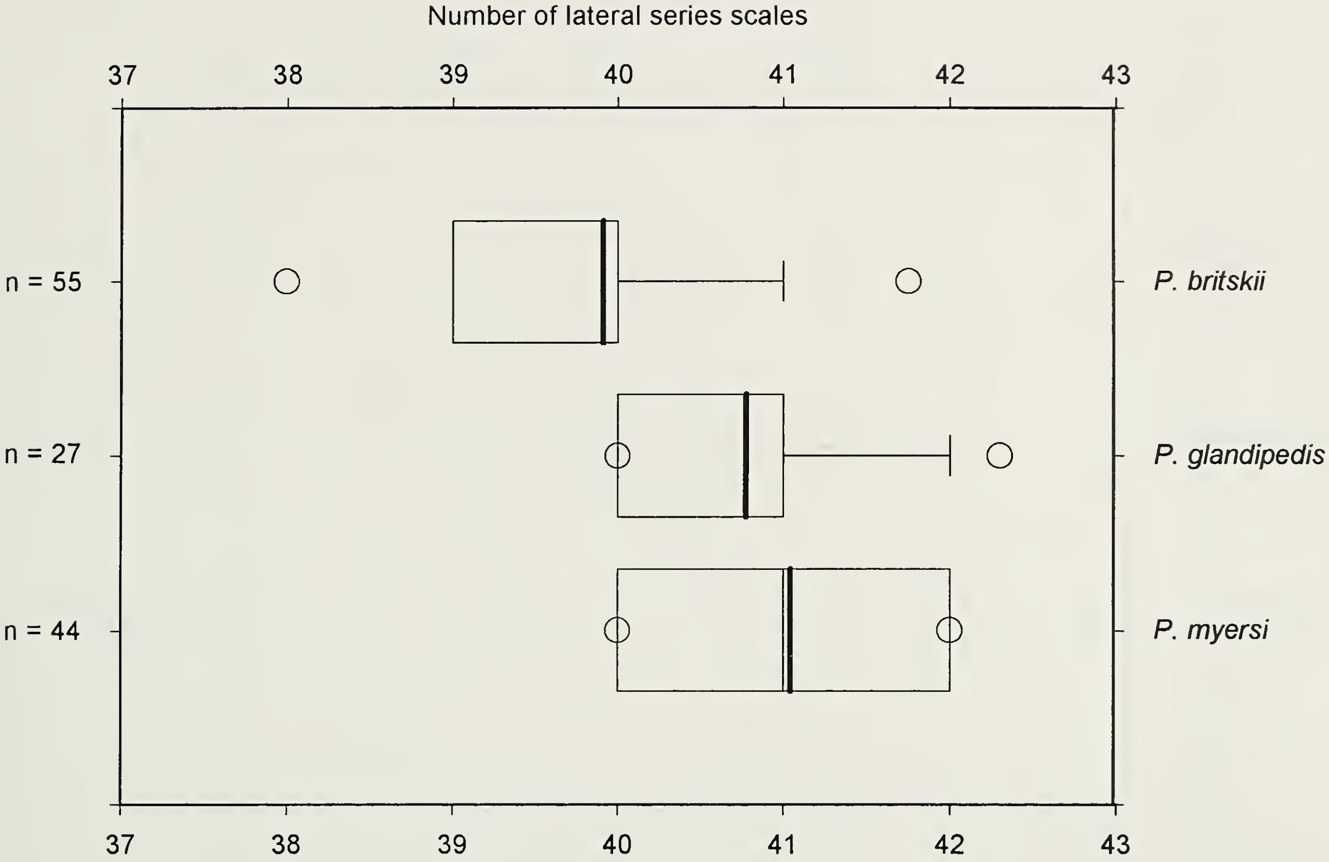

Fig. 6. Tukey box plots showing the statistical distribution of number of lateral-series scales for species of *Planaltina*. No significant difference in number of lateral series scales was found using a Mann-Whitney rank sum test for *P. myersi* and *P. glandipedis*. However, using this test a statistically significant difference was found between *P. myersi* and *P. britskii* (T = 3021.00, P = <0.001) and between *P. glandipedis* and *P. britskii* (T = 1733.0, P = <0.001). The median for *P. myersi* and *P. glandipedis* is 41 and for *P. britskii* it is 40.

imen. Posterior most ray unbranched in all but one specimen in which count appears as ii, 9, but is actually ii, 8, posteriormost ray being branched, n = 45. Adipose fin present. Anal-fin rays iv, 21 (iv or v, usually v, branched rays X = 20.8, range 19–23, n = 45). Moderately developed anterior anal-fin lobe including anterior unbranched rays and first 4–5 branched rays. Anal fin of sexually mature males with bilateral hooks on fifth unbranched and anterior 9 or 10 branched rays distributed as in Fig. 14. Pectoral-fin rays i, 11 (anterior unbranched ray i in all specimens, posterior ray actually unbranched, but counted as a branched ray), branched rays X = 10.3, range 9–11, n = 45. Posterior tips of longest pectoral-fin rays not reaching pelvic-fin origin; pectoral fin about same length in both sexes, without hooks. Pelvic-fin rays i, 6, n = 45 (posterior most ray unbranched). Sexually mature males with hooks present on rays of pelvic fin, distributed as in Fig. 15. Number of hooks per ray varying among different males, but usually approximately as shown in Fig. 15; a mature male (30.5 mm SL) with 0 hooks on first ray, 8 on second, 10 on third, 13 on fourth, 15 on fifth, 16 on sixth, 3 on seventh ray, all on ventral surface of right side pelvic fin. Pelvic fins of adult males longer than those of adult females (see Table 1 and Fig. 15); distal tips of longest pelvic-fin rays extending to, or slightly beyond, anal-fin origin in adult males, but pelvic fins falling short of anterior origin of anal fin in adult females. Compare Figs. 1a, b. See also discussion under "*Sexual dimorphism.*" Scales cycloid, with few radii, often 3–6 along posterior exposed field, more numerlous, to approximately 10, on enlarged scale bordering dorsal border of pouch opening.

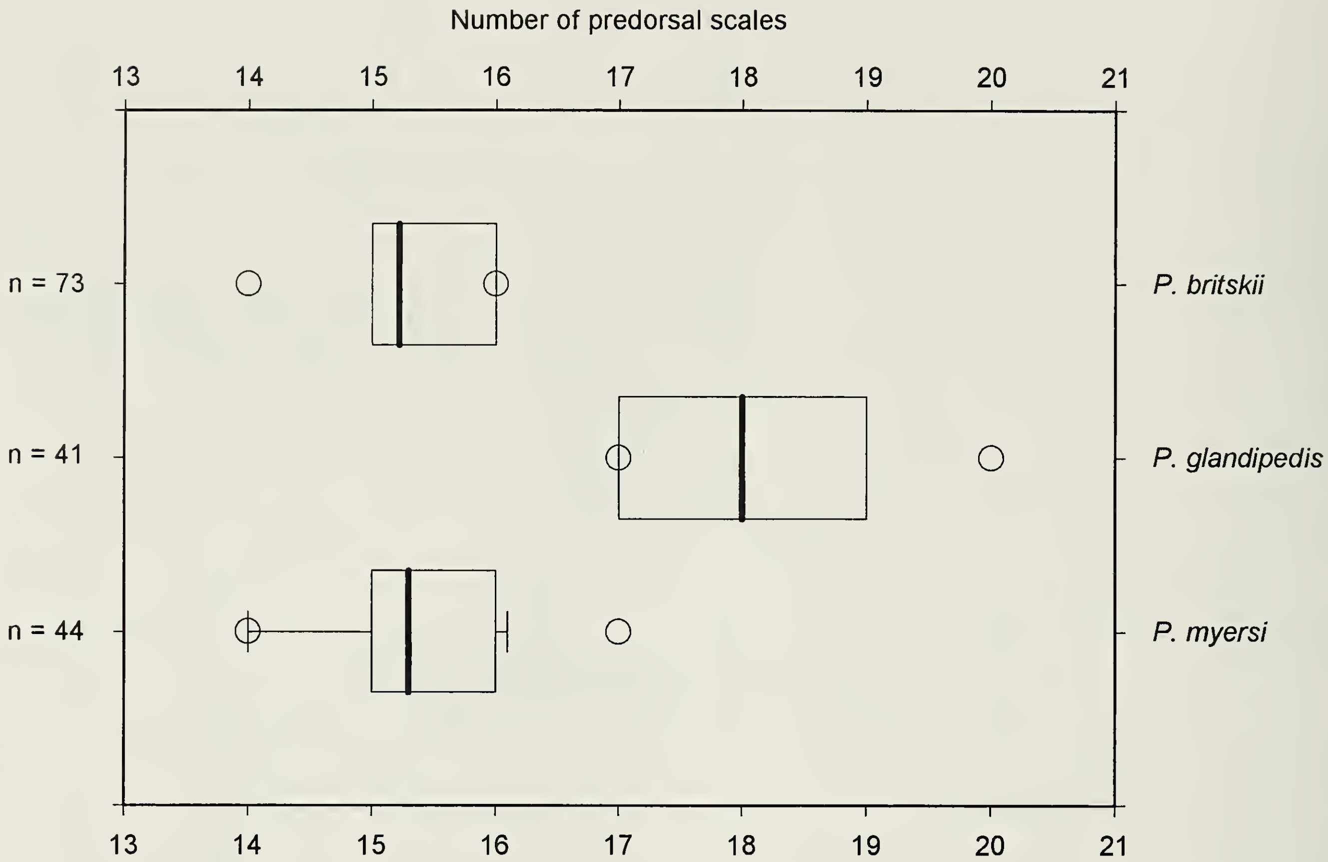

Fig. 7. Tukey box plots of number of predorsal scales for species of *Planaltina.* A Mann-Whitney rank sum tests found no significant difference in the number of those scales for *P. myersi* and *P. britskii,* but a significant difference was found between *P. myersi* and *P. glandipedis* (T = 2633.000, P = <0.001) and between *P. glandipedis* and *P. britskii* (T = 3854.000, P = <0.001). The median for *P. myersi* = 15, for *P. glandipedis* = 18 (= the same as mean), and for *P. britskii* = 15.

Lateral line complete, perforated scales 42 (X = 41.0, range 39–43, n = 44). Predorsal scales 15 (X = 15.3, range 13–17, n = 44). Scale rows between dorsal-fin origin and lateral line 6 (X = 5.9, range 5–6, n = 45). Scale rows between anal-fin origin and lateral line 5 (X = 4.9, range 4–5, n = 45). Scale rows around caudal peduncle 16 (X = 15.5, range 15–16, n = 45).

Premaxillary teeth in two distinct rows (see Fig. 3). Larger teeth pentacuspid; smaller teeth tricuspid or with less well-developed and sometimes vestigial additional lateral cusps. Outer row teeth 3 (X = 3.2, range 2–4, n = 47). Inner row teeth 4 (X = 4.0, range 4–5, but only one specimen had 5 teeth, n = 47). Maxillary teeth 1 (number of teeth does not appear to increase ontogenetically, X = 2.1, range 1–3, n = 47). Maxillary teeth tricuspid, occasionally bicuspid, (anterior tooth larger than remaining teeth). Dentary with 4 large anterior pentacuspid or sometimes quadricuspid teeth, n = 47 and 7 smaller posterior teeth (X = 7.0, range 5–9, n = 46). Premaxillary, maxillary, and dentary teeth compressed so that flattened surfaces face both externally and internally.

Vertebrae 39 (X = 39.3, range 38–41, n = 54). Upper limb gill-rakers 5 (X = 5.7, range 4–7, n = 47); lower limb gill-rakers 10 (X = 11.1, range 10–13, n = 47). Branchiostegal rays 4 in two cleared and stained specimens, 3 rays originating from anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—Males and females with approximately the same color pattern (Figs. 1a, b, 2). Body pale to light brown and a little darker dorsally than ventrally. Dorsal body surface dark due to scattered dark chromatophores and a clear reticulate

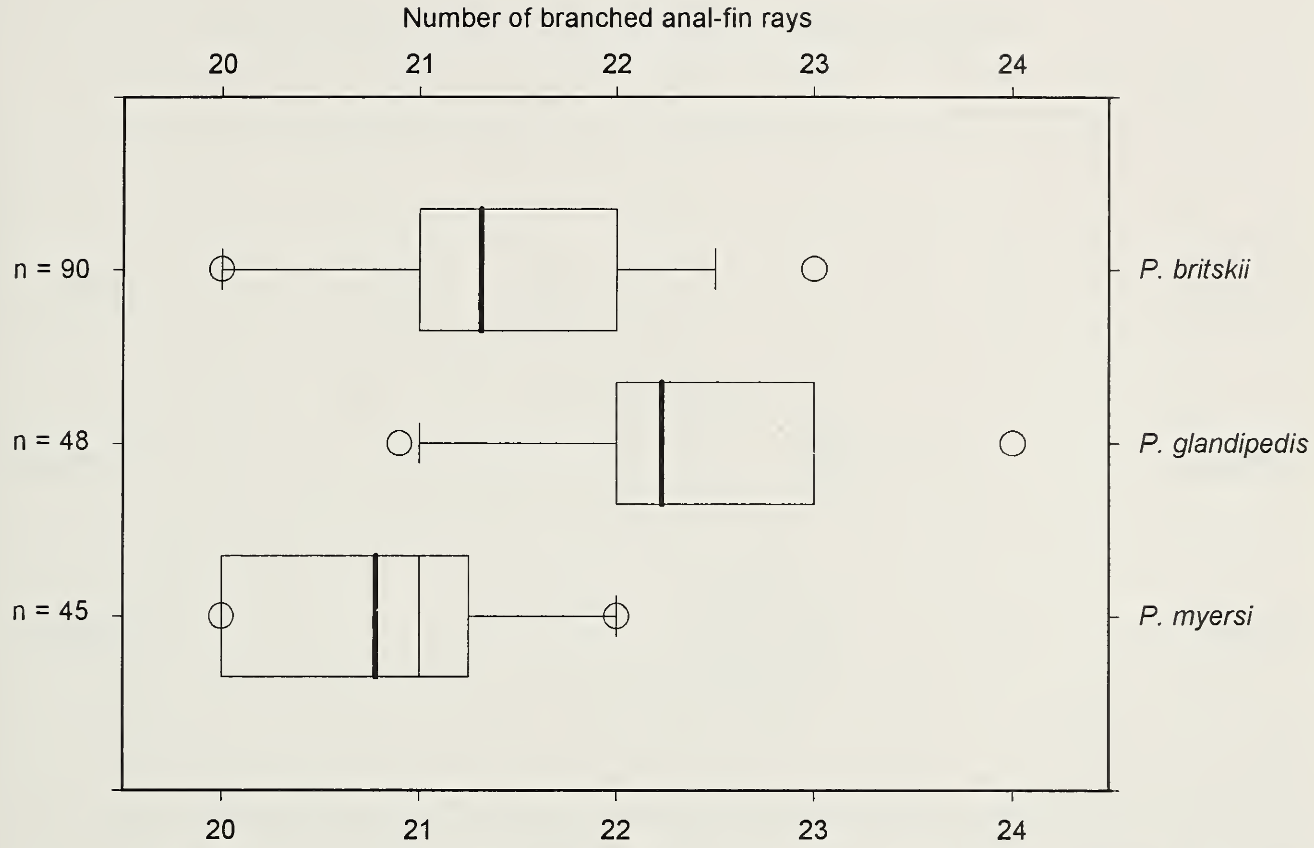

Fig. 8. Tukey box plots of number of branched anal-fin rays for species of *Planaltina.* A significant difference in number of these fin rays was found among all three species using a Mann-Whitney rank sum test. Between *P. myersi* and *P. britskii* (*T* = 2449.000, *P* = 0.004), between *P. myersi* and *P. glandipedis* (*T* = 1376.000, *P* = <0.001) and between *P. glandipedis* and *P. britskii* (*T* = 4387.000, *P.* = <0.001). The median for *P. myersi* = 21, for *P. glandipedis* = 22 and for *P. britskii* = 21.

pattern of dark chromatophores associated with scale borders. Fewer dark chromatophores occurring on ventral posterior part of body where scattered concentration of chromatophores presents on body dorsal to anterior half of anal fin, most obvious in males. Dark lateral body stripe present, but mostly obscured by guanine pigment in freshly caught specimens or in specimens fixed in ethyl alcohol. This darkly pigmented stripe, when guanine pigment destroyed by formalin, extending from posterior part of dorsal opercular region to caudal-fin base and onto anterior part of median caudal-fin rays. Dark pigmentation of lateral stripe mostly concentrated along posterior two thirds of body and about equally evident on males and females. Also extending onto anterior part of median caudal-fin rays. Other median fins relatively free of pigment, but anal fin with considerable amount of dark pigment on the membranes between rays. Pectoral and pelvic fins pale. Head dark dorsally and dark around mouth. Circumorbital bones and opercle silvery with very few scattered dark chromatophores.

Sexual dimorphism, reproductive mode and gonad anatomy.—The females lack the pelvic-fin and anal-fin hooks present in males as described above (see Figs. 14, 15). The pelvic fins are longer in adult males than in adult females. Our data indicate that sexual maturity is reached by about or at least by 30 mm SL and by this length the male's pelvic fins have also reached their proportionately greatest length relative to that of the females. Comparisons of Fig. 16 of *P. myersi,* Fig. 17 of *P. glandipedis* and Fig. 18 of *P. britksii* indicate that the relative pelvic-fin length in males of *P. myersi* and *P. glandipedis* varies less than in *P. britskii.* Although our population samples are represented by males and females of

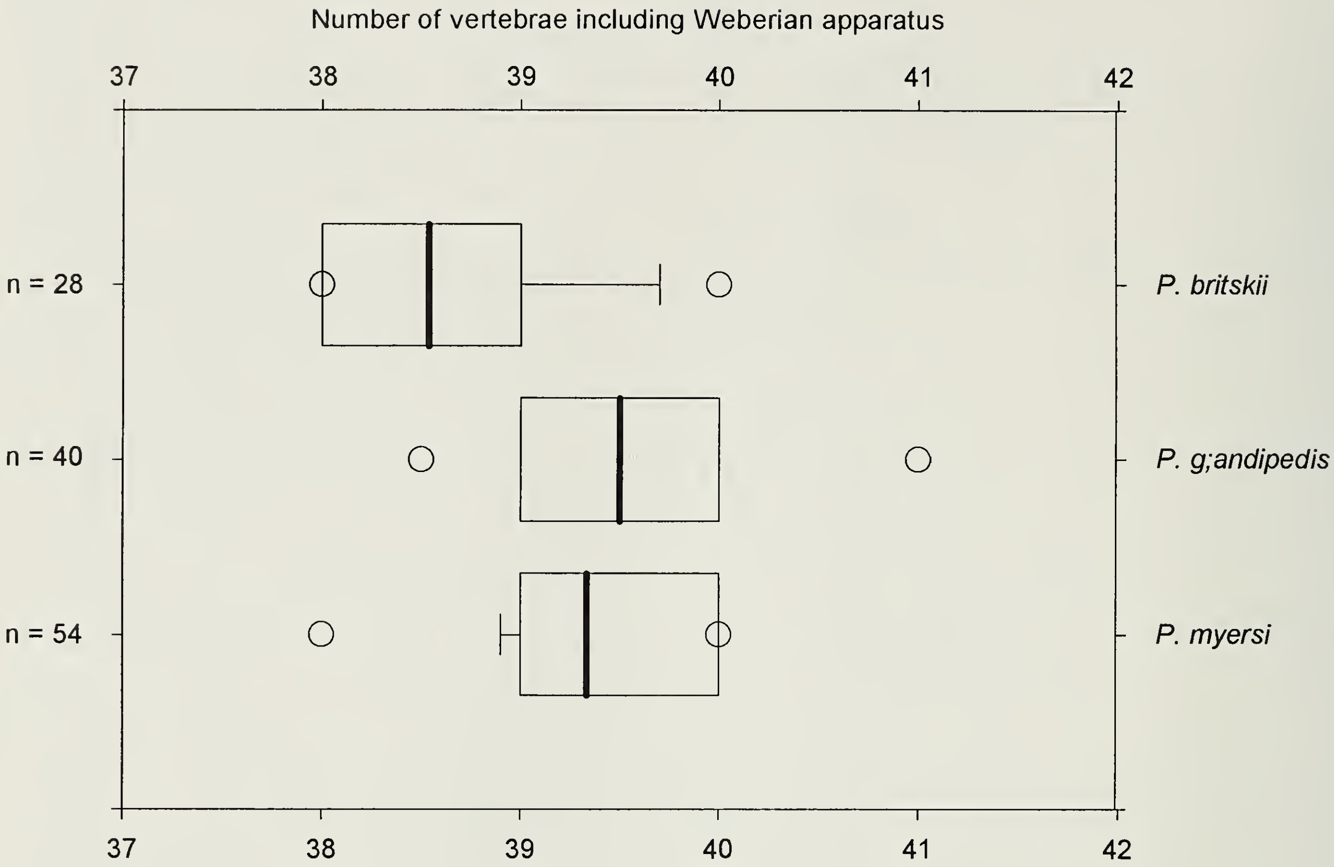

Fig. 9. Tukey box plots showing the distribution of number of vertebrae for species of *Planaltina.* A Mann-Whitney rank sum test found no significant difference between number of vertebrae in *P. myersi* and *P. glandipedis,* but a significant difference ($T = 612.500$, $P = <0.001$) was found between *P. britskii* and *P. glandipedis* as well as *P. britskii* and *P. myersi* ($T = 740.00$, $P = <0.001$). Median for *P. myersi* and *P. glandipedis* = 39, and for *P. britskii* = 38.

about equal length ranges for each sex, relatively few are fully sexually mature judging from visual inspection of the gonad state of development in some specimens. The scales bordering the dorsal margin of the mature male pouch opening (see Fig. 19) are more elongate than those of the mature females, but it is impossible to predict if greater elongation of scales dorsal to the pouch opening might be attained at comparatively larger sizes in females.

A gill gland as reported present in *Corynopoma riisei* Gill by Burns and Weitzman (1996) was reported as present by Bushmann et al. (2002: table 1) in a sexually mature male specimen of *P. myersi* (USNM 278966, 38.3 mm SL), but absent in a sexually mature female specimen (USNM 278966, 43.0 mm SL). In maturing males the presence of such a gland is uncertain. One maturing male specimen (MNRJ 10635, 33.0 mm SL) appeared to have several fused distal tips of anterior gill filaments, but no obvious gill gland was present.

Histological analysis revealed that the epithelium covering both the anal- and pelvic-fin rays was thicker in males than in females. Figure 20 shows the thickened epithelium along a pelvic-fin ray of a mature male (USNM 278966, 38.3 mm SL). Abundant club cells, some close to the surface, were present in the anal- and pelvic-fin epithelia of both sexes.

Histological analysis of ovaries of two mature females (MNRJ 10634, 30.9 mm SL; USNM 278989, 35.0 mm SL) revealed the presence of abundant spermatozoa (see Fig. 21) and large mature oocytes within the ovarian cavity (see also Burns et al., 1995: table 3 and fig. 1A). Longitudinal sections through the testes revealed a pos-

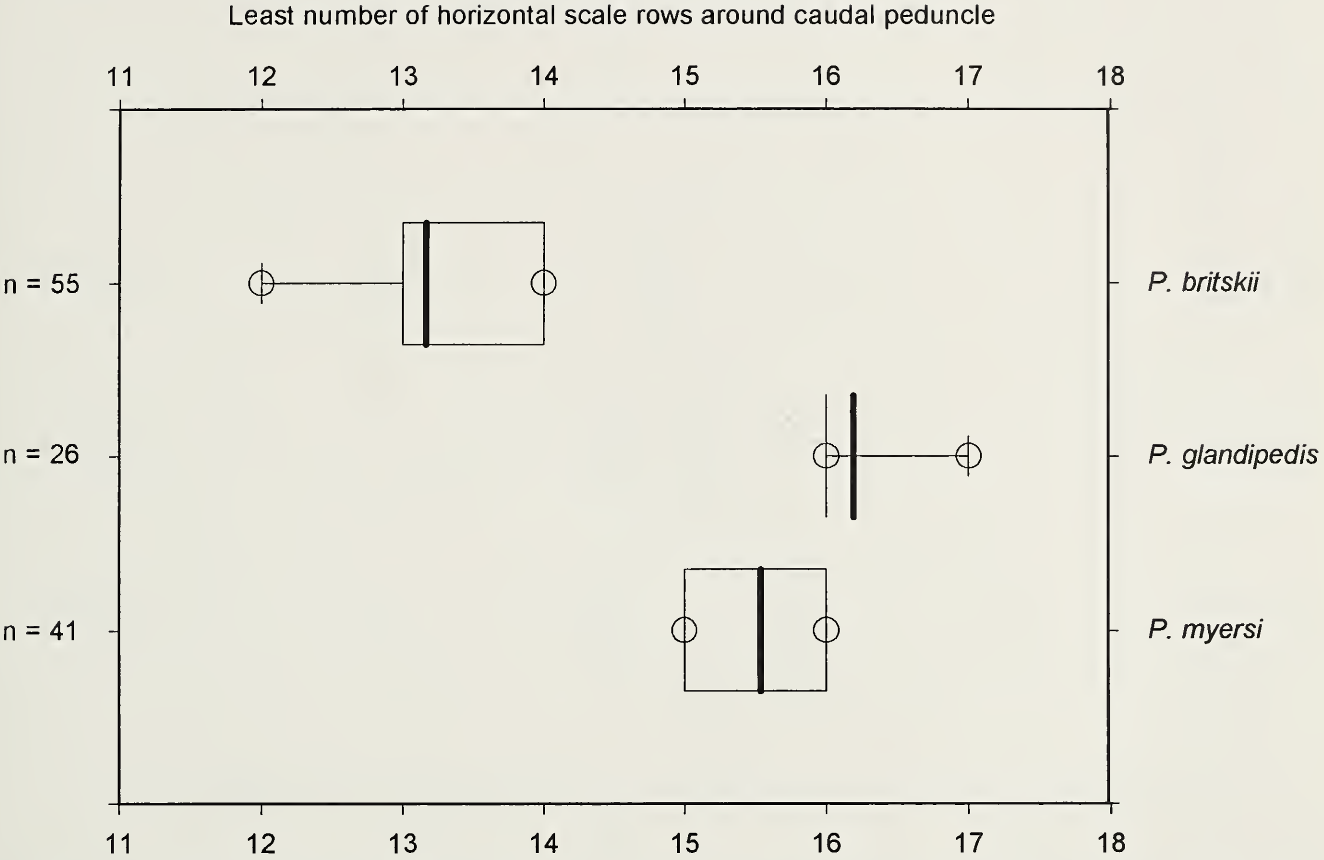

Fig. 10. Tukey box plots of least number of horizontal scale rows around caudal peduncle for species of *Planaltina.* A Mann-Whitney rank sum test indicated a statistically significant difference among all species. That between *P. britskii* and *P. glandipedis* and between *P. britskii* and *P. myersi* is obvious comparing the graphs, but that between *P. glandipedis* and *P. myersi,* although apparently statistically significant (T = 1186.00, P = <0.001) is not particularly useful for identification of the species. Median for *P. myersi* and *P. glandipedis* = 16, and for *P. britskii* = 13.

terior sperm storage area occupying 44.2% of the total testis area in a mid-sagittal testis section as was reported and discussed by Burns et al. (1995:134, fig. 2). Burns et al. (1995: table 3) also reported that the sperm cells are typical aquasperm, but with the nucleus spherical to slightly "deformed." There appear to be no sperm cell modifications as found in typical glandulocaudines, but ultrastructure examination was not possible because only formalin-fixed specimens were available.

Planaltina glandipedis, new species

Fig. 22, Table 2

Specimens examined.—All specimens from Brazil, Estado de São Paulo, Município de Corumbataí (except where noted), and tributaries to the drainage basin of the rio Tietê, a tributary of the upper rio Paraná.

Holotype.—MZUSP 62752, male, 26.2 mm SL, Corumbataí, rio Corumbataí, approximately 22°13′S, 47°38′W, 19 Jan. 1976; H. A. Britski.

Paratypes.—MZUSP 62753, 11 (23.0–28.7 mm SL) and USNM 362135, 11 (immatures to adults, sex undetermined, both collected with holotype, 20.0–27.0 mm SL, 2 specimens, male 26.3 mm SL and female 27.0 mm SL used for histological information). Following 5 lots of immature to adult paratypes collected at Corumbataí, rio Corumbataí, approximately 22°13′S, 47°38′W. MZUSP 62754, 7 (19.7–23.0 mm SL). USNM 362136, 5 (21.7–25.3 mm SL), 25 Jan. 1976, H. A. Britski. MZUSP 62755, 1 (28.5 mm SL), Dec. 1962, H. A. Britski. USNM 362137, 2 (25.8 and 26.5 mm SL),

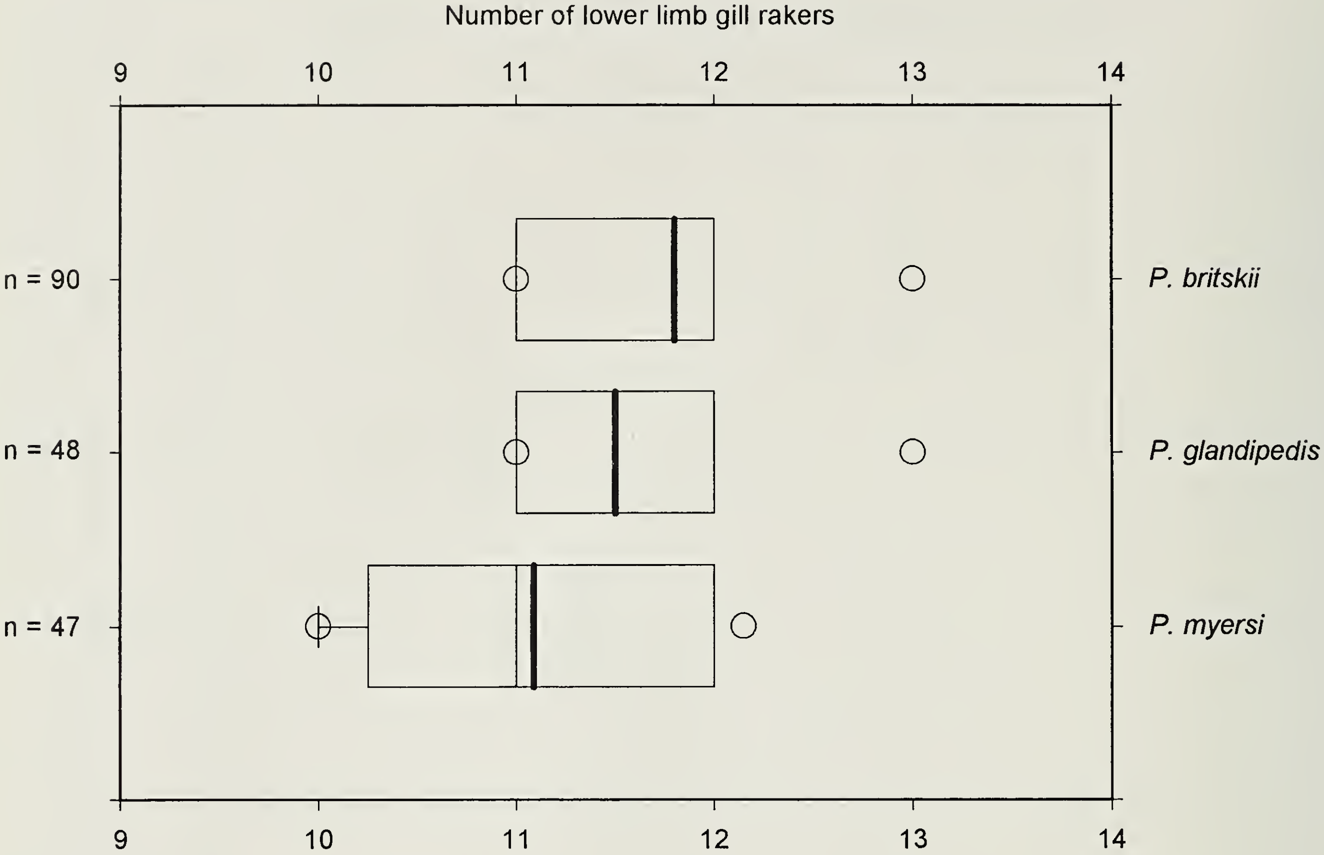

Fig. 11. Tukey box plots of number of lower limb gill rakers for species of *Planaltina.* The differences in the number of lower limb gill rakers among the species is relatively small and provide little if any useful information for identification of the species. However, a nonparametric Mann-Whitney rank sum test found a statistical difference between *P. britskii* and *P. myersi* (T = 2192.500, P = <0.001) and may indicate a genetic difference in these species. However, using the same type of test, differences between the other two species combinations suggest that resulting differences should be interpreted cautiously and considering the numbers of specimens used we reserve judgment about any possible genetic differences in these species. Differences for *P. britskii* and *P. glandipedis* are T = 1936.5, P = 0.017 and for *P. glandipedis* and *P. myersi* are T = 2752.0, P = 0.009. Median for *P. myersi* and *P. glandipedis* = 11, and for *P. britskii* = 12.

2 Nov. 1963, H. A. Britski & A. E. Gomes. MZUSP 62756, 3 (matures 25.5–26.5 mm SL), 2 Nov. 1963, H. A. Britski & A. E. Gomes. DZSJRP 671, 4 (22.0–25.0 mm SL) and MZUSP 63690, 3 (matures 25.5–26.5 mm SL), Brazil, São Paulo, Município de Brotas, basin of rio Jacaré-Pepira, approximately 22°17′S, 48°09′W, Jan. 1988, W. Barrela.

Definition.—*Planaltina glandipedis* is sympatric with *P. britskii,* but can be easily distinguished from that species and the allopatric *P. myersi* by lacking an adipose fin and by characters provided in the key. Furthermore, *P. glandipedis* has tricuspid jaw teeth (see Figs. 3–5) and the lower jaw protrudes somewhat beyond upper, whereas in *P. britskii* the teeth of the inner row of the premaxilla and the large anterior teeth on the dentary are pentacuspid, and the lower jaw is included by the upper jaw.

Description.—Morphometrics of the holotype and paratypes presented in Table 2. Description based on all lots of this species examined because no statistical differences found among lots from different localities.

Body relatively small, compressed and moderately elongate; greatest body depth between snout tip and dorsal-fin origin, near distal tip of adpressed pelvic fin. Dorsal body profile elevated at dorsal-fin origin, slightly convex from this point to snout tip, nearly straight along dorsal-fin base and slightly concave dorsal to caudal peduncle. Dorsal-fin origin nearer to caudal-fin base than to snout tip. Ventral body profile con-

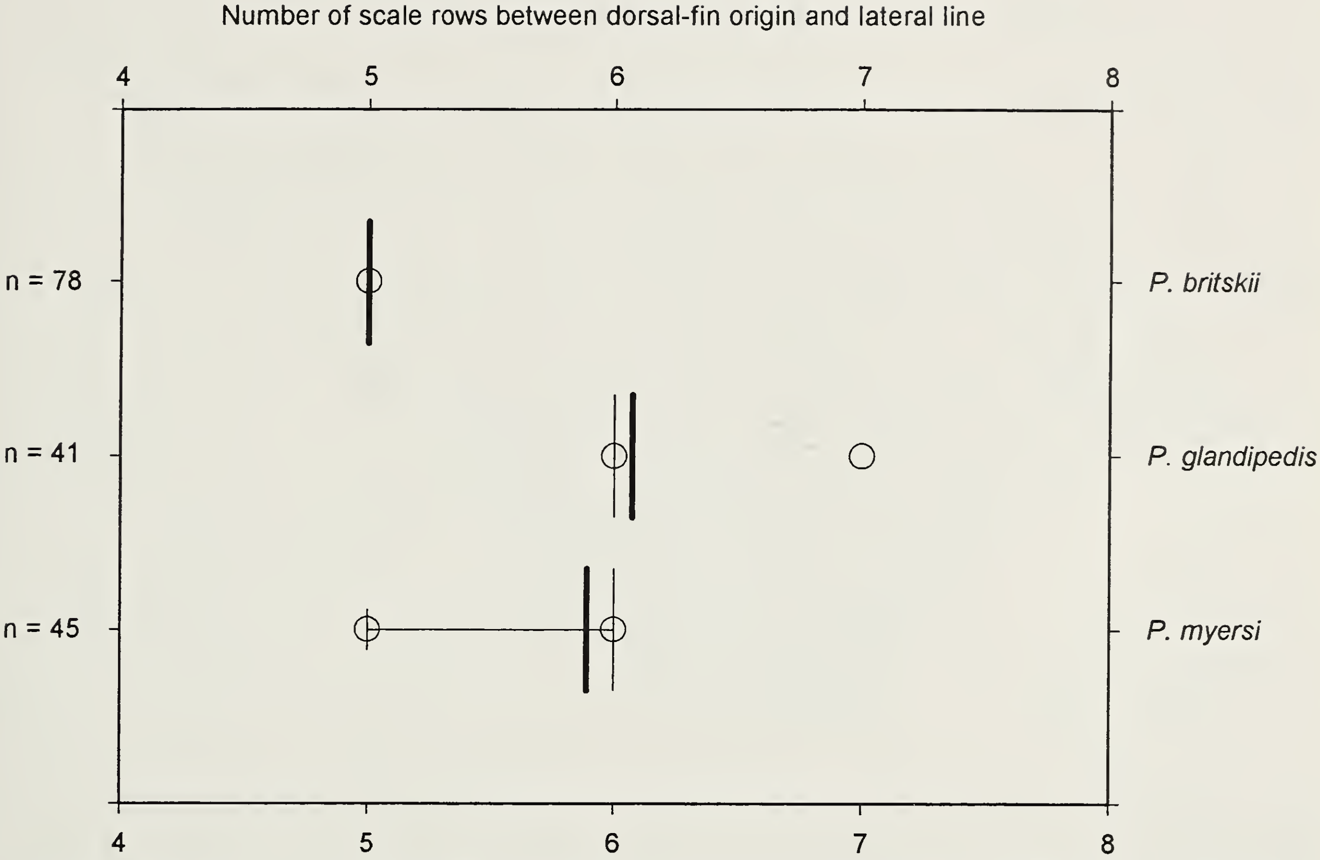

Fig. 12. Tukey box plots of number of scale rows between dorsal-fin origin and lateral line for species of *Planaltina*. A nonparametric Mann-Whitney rank sum test detected a statistically significant difference between *P. britskii* and both other species, *P. britskii* and *P. glandipedis* (T = 4059.000, P = <0.001) and for *P. britskii* and *P. myersi* (T = 4350.000, P = <0.001). The same test for differences between *P. myersi* and *P. glandipedis* indicated no significant difference. Median for *P. myersi* and *P. glandipedis* = 6, and for *P. britskii* = 5.

vex from tip of lower jaw to anal-fin origin, nearly straight along anal-fin base and concave from end of anal fin to origin of procurrent caudal-fin rays.

Lower jaw protruding, anterior to upper jaw. Mouth gape inclined posteroventrally towards mandibular joint. Maxilla extending posteriorly beyond vertical line passing through anterior border of orbit, but not reaching vertical line passing through anterior border of eye pupil.

Dorsal-fin rays ii, 8, n = 47. Adipose fin absent. Anal-fin rays iv, 22 (iv or v, usually iv, branched rays X = 2.2, range 20–25, n = 48). Anterior anal-fin lobe moderately developed and includes fourth or fifth unbranched ray and first 5–6 branched rays. Anal fin of sexually mature males with bilateral hooks on fourth or fifth unbranched and anterior 10 branched rays (Fig. 23). Anal fin of sexually active males with glandular cells on fin's anterior region (see "*Sexual dimorphism, . . .*" below and Fig. 24). Pectoral-fin rays i, 9 (anterior unbranched ray i in all specimens) branched rays X = 9.7, range 9–11, n = 48. Distal tips of longest pectoral-fin rays extending posteriorly beyond pelvic-fin origin. Pectoral fins of about equal length in both sexes and without hooks. Pelvic-fin rays i, 6 (posteriormost ray unbranched in most specimens, branched in two adult males, but always considered as "branched" in counts, n = 48). Sexually mature males with hooks present on rays of pelvic fin, distributed as in Fig. 25. Number of hooks per ray in males varies; mature male (26.0 mm SL) with 7 hooks on first, 18 on second, 16 on third, 10 on fourth, and 13 on fifth branched rays of right pelvic fin. Pelvic fins of adult males somewhat longer than those of most adult females (see Fig.

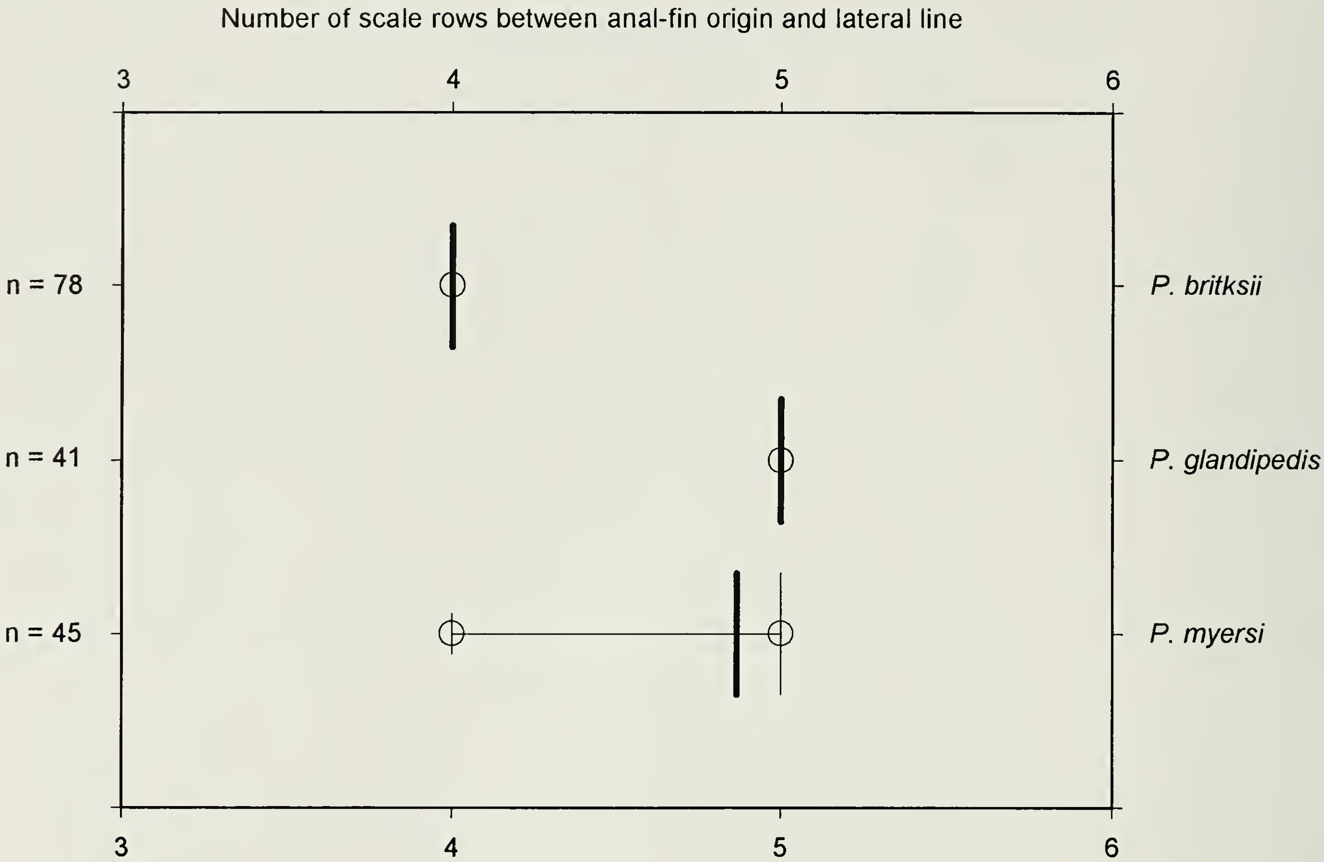

Fig. 13. Tukey box plots of number of scale rows between anal-fin origin and lateral line for species of *Planaltina*. A nonparametric Mann-Whitney rank sum test found a statistically significant difference between *P. britskii* and *P. myersi* ($T = 4311.00$, $P = <0.001$). The same test for *P. myersi* and *P. glandipedis* indicated no significant difference. The difference between *P. britskii* (all 4) and *P. glandipedis* (all 5) was absolute. Median for *P. myersi* = 5.

17); distal tips of longest pelvic-fin rays extending to anal-fin origin in adult males but not in adult females. Males and females with pads of glandular tissue on pelvic-fin rays (see Figs. 26 and 27 and discussion in "*Sexual dimorphism, . . .*" below).

Scales cycloid with few radii along posterior border, more numerous on enlarged scales bordering and covering caudal pouch of male and female (see Fig. 28a, b).

Lateral line complete, perforated scales 41 ($X = 40.7$, range 40–44, $n = 27$). Predorsal scales 18 ($X = 18$, range 17–20, $n = 41$). Scale rows between dorsal-fin origin and lateral line 6 ($X = 6.1$, range 6–7, $n = 41$). Scale rows between anal-fin origin and lateral line 5 in all specimens ($n = 41$). Scale rows around caudal peduncle 16 ($X = 16.2$, range 16–17, $n = 26$).

Premaxillary teeth in two distinct rows. Larger teeth distinctly tricuspid, smaller teeth with less well-developed, sometimes vestigial, lateral cusps (see Fig. 4). Outer row teeth 3 ($X = 2.5$, range 1–4, $n = 48$). Inner row teeth 4 ($X = 4.9$, range 4–6, n = 44). Maxillary teeth 3, (increasing in number with increasing SL from $X = 3.6$ in 10 specimens between 20.0 and 24.7 mm SL to $X = 4.2$ in 7 specimens between 22.0 and 26.5 mm SL). Maxillary teeth tricuspid, first 2 or 3 larger than remaining teeth. Dentary with 4 large anterior tricuspid teeth in all specimens, $n = 48$ and 8 ($X = 7.2$, range 5–11, $n = 48$) posterior small teeth. Premaxillary, maxillary, and dentary teeth compressed, having flat inner and outer surfaces.

Vertebrae 39 ($X = 39.5$, range 38–41, $n = 39$). Upper limb gill-rakers 6 ($X = 5.6$, range 5–6, $n = 48$); lower limb gill-rakers 12 ($X = 11.5$, range 10–13, $n = 48$). Branchiostegal rays 4 in two cleared and stained

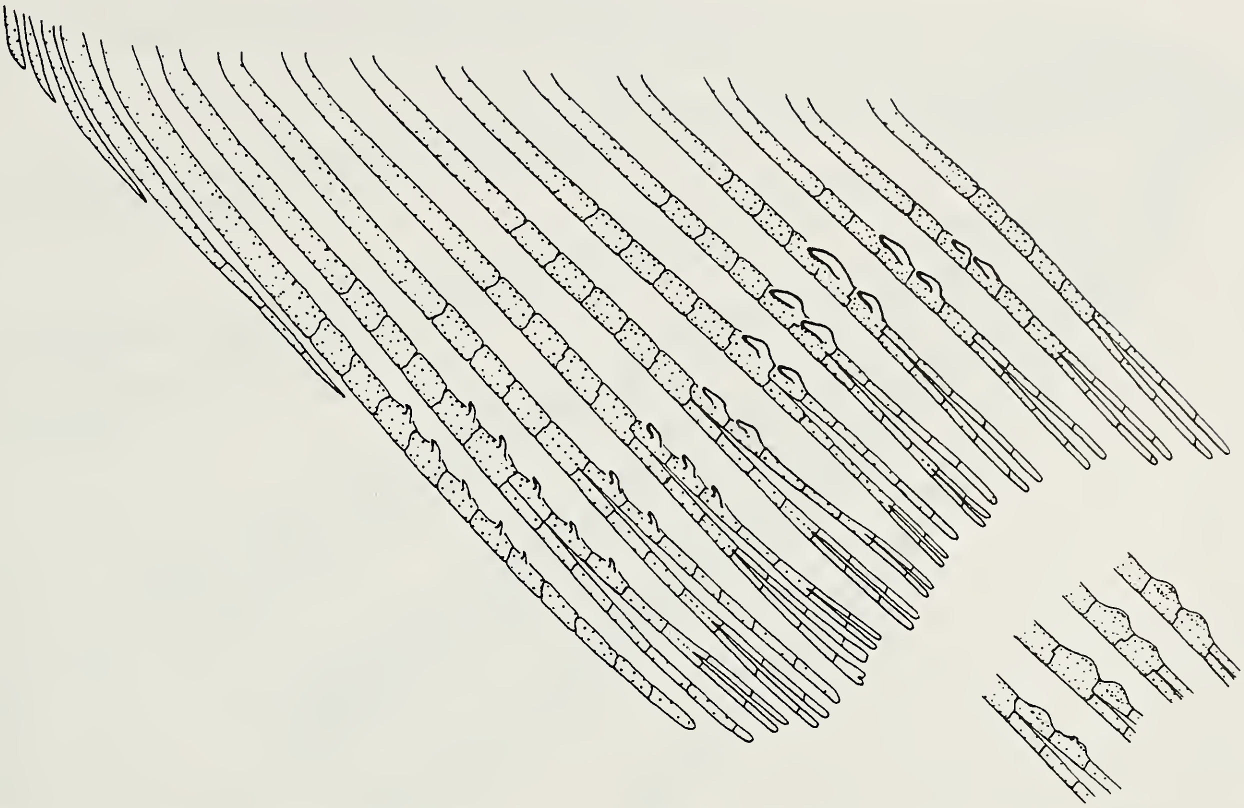

Fig. 14. *Planaltina myersi,* MNRJ 10635, c&s, sexually active male, SL 33.3 mm. Anterior portion of anal fin, left side. Figure shows anal-fin hooks positioned along posterolateral border of anal-fin rays, larger more posterior hooks bent dorsoanteriorly. Inset drawing at right shows anal-fin hook remnants of a sexually inactive adult male or perhaps developing hooks of a maturing male.

specimens, 3 rays originating from anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—Males and females with approximately same color pattern (Fig. 22) at least in specimens preserved in alcohol for more than 20 years. Body pale to light brown and slightly darker dorsally than ventrally. Dorsal body surface dark due to scattered dark chromatophores. Fewer dark chromatophores on the ventral posterior part of body. Dark lateral body stripe mostly obscured by guanine pigment when such pigment not destroyed by formalin and extending from posterior part of dorsal opercular region to caudal-fin base. Visible dark pigmentation of lateral stripe mostly concentrated on caudal peduncle and more evident on males. This dark pigment continuing on anterior part of median caudal-fin rays. Pectoral and pelvic fins pale, dorsal and anal fins dusky with scattered dark chromatophores along fin rays. Head darker dorsally and around mouth. Circumorbital bones and opercle silvery with few scattered dark chromatophores.

Ecology.—Dr. Heraldo Britski (pers. comm.) reports that the rio Corumbataí, where most of the samples were collected, is a clear-water river with a sandy bottom, approximately 8 meters wide and 1 meter deep at the collecting site. The area was almost entirely deforested and the marginal vegetation predominately represented by grasses.

Sexual dimorphism, mode of reproduction, and gonad anatomy.—Histological analysis revealed a thickened epithelium along the anal-fin rays of a mature male (26.3 mm SL; Fig. 24). Only a slight thickening was evident in the anal fin of a mature female (27.0 mm SL). Club cells were abundant in some areas, particularly in the epithelium near the anal-fin base. Although some club cells were present near the epithelial surface, no definitive secretion of the

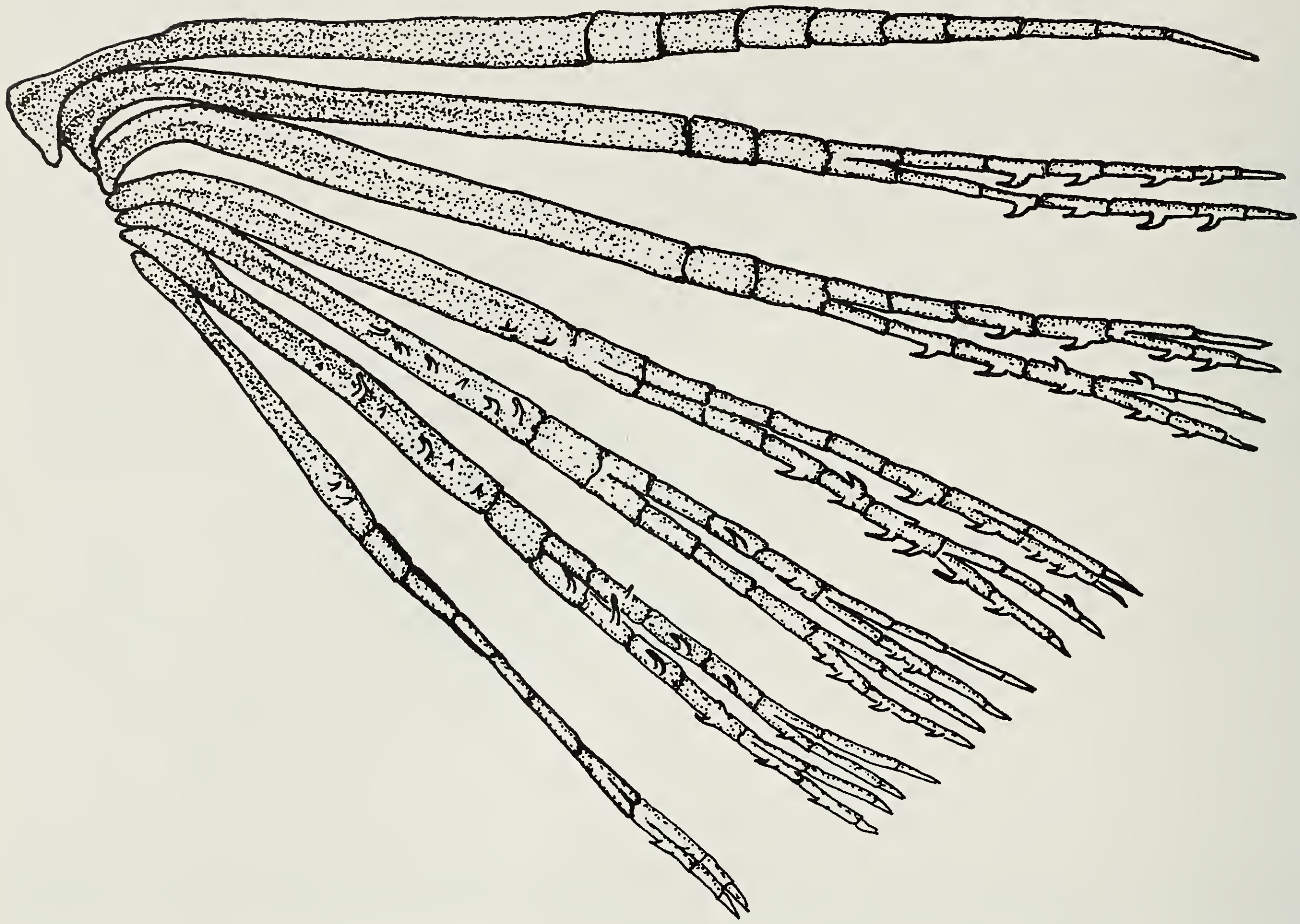

Fig. 15. *Planaltina myersi,* MNRJ 10634, c&s, sexually active male, SL 30.5 mm. Pelvic-fin rays, left side. Ventral surface showing pelvic-fin hooks.

cell contents was observed. The females lack the anal-fin and pelvic-fin hooks present in the males as described above (Fig. 25). The mean pelvic-fin length is longer in adult males than in adult females (Fig. 17) and although difficult to document from our limited data, this divergence in relative length may begin at approximately 24.0–25.0 mm. The skin is thickened along the ventral surface of the pelvic-fin rays of reproductively active males and forms a linear and turgid mound of tissue. Histological analysis of pelvic fins of a mature male (26.3 mm SL) and a mature female (27.0 mm SL) revealed that the marked thickening of the skin in the male was due to both growth of the epithelium and underlying connective tissue (Figs. 26, 27b). Club cells were particularly abundant near the pelvic-fin base, some near or at the surface. Unfortunately we were not able to observe cells at the surface undergoing active holocrine secretion as was observed for similar cells of the anterior region of the anal fin of a species of *Attonitus* and the new genus. See Weitzman et al. (2004) for a more complete description of the gland cells and their mode of secretion in species of *Attonitus.* In the related undescribed genus and species these glandular cells resemble the classic "club" cells known to be present in most ostariophysan fishes (Pfeiffer 1977:660). There is a great amount of evidence that most ostariophysan club cells produce a pheromone that serves as an alarm signal (Pfeiffer 1967:389–390). Classic alarm substance cells (ASC's) are club cells that do not open onto the epithelial surface and are said to release their contents only if the epithelium is damaged (Pfeiffer 1977:660–662). The club cells seen along the anal fin of *Attonitus* and the possibly closely related new genus and species do reach the epithelial surface and undergo de-

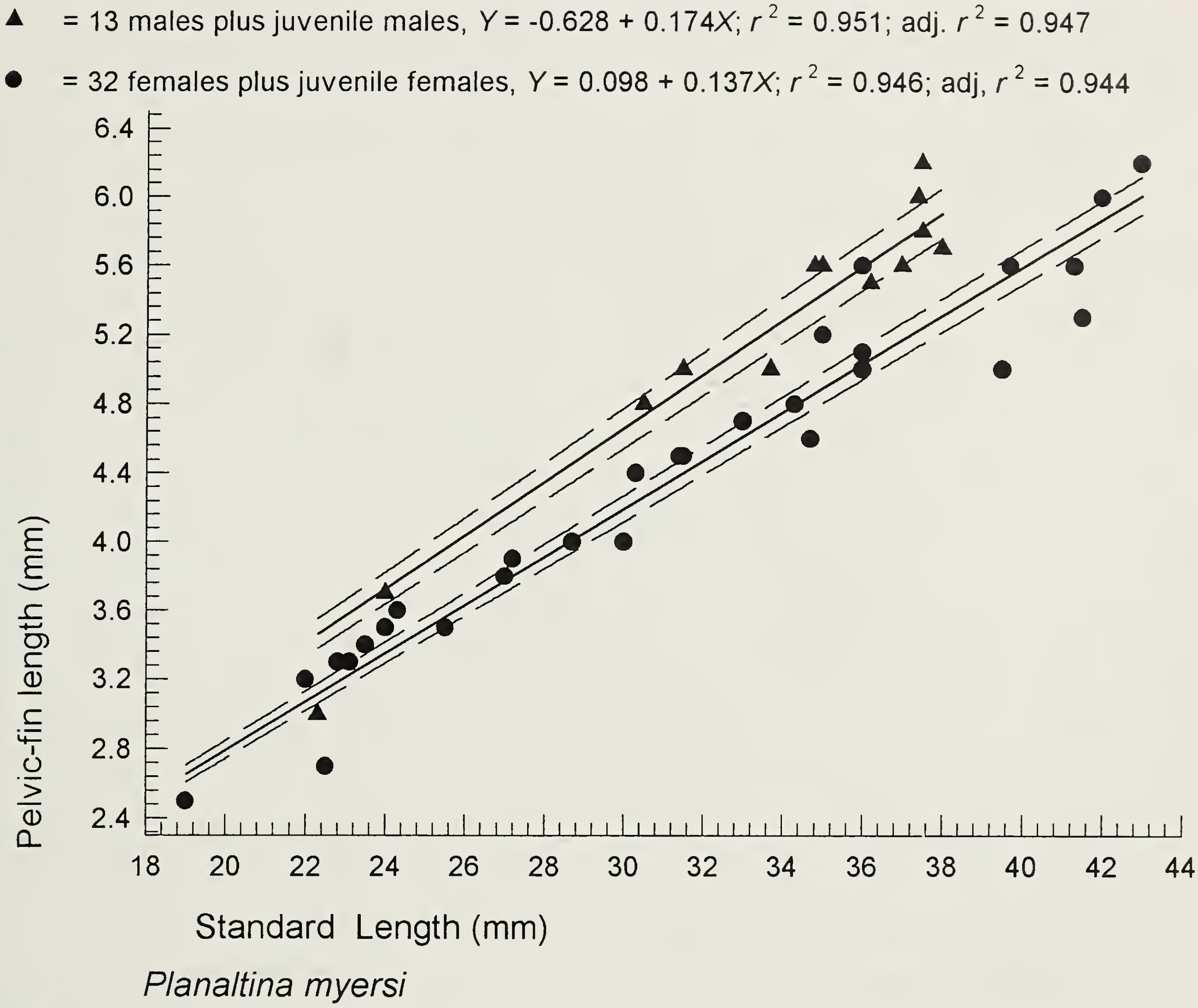

Fig. 16. *Planaltina myersi,* pelvic-fin length as a function of SL by sex. Males and females were identified by external features and sometimes by examination of gonads through a slit in right side of body. Below 30 mm SL, the data is essentially useless for indicating differences in male and female pelvic-fin length, but beyond 30 mm SL, where most mature males occur and primarily where sex of both could males and females could be identified by gonad examination, all males have longer pelvic fins than females.

generation with the contents of the entire cell being secreted (holocrine secretion). These cells may therefore have a function other than of ASC's as may be the case in several catfish species (Pfeiffer 1967:389–390, 1977:663). Some club cells observed in the species of *Planaltina* also appeared to be located near the epithelial surface, although cell degeneration and release was not observed in our histological sections. More specimens need to be analyzed histologically to see if some club cells of *Planaltina* resemble those present on the anal fins of species of *Attonitus* and the new species and genus possibly closely related to *Attonitus.*

Although our population samples of *P. glandipedis* are represented by males and females of about equal length ranges from 24 to about 28.5 mm SL, only a few are sexually mature judging from visual inspection of the gonads. The scales bordering the dorsal border of the mature male pouch opening are more elongate than those of the mature females (Fig. 28a, b), but it is impossible to predict that greater elongation of scales dorsal to the pouch opening might be attained at comparatively larger sizes in females based only on the few available adult specimens of both sexes.

Histological analysis of ovaries from a mature female (27.0 mm SL) revealed the

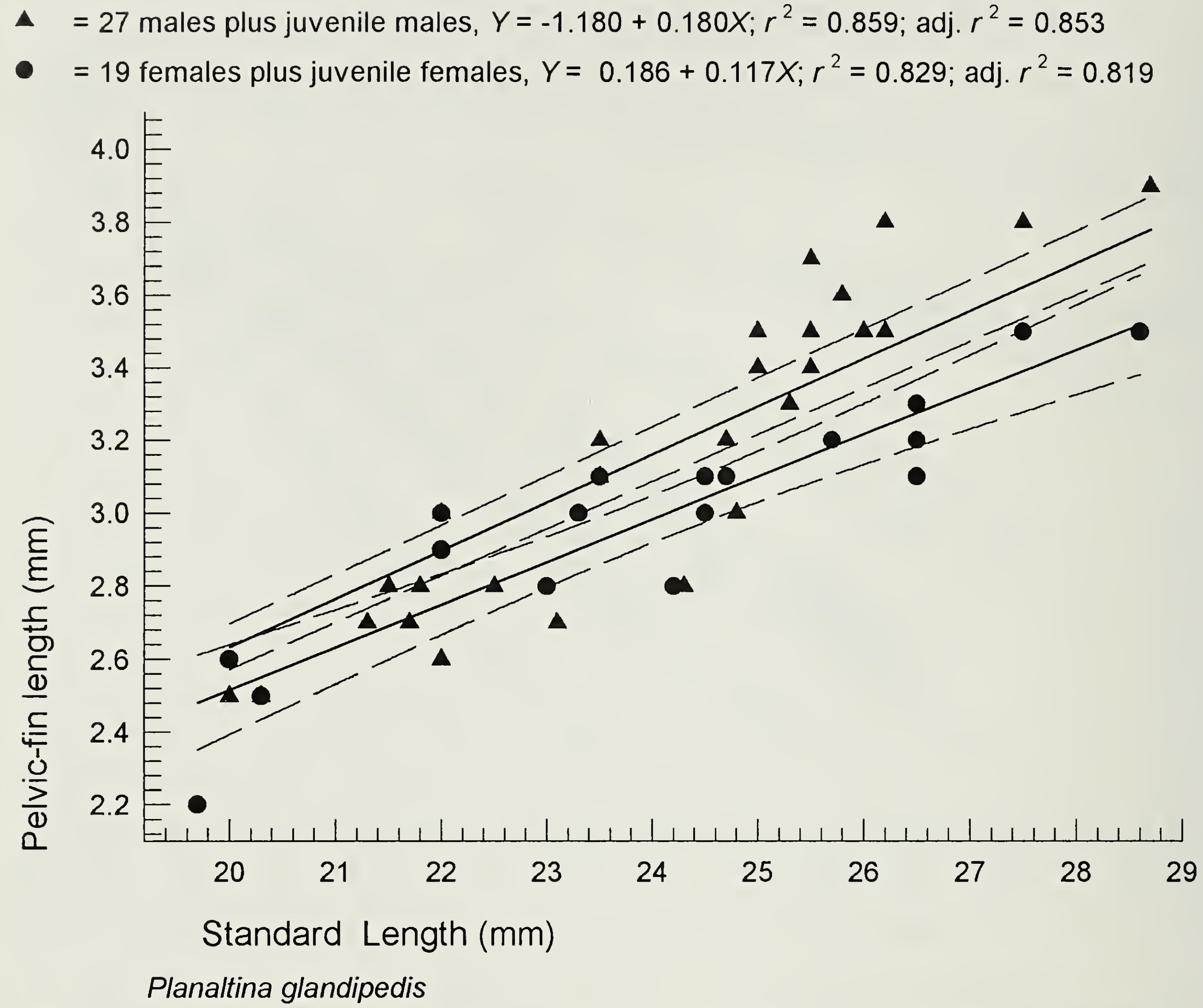

Fig. 17. *Planaltina glandipedis,* pelvic-fin length as a function of SL by sex. Males and females identified by external features and sometimes by examination of gonads by a slit in right side of body. Sexual maturity according to relative pelvic-fin length in males versus those of females appears to strikingly occur at least by standard lengths of about 25 mm SL where there appears a sudden increase in male pelvic-fin length. However, the data in other regions of the graph are insufficient to confirm this estimate. Also, at these lengths the male's testes become active and gland cells appear present in the pelvic fins.

presence of spermatozoa within the ovarian cavity (Fig. 29). Longitudinal sections through the testes revealed a posterior sperm storage area like that described for *P. myersi* by Burns et al. (1995:134, fig. 2). This posterior sperm storage region in a mature male *P. glandipedis* male (26.3 mm SL) occupied 23.3% of the area of a mid sagittal testis section. In *P. myersi* the storage area occupied 44.2% of the total testis area while equivalent regions in outgroup glandulocaudine species ranged from 4.3–12.2% (Burns et al. 1995). As reported for *P. myersi* by Burns et al. (1995: table 3) the sperm cell nucleus is spherical to slightly deformed. There appears to be no sperm cell modifications as are found in typical glandulocaudines, but ultrastructure examination was not possible. There were no gill glands as reported in *Corynopoma riisei* Gill by Burns and Weitzman (1996) and other glandulocaudines by Bushmann et al. (2002).

Distribution.—*Planaltina glandipedis* is known from the rio Corumbataí and rio Jacaré-Pepira, both tributaries of the rio Tietê, upper rio Paraná basin, in the State of São Paulo.

Etymology.—The name *glandipedis* is derived from Latin *glandula,* diminutive for

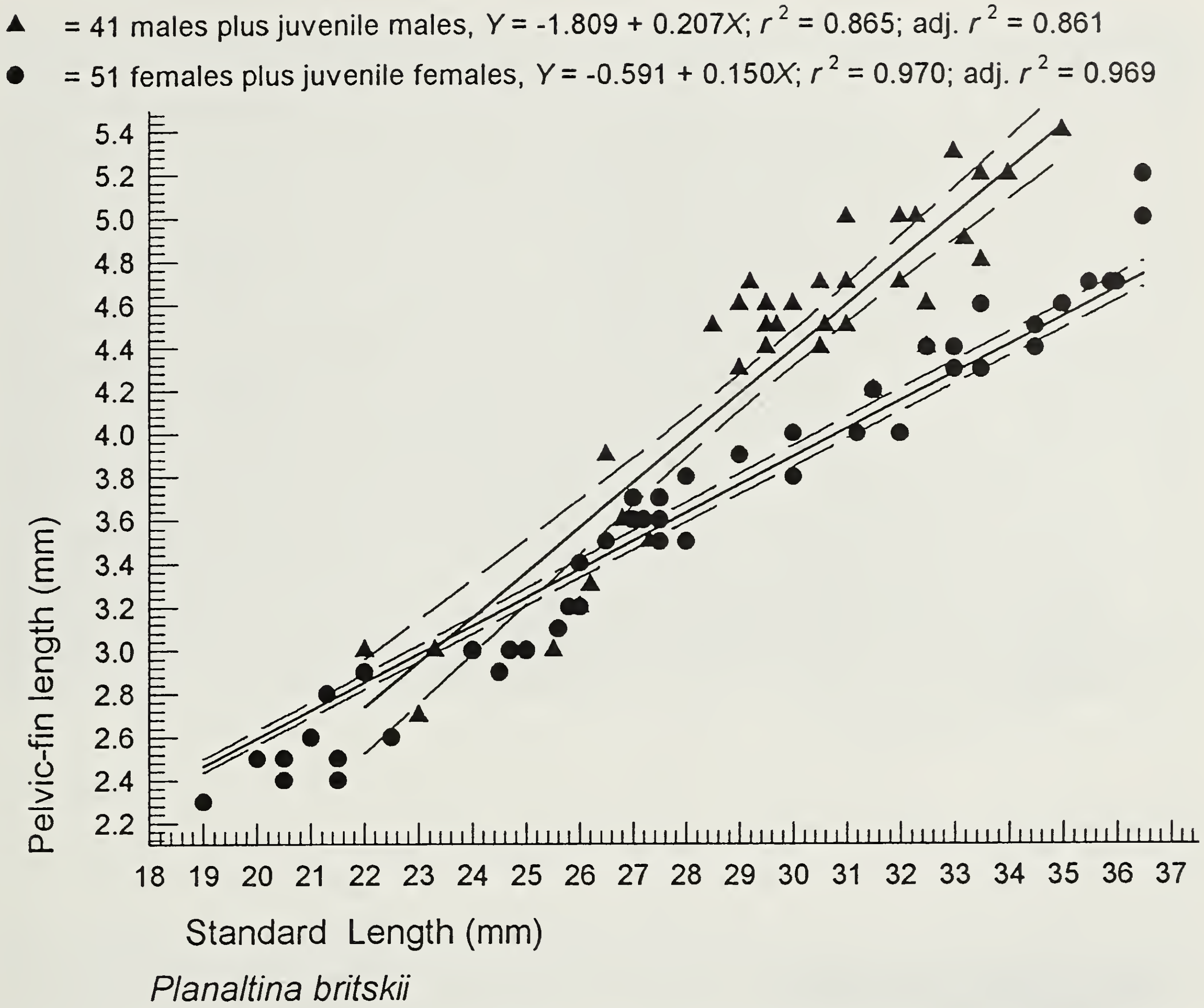

Fig. 18. *Planaltina britskii,* pelvic-fin length as function of SL by sex and maturity. Males and females identified by external features and sometimes by examination of gonads by a slit in right side of body. Sexual maturity according to relative pelvic-fin length in males versus that of females appears to occur by lengths close to 28–29 mm SL. At these lengths male's pelvic fins become longer relative to those of females. Also, at these lengths, male's testes become active.

acorn, hence gland, and *pedis,* Latin for foot, in this case referring to the pelvic fins. A noun in apposition. The name is meant to signify a fish with a pelvic-fin gland or organ.

Planaltina britskii, new species
Fig. 30, Table 3

Specimens examined.—All type specimens are from Brazil, Estado de São Paulo, drainages, tributary to rio Grande or rio Tietê, both tributaries of the rio Paraná or in small streams directly tributary to the rio Paraná.

Holotype.—MZUSP 62757, male, 35.0 mm SL, Município de São José do Rio Preto, córrego da Barra Funda, tributary of rio Preto and tributary of rio Turvo, tributary of rio Grande, approximately, 20°37′S, 49°23′W, 7 Dec. 1998, V. Garutti.

Paratypes.—MZUSP 62758, 5 (33.0–36.5 mm SL) and DZSJRP 668, 7 (immature to adults, 22.0–36.5 mm SL), collected with holotype. Following 4 lots of immature to adult paratypes collected in Município de São José do Rio Preto, córrego da Barra Funda, tributary of rio Preto and then rio Turvo, tributary of rio Grande, approximately 20°37′S, 49°23′W. MZUSP 62759, 4 (17.0–31.0 mm SL), 30 Dec. 1980, V. Ga-

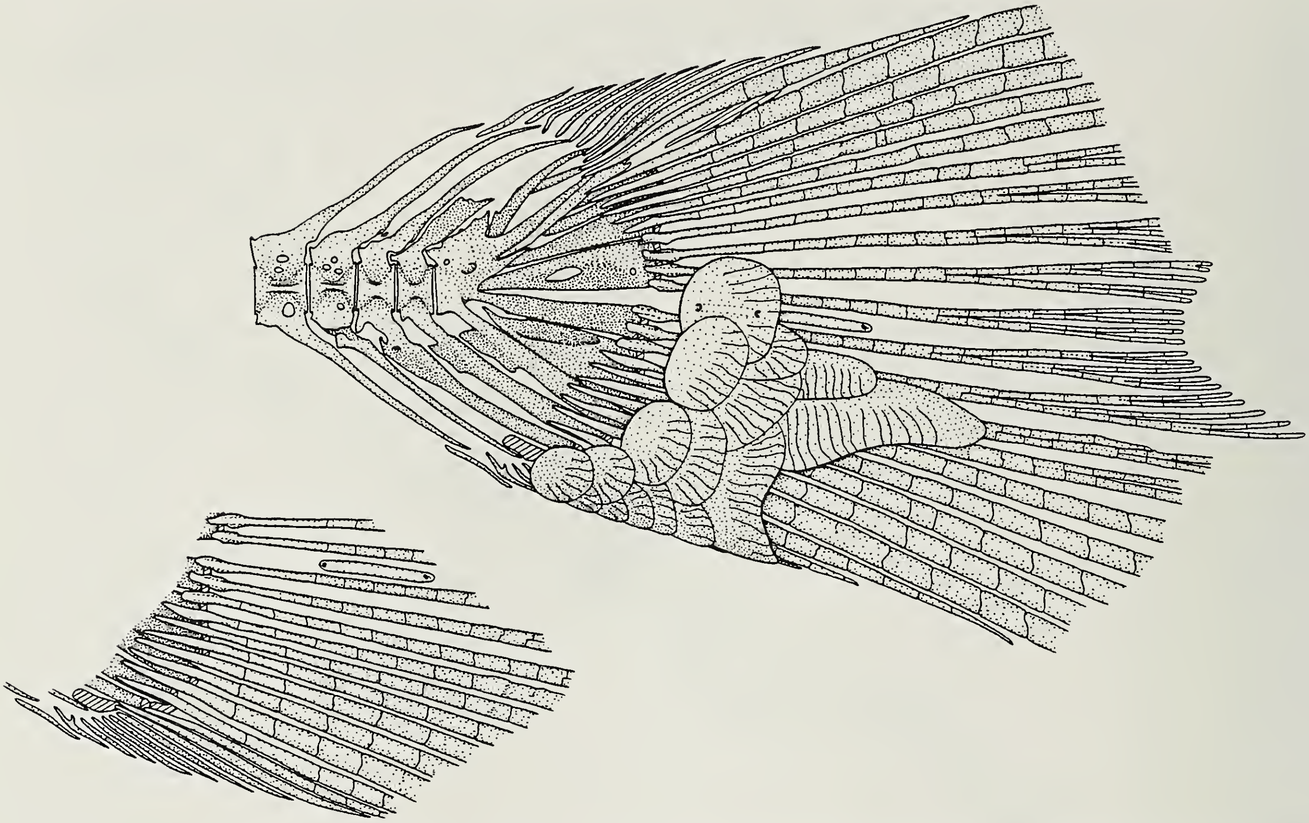

Fig. 19. *Planaltina myersi,* MNRJ 10635, c&s, sexually active male, SL 33.3 mm. Caudal skeleton, lateral view, left side. Inset at left shows modified scales removed.

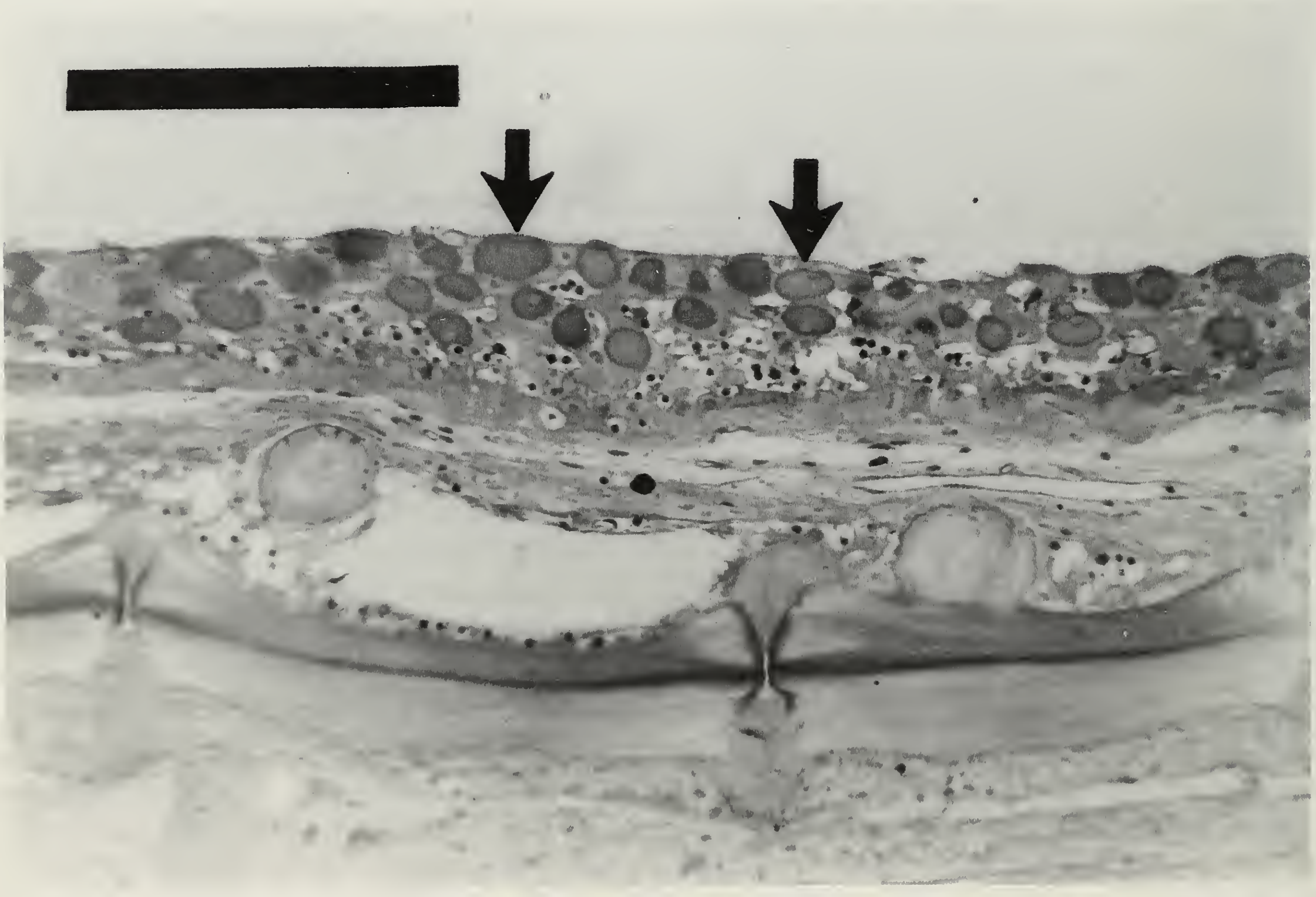

Fig. 20. *Planaltina myersi,* USNM 278966, histological section of pelvic fin showing abundant club cells (arrows), adult male SL 38.3 mm. Bar = 100 μm.

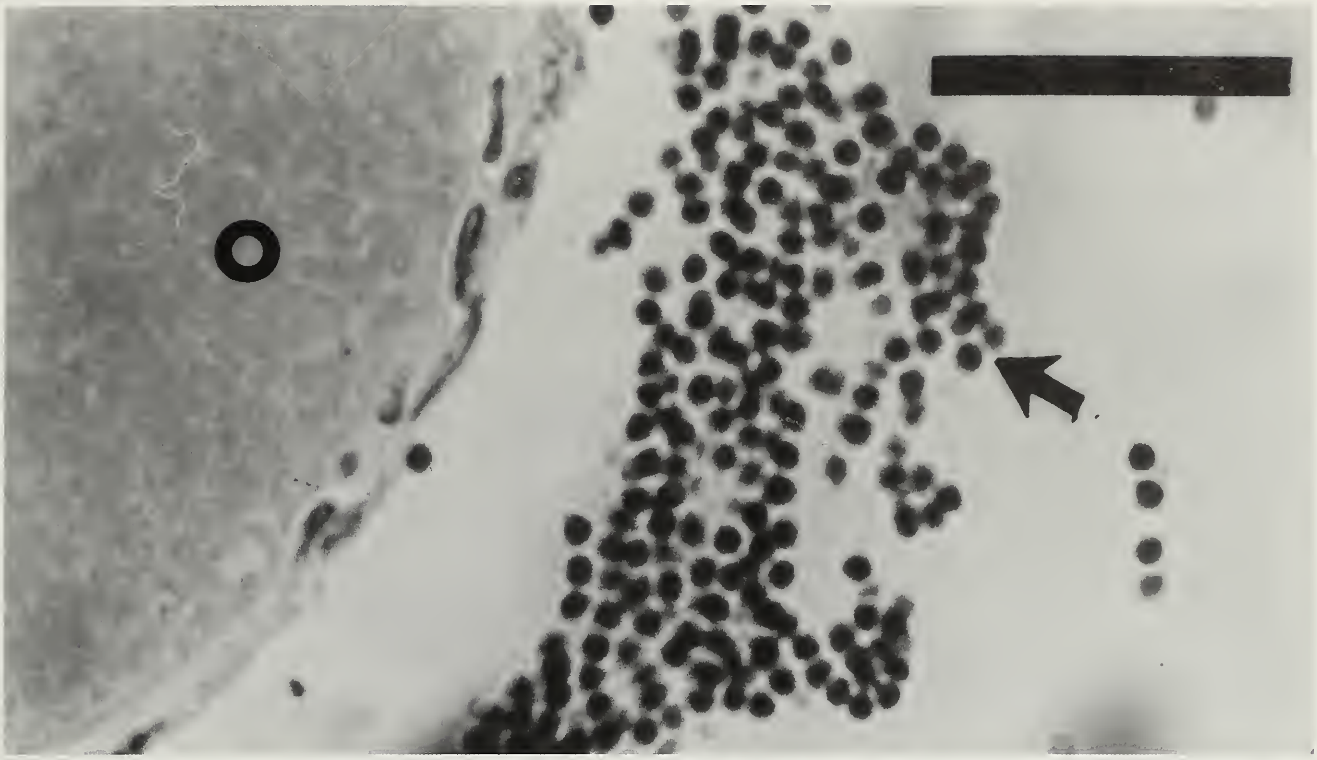

Fig. 21. *Planaltina myersi,* USNM 278989, histological section of ovary of adult female, 35.0 mm SL, arrow points to spermatozoa, o = oocyte cytoplasm. Bar = 20 μm.

rutti & party; DZSJRP 674, 5 (immatures, 26.0–27.0 mm SL), 30 Dec. 1980, V. Garutti & party; MZUSP 26911, 10 (21.0–26.2 mm SL), 4 Jul. 1980, V. Garutti; USNM 362134, 10 (immatures to adults, 25.5–31.2 mm SL), 4 Jul. 1980, V. Garutti. MZUSP 62760, 10 (immatures to adults, 19.0–32.5 mm SL); LIRP 2255, 10 (immatures to adults, 31.5–33.5 mm SL), Município de Auriflama, Fazenda Itapuã, cór-

Fig. 22. *Planaltina glandipedis,* new species, holotype, adult male above, MZUSP 62752, SL 26.2 mm and paratype, adult female below, MZUSP 62753, SL 28.6 mm. Corumbataí, rio Corumbataí, approximately 22°13′S, 47°38′W, Estado de São Paulo, Brazil.

Table 2.—Morphometrics of *Planaltina glandipedis*. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Minimum, maximum, *n*, *X*, and *SD* are based on the holotype, MZUSP 62752, and the following paratype lots: MZUSP 62753, USNM 362135, MZUSP 62754, USNM 362136, MZUSP 62755, USNM 362137, MZUSP 62756, and DZSJRP 671.

		Males				Females			
	Holotype	*n*	Range	*X*	*SD*	*n*	Range	*X*	*SD*
Standard length (mm)	26.2	27	20–28.7	24.0		20	19.7–28.6	24.2	
Body depth at dorsal fin origin	26.7	27	18.6–28.8	23.5	3.0	20	21.8–28.7	24.3	2.0
Snout to dorsal-fin origin	61.5	27	54.4–64.0	58.9	2.6	20	54.7–62.8	59.5	2.5
Snout to pectoral-fin origin	25.6	27	21.4–28.0	24.2	1.6	20	23.0–27.6	24.9	1.1
Snout to pelvic-fin origin	45.8	27	42.4–50.0	45.2	2.0	20	42.1–49.1	45.7	1.7
Snout to anal-fin origin	58.8	27	53.0–64.0	57.7	2.6	20	55.8–61.5	59.0	1.6
Caudal peduncle depth	10.7	27	07.9–12.0	09.9	1.2	20	07.6–11.5	09.9	1.1
Caudal peduncle length	12.6	27	10.6–14.4	12.4	0.9	20	07.6–14.5	12.0	1.6
Pectoral-fin length	26.7	27	20.6–26.9	23.4	1.2	20	21.8–26.4	23.4	0.1
Pelvic-fin length	14.5	27	12.5–14.5	13.4	0.5	20	11.2–14.4	12.5	0.7
Dorsal-fin base length	09.9	26	08.0–12.0	09.8	0.1	20	08.2–12.7	10.0	1.2
Dorsal-fin height	19.8	27	15.9–22.4	19.6	1.7	20	17.2–22.1	19.7	1.3
Anal-fin base length	29.3	27	26.5–32.8	29.0	1.6	20	26.0–33.2	28.7	2.0
Anal-fin lobe length	17.9	27	13.6–19.5	17.2	1.6	20	13.0–20.4	17.3	1.8
Eye to dorsal-fin origin	46.9	27	43.1–49.6	46.0	2.1	20	43.0–50.0	46.5	1.6
Dorsal-fin origin to caudal-fin base	38.2	27	36.3–42.0	39.3	1.5	20	36.4–40.7	38.7	1.1
Bony head length	24.8	27	21.6–25.8	23.3	1.2	20	21.5–25.4	23.3	1.1
Horizontal eye diameter	35.4	27	35.4–42.6	38.9	1.8	20	33.8–42.6	38.7	2.1
Snout length	23.1	27	17.0–26.9	21.0	2.5	20	17.8–25.4	21.9	2.6
Least interorbital width	33.8	27	27.0–34.9	30.8	2.1	20	26.7–36.2	31.5	2.6
Upper jaw length	43.1	27	37.0–44.8	40.7	2.1	20	38.6–44.0	41.3	1.4

rego do Limoeiro, tributary of rio São José dos Dourados, tributary of rio Grande, 20°33′32.9″S, 50°35′29″W, altitude 350 m, 28 Jul. 1999, Ricardo M. C. Castro & party. MZUSP 62761, 6 (29.5–35.0 mm SL). DZSJRP 656, 7 (immatures to adults, 22.0–29.2 mm SL), José Bonifacio, km 88 of road BR-153, stream ultimately tributary to rio Tietê, approximately 21°03′S, 49°41′W, 12 Feb. 1988, D. Brandão & party. MZUSP

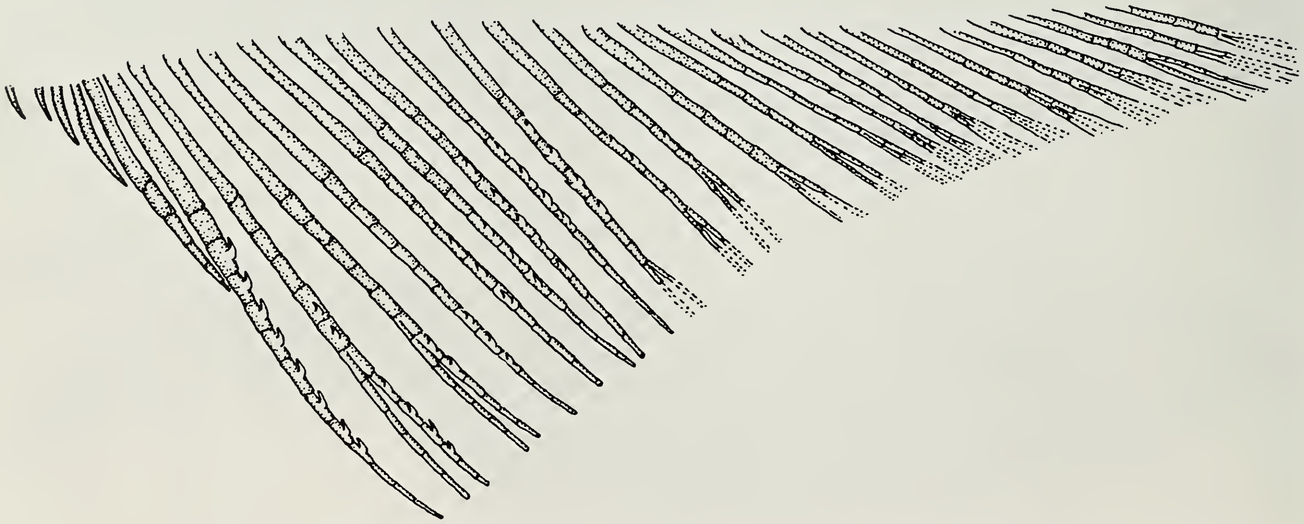

Fig. 23. *Planaltina glandipedis*, USNM 362385, c&s, sexually active male, SL 24.3 mm. Anterior portion of anal fin, left side. Figure shows anal-fin hooks positioned along posterolateral border of anal-fin rays, larger more posterior hooks bent dorsoanteriorly.

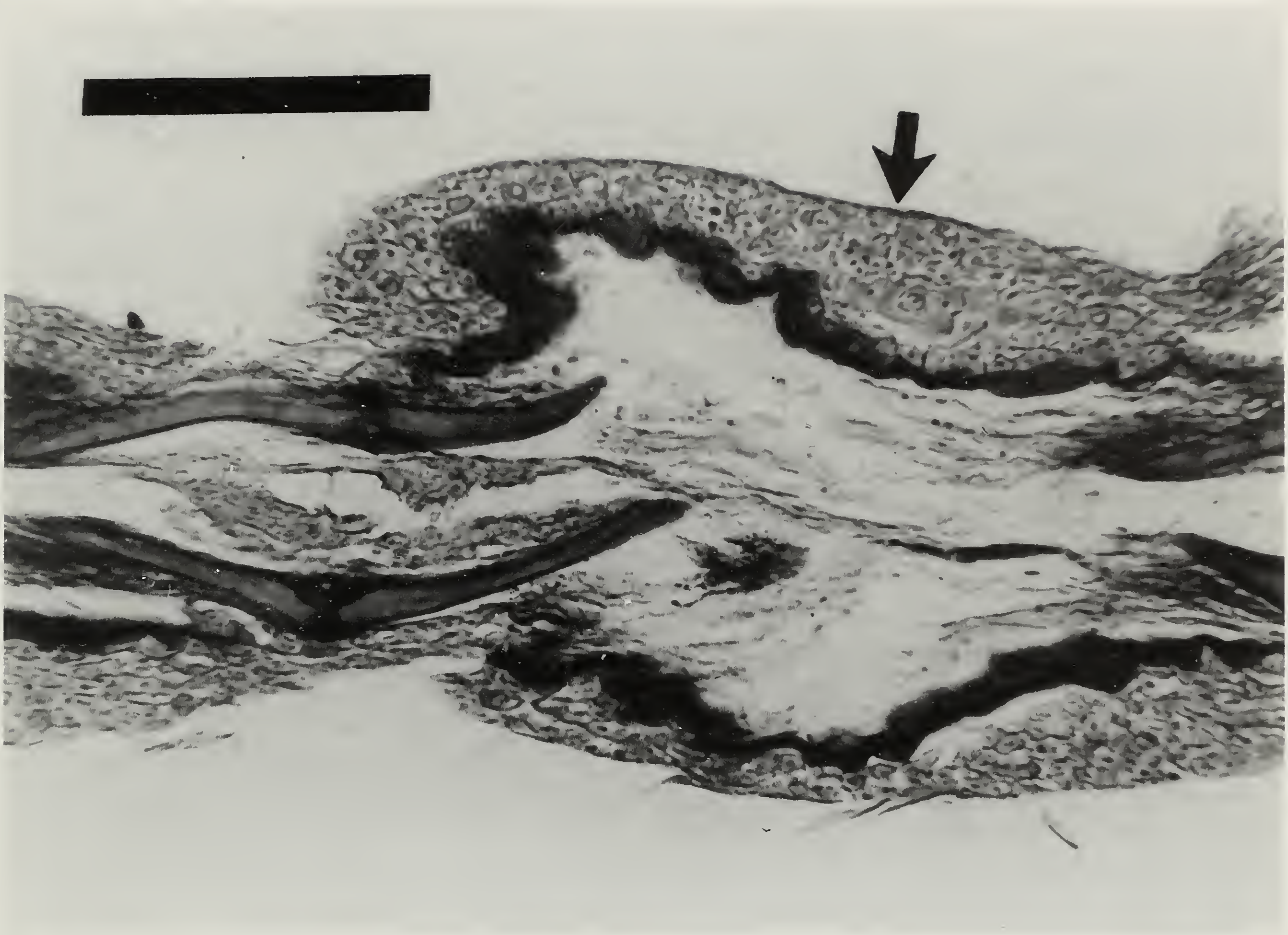

Fig. 24. *Planaltina glandipedis*, USNM 362136, histological section through anterior anal fin of mature male, SL 26.3 mm. Arrow indicates thickened epithelium. Bar = 100 μm.

62762, 3 (immatures to adults, 30.0–33.5 mm SL); DZSJRP 670, 3 (adults, 27.5–30.0 mm SL), Município de Mirassolândia, Macaúbas, approximately 20°34′S, 49°28′W, 30 Apr. 1988, Marcelo Garcia. MZUSP 27138, 2 (immatures, 18.5 and 20.5 mm SL). USNM 367195, 1 (27.3 mm SL), Miguelópolis, represa de Volta Grande, rio Grande, approximately 20°12′S, 48°07′W, 6–7 Nov. 1975, CETESB. MZUSP 62763, 4 (immatures, 21.5–23.3 mm SL), Conchal, rio Mogi-Guaçu, tributary of rio Tietê, approximately 22°19′S, 47°07′W, 20 Apr. 1997, Flavio C. T. Lima & party. MZUSP 62764, 2 (immatures, 27.2 and 29.5 mm SL), Corumbataí, rio Corumbataí, tributary of rio Piracicaba, tuibutary of rio Tietê, approximately 22°13′S, 47°38′W, 25 Jan. 1976, Heraldo A. Britski.

Non-type material.—MZUSP 62808, 4 (adults, 27.5 and 31.5 mm SL), Ilha Solteira, rio Paraná, approximately 20°23′S, 51°167′W, Sept. 1965. LIRP 2256, 1 (adult, 32.0 mm SL), Município de Olimpía, Córrego das Laranjeiras 20°44′11.3″S, 49°02′50.3″W, 15 July 2001, Ricardo M. C. Castro & party. LIRP 2257, 2 (immatures, 22.3 and 27.0 mm SL), Município de Guapiaçu, Córrego do Modesto, 20°43′52.4″S, 49°14′35.5″W, 14 July 2001, Ricardo M. C. Castro & party.

Definition.—*Planaltina britskii* and *P. glandipedis* sympatric in rio Corumbataí drainage and both with a scale arrangement on dorsal border of pouch scale different from that of *P. myersi* (key above and compare Figs. 19, 28, 33a, b). These two species readily distinguished from each other by characters provided in key and in definitions of *P. myersi* and *P. glandipedis*.

Description.—Morphometric data presented in Table 3. Description based on all

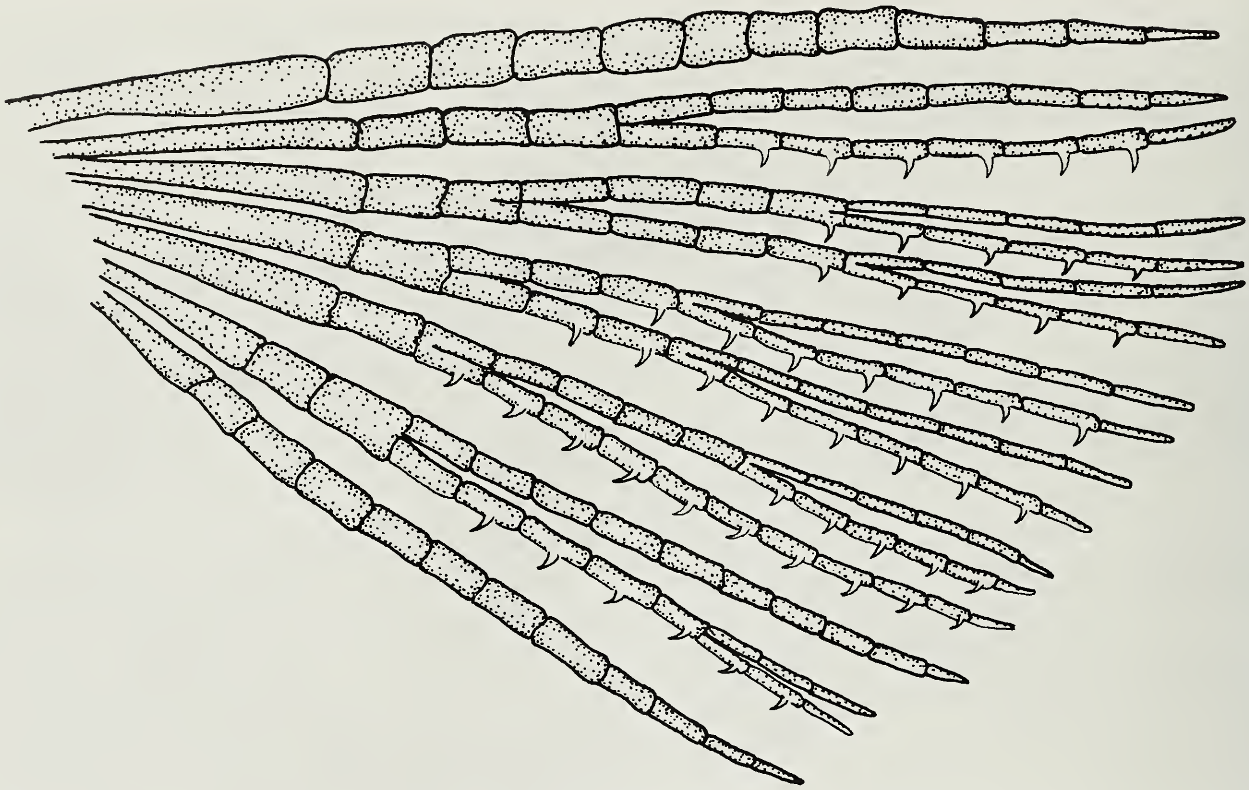

Fig. 25. *Planaltina glandipedis,* USNM 362135, c&s, sexually active male, SL 24.3 mm, pelvic-fin rays, left side. Ventral surface showing pelvic-fin hooks.

lots since no significant differences found among them.

Body compressed and slender; greatest body depth located slightly anterior of dorsal-fin origin at vertical crossing pelvic-fin origin. Dorsal body profile slightly convex from tip of snout to dorsal-fin origin, almost straight from this point to anterior to caudal peduncle and slightly concave dorsal to caudal peduncle. Dorsal-fin origin nearer to caudal-fin base than to snout tip. Ventral body profile convex from tip of lower jaw to anal-fin origin, almost straight from this point to posterior end of anal-fin base and slightly concave ventral to caudal peduncle.

Snout conical, shorter than orbital diameter. Mouth subterminal, lower jaw included in upper when mouth closed. Maxilla ventrally convex, extending posteriorly to vertical line crossing anterior border of pupil of eye.

Dorsal-fin rays ii, 8 (with posteriormost ray unbranched in all but two specimens in which count appears as ii, 9 but is actually ii, 8), n = 90. Adipose fin present. Anal-fin rays iv, 21 (iv or v, usually iv, unbranched rays, branched rays X = 21.3, range 19–24, n = 90). Anterior anal-fin lobe weakly developed and including fourth and/or fifth unbranched rays and first 6–7 branched rays. Anterior part of anal fin in sexually mature males with bilateral hooks on anterior fourth or fifth unbranched and anterior 9–10 branched rays (Fig. 31). Pectoral-fin rays i, 11 (anterior unbranched ray i in all specimens; branched rays X = 10.4, range 9–11, n = 90). Distal tips of longest pectoral-fin rays not reaching pelvic-fin origin in juveniles, just extending to pelvic-fin origin in immatures and slightly beyond pelvic-fin origin in adult specimens; pectoral fin about same relative length in both sexes and without hooks. Pelvic-fin rays i, 6 (posteriormost ray unbranched in most specimens, branched in 2 adult males, n = 90). Sexually mature males with hooks present on rays of pelvic fin, distributed as in Fig. 32. Number of hooks per ray varying among males; in mature male (43.0 mm SL) no hooks present on first branched ray,

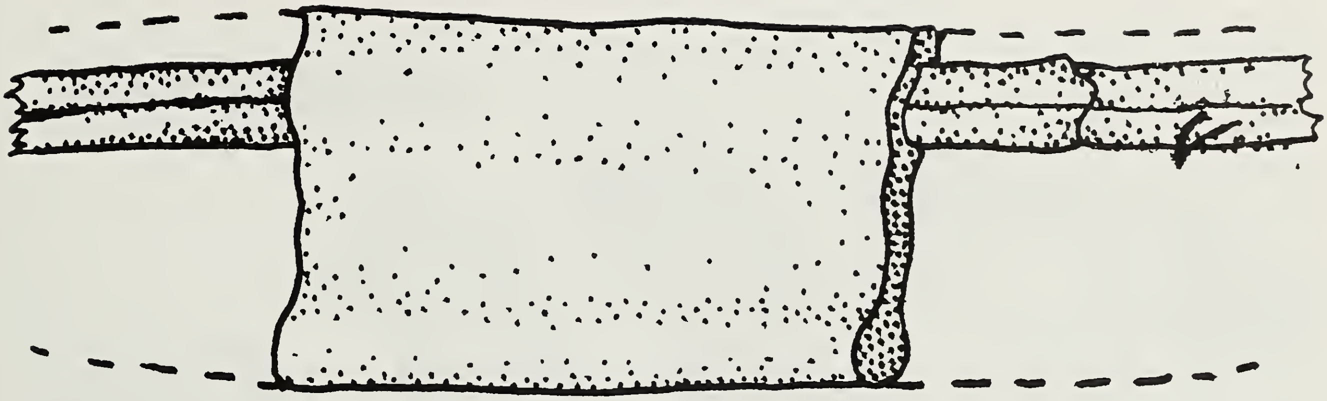

Fig. 26. *Planaltina glandipedis* drawing of a section of the ventral external surface of pelvic-fin glandular pads of a sexually active male, USNM 362135, SL 24.3 mm. The fin ray section displays its two halves or lepidotrichs and the proximal portion of this ray extends to the left and the distal portion extends to the right. A hook, at the right, is shown extending ventrally from the surface of the ventral lepidotrich. The fold of tissue extending ventrally from the fin ray constitutes a section of this particular ray's glandular pad. The ventral dashed lines extending to the right and left of the fold of tissue indicate the continuation of the ventral border of the fold or pad that has been cut away. The dorsal dashed lines are continuous with the area where the pad of tissue has been cut from the membrane that extends between the pelvic-fin rays adjacent to the illustrated ray.

25 present on second, 23 on third, 30 on fourth, and 15 on fifth branched ray of right pelvic fin. Pelvic fins of adult males longer than those of females (Fig. 18); distal tips of longest pelvic-fin rays of males extending slightly beyond anal-fin origin, but falling short of anal-fin origin in adult females. See discussion under "*Sexual dimorphism*" for explanation of Fig. 18 and pelvic-fin length differences between males and females. Principal caudal-fin rays 10/9, n = 90.

Scales cycloid with few radii (3–5) along posterior border, more numerous and conspicuous on enlarged scales bordering dorsal edge of pouch opening (Fig. 33a).

Lateral line complete, perforated scales 38 (X = 39.9, range 38–42, n = 55). Predorsal scales 14 (X = 15.2, range 14–16, n = 73). Scale rows between dorsal-fin origin and lateral line 5 (n = 75). Scale rows between anal-fin origin and lateral line 4 (n = 75). Scale rows around caudal peduncle 13 (X = 13.1, range 12–14, n = 54).

Premaxillary teeth in two distinct rows. Outer row of premaxillary teeth tricuspid, inner row pentacuspid. Outer row teeth 3 (X = 3.4, range 2–5, n = 90). Inner row teeth 4 (X = 4.0, range 4–5, n = 90). Maxillary teeth 2 (X = 1.7, range 1–3, n = 90). Maxillary teeth tricuspid, first usually larger than remaining. Dentary with 4 large anterior pentacuspid teeth in all specimens, n = 90 and 6 (X = 6.2, range 4–9, n = 90) slightly tricuspid to nearly unicuspid teeth posteriorly. Premaxillary, maxillary and dentary teeth compressed.

Vertebrae 38 (X = 38.7, range 38–41, n = 41). Upper limb gill-rakers 6 (X = 5.8, range 4–7, n = 88); lower limb gill-rakers 12 (X = 11.8, range 11–13, n = 89). Branchiostegal rays 4 in 2 cleared and stained specimens, 3 rays originating from anterior ceratohyal and 1 ray from posterior ceratohyal.

Color in alcohol.—Males and females displaying an identical color pattern in preserved specimens (Fig. 30). Body light brown, darker on dorsum and top of head. Lateral body stripe dark with silvery reflections, especially along ventral region due to deposits of guanine. This stripe beginning anteriorly as thin line at dorsal region of opercle and widens progressively towards caudal-fin base, reaching a maximum width at caudal peduncle, where it narrows and extends dorsal to enlarged dorsal pouch scales and onto median caudal-fin rays. Dark chromatophores present on dorsal body surface, mostly concentrated along

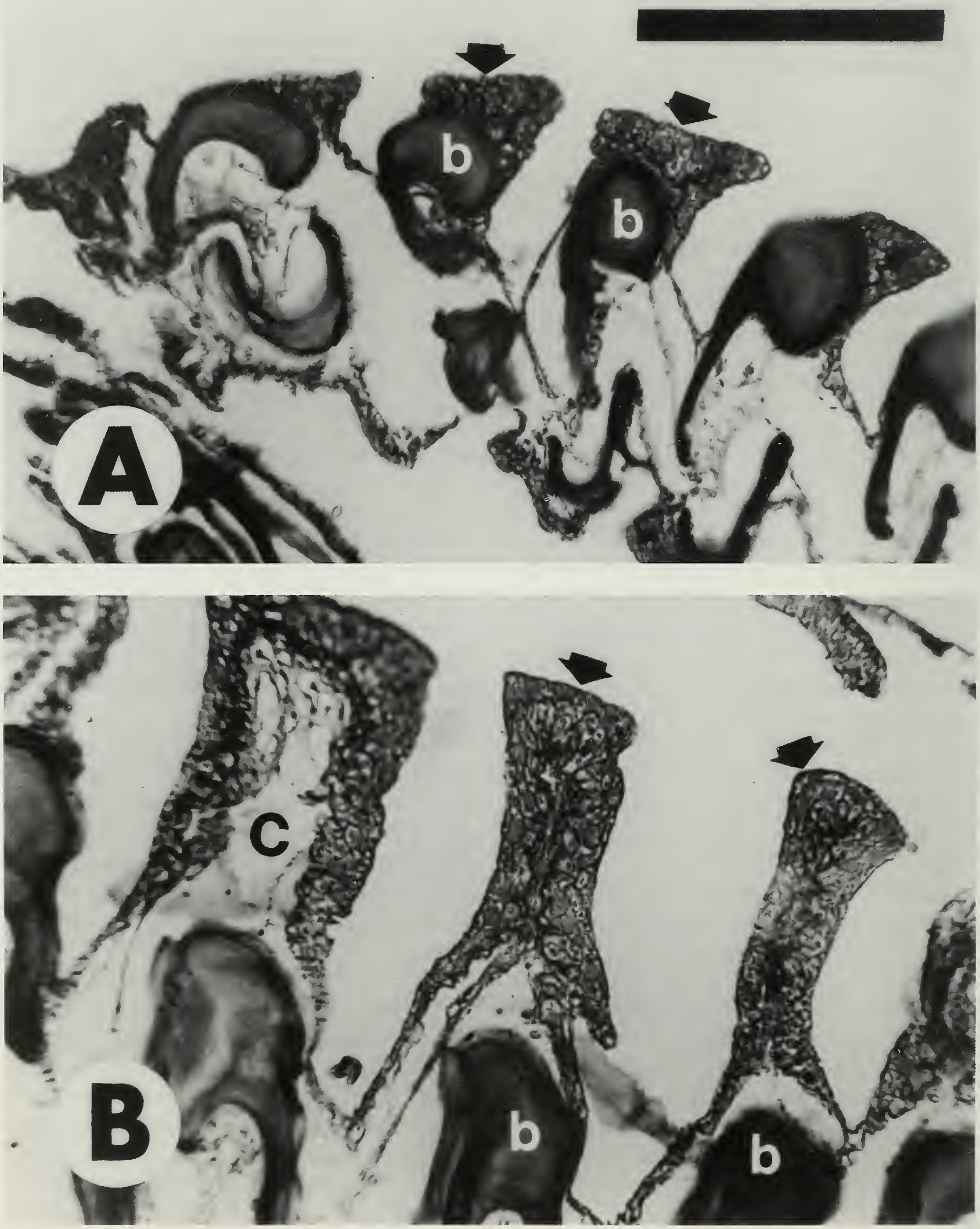

Fig. 27. *Planaltina glandipedis,* USNM 362136; A, histological cross sections of pelvic fins of female SL 27.0 mm and B, glandular pads of the male SL 26.3 mm. Arrows indicate epithelium covering pelvic-fin rays, b = bone of fin rays; c = expanded connective tissue of male. Bar = 100 μm.

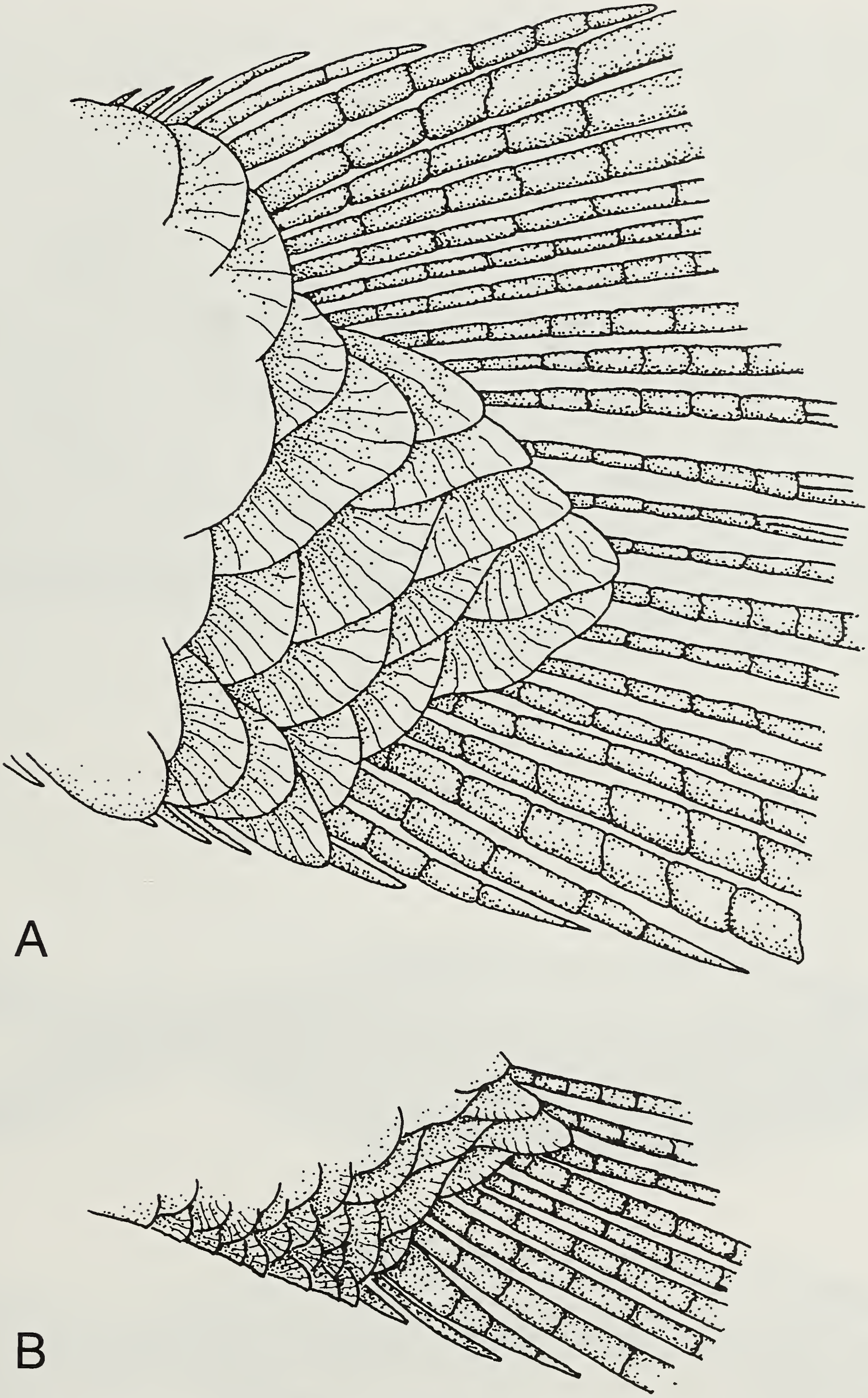

Fig. 28. *Planaltina glandipedis*, A, USNM 362135, c&s, sexually active male, SL 26.9 mm. Caudal skeleton, lateral view, left side; B, USNM 362135, c&s, sexually active female, SL 24.5 mm. Caudal skeleton, lateral view, left side.

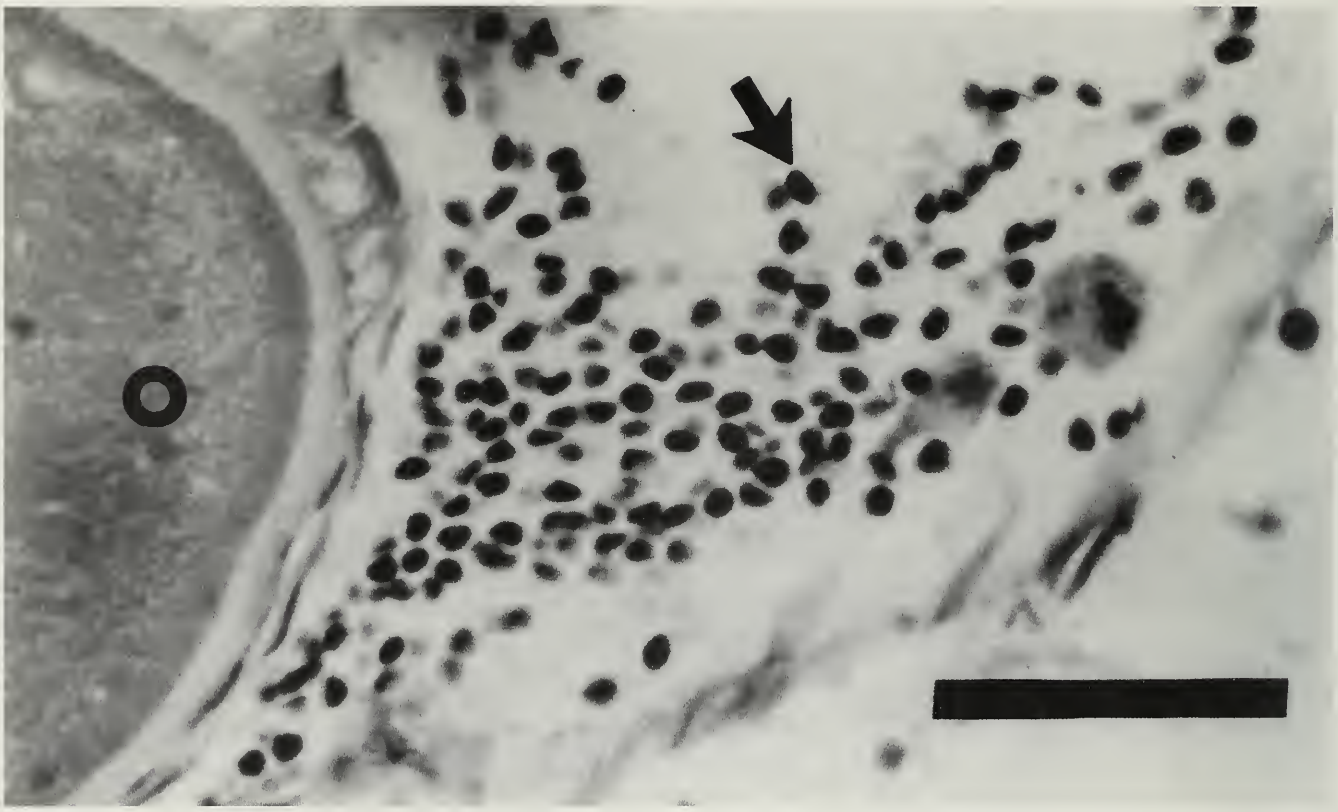

Fig. 29. *Planaltina glandipedis,* USNM 362136, histological section of ovary of adult female SL 27.0 mm. Arrow indicates spermatozoa; O = oocyte cytoplasm. Bar = 20 μm.

Fig. 30. *Planaltina britskii,* new species, holotype, adult male above, MZUSP 62757, SL 35.0 mm, and paratype and adult female, MZUSP 62758, SL 36.5 mm; córrego da Barra Funda, tributary of rio Preto and tributary of rio Turvo, tributaries to rio Grande, Município de São José do Rio Preto, approximately 20°37′S, 49°23′W, Estado de São Paulo, Brazil.

Table 3.—Morphometrics of *Planaltina britskii,* new species. Standard length is expressed in mm; measurements through head length are percentages of standard length; the last four entries are percentages of head length. Minimum, maximum, *n, X,* and *SD* are based on the holotype, MZUSP 62757, and the following paratype lots: MZUSP 62758, DZSJRP 668, MZUSP 62759, DZSJRP 674, MZUSP 26911, USNM 362134, MZUSP 62758, LIRP XXX, MZUSP 62761, DZSJRP 656, MZUSP 62762, DZSJRP 670, USNM 367195, and MZUSP 62763.

		Males				Females			
	Holotype	*n*	Range	*X*	*SD*	*n*	Range	*X*	*SD*
Standard length (mm)	35.0	39	22.0–35.0	29.7		50	19.0–36.5	28.3	
Body depth at dorsal fin origin	22.9	39	18.6–25.0	22.5	1.8	50	16.9–25.5	22.2	2.5
Snout to dorsal-fin origin	59.1	39	53.8–61.9	57.9	1.8	50	55.3–61.0	58.3	1.5
Snout to pectoral-fin origin	23.7	39	22.3–26.8	24.2	1.0	50	22.4–27.3	24.4	1.0
Snout to pelvic-fin origin	46.6	39	42.9–50.9	45.6	1.8	49	42.8–51.1	46.5	1.8
Snout to anal-fin origin	60.0	39	53.6–63.5	59.1	1.8	50	54.7–65.7	60.2	2.1
Caudal peduncle depth	09.7	39	07.7–10.3	09.2	0.7	50	06.5–10.0	08.8	0.8
Caudal peduncle length	14.3	39	10.0–14.3	12.3	1.1	50	09.7–14.1	12.1	1.1
Pectoral-fin length	21.7	39	18.2–22.9	20.6	1.0	50	18.3–22.5	20.6	1.0
Pelvic-fin length	15.4	39	11.7–16.1	14.5	1.3	50	11.2–14.3	12.8	0.7
Dorsal-fin base length	09.7	39	08.5–11.3	10.0	0.8	50	08.0–11.7	09.9	0.7
Dorsal-fin height	19.1	37	17.6–20.6	19.2	0.7	48	17.5–20.2	18.9	0.6
Anal-fin base length	28.0	39	25.0–31.0	28.0	1.6	50	24.4–31.8	27.5	1.4
Anal-fin lobe length	16.3	38	15.2–18.9	16.9	0.9	50	14.6–19.2	17.1	1.1
Eye to dorsal-fin origin	47.1	39	41.5–49.4	45.2	1.6	50	41.3–48.6	45.6	1.7
Dorsal-fin origin to caudal-fin base	42.3	39	38.6–44.3	41.1	1.4	50	37.2–45.3	40.5	1.7
Bony head length	23.4	39	21.6–25.7	23.6	0.8	50	21.5–25.0	23.6	0.9
Horizontal eye diameter	36.6	39	34.9–41.8	37.7	1.6	50	34.5–41.8	38.0	1.9
Snout length	26.8	39	21.7–30.5	26.3	2.1	50	22.0–30.8	26.3	1.9
Least interorbital width	34.1	39	27.1–34.7	31.6	1.8	50	23.1–35.4	31.6	2.5
Upper jaw length	42.7	39	36.4–45.5	41.4	2.4	50	34.7–44.8	40.9	2.3

exposed borders of scales. Scattered dark chromatophores on snout, tip of lower jaw, and below eye. Inconspicuous patch of dark chromatophores present dorsal to anterior half of anal fin, extending ventrally onto most of anal fin.

Fins hyaline except faint scattered dark chromatophores present on basal portion of dorsal fin and upper and lower lobes of caudal fin. Most of iris, as well as circumorbital, and opercular bones silvery.

Color in life.—Unknown.

Sexual dimorphism, mode of reproduction and gonad anatomy.—The typical hooks on the anal and pelvic fins of males are represented in Figs. 31 and 32. These

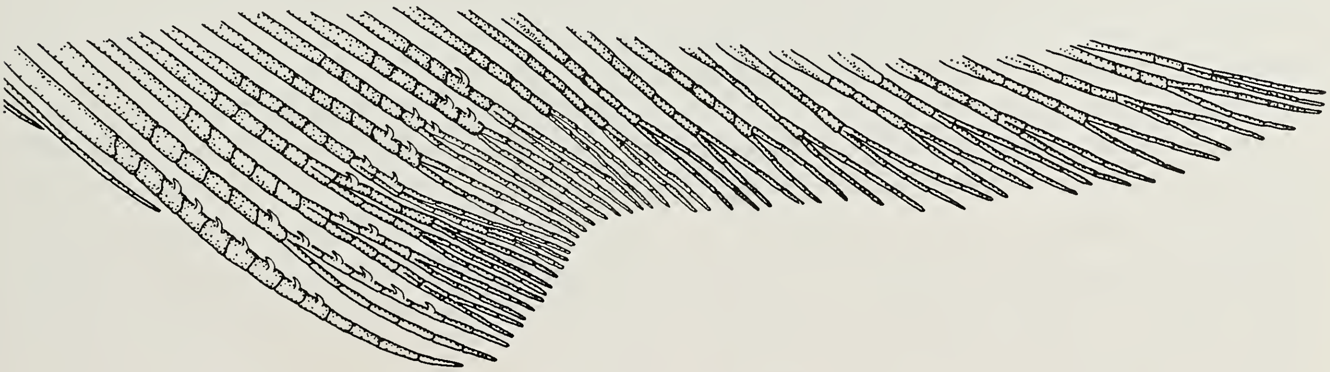

Fig. 31. *Planaltina britskii,* USNM MZUSP 62758, c&s, sexually active male, SL 35.6 mm. Anal fin, left side. Figure shows anal-fin hooks positioned along posterolateral border of anal-fin rays, hooks curved dorsoanteriorly.

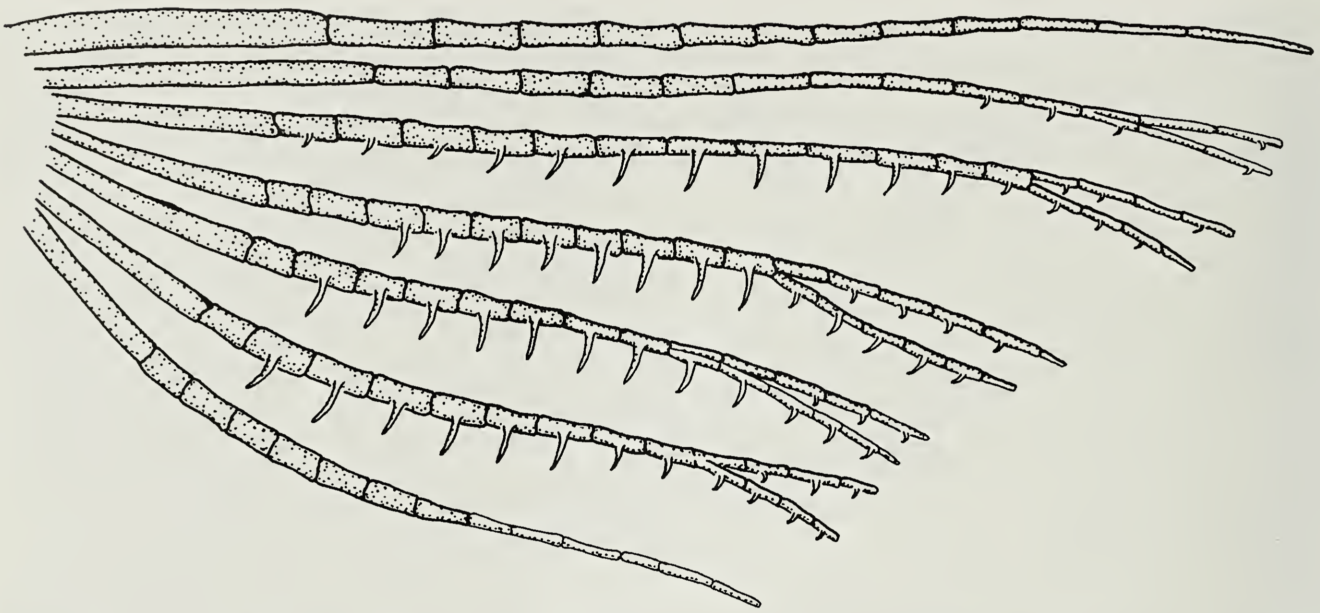

Fig. 32. *Planaltina britskii,* MZUSP62758, c&s, sexually active male, SL 35.6 mm. Pelvic-fin rays, left side. Ventral surface showing elongate narrow pelvic-fin hooks.

are absent on the pelvic and anal fins of females. Adult males have pelvic fins longer than adult females (see Fig. 18).

In our population samples males and females occur in equal length ranges, but very few adult females show the typical elongated scales on the dorsal border of the pouch opening that is present on the caudal fin of males of comparable lengths. The elongated scale pattern on the dorsal border of the pouch opening of adult males (illustrated in Fig. 33a) is present even in immature males of 30.0 mm in SL, but mature females in the size range between about 28.0 and 34.0 mm SL have the scales on the dorsal border of the pouch opening only slightly modified (see Fig. 33b). This suggests that the full elongation of scales on the dorsal border of the pouch opening in females is attained at comparatively longer sizes than in males.

A description of the ultrastructure of the sperm cell is not available. Histological analysis of mature ovaries revealed the presence of spermatozoa within the ovarian cavity (Fig. 34). Upon dissection, the testes of the only male specimen available for histological analysis (Fig. 35) were relatively thin, suggesting that it was not fully mature (holotype, MZUSP 62757, 35.0 mm SL). However, a distinct posterior sperm storage region was present in the testis, occupying 13.1% of the total testis area in a mid-sagittal section. This is slightly larger than the percent area range (4.3–12.7%) for the outgroup glandulocaudine species in the study of Burns et al. (1995:134, fig. 2). Considering that this male was not fully mature, a distinct posterior sperm storage region comparable to that found in the other *Planaltina* species probably occurs in *P. britskii.* As reported for *P. myersi* by Burns et al. (1995: table 3) the sperm cells are typical aquasperm with the cell nuclei spherical to slightly deformed. There appears to be no sperm cell modifications as are found in typical glandulocaudines. A gill gland, comparable to that seen in *P. myersi* (Bushmann et al. 2002) was present in the holotype (Fig. 36).

Data from Garutti (1983) indicate that in córrego da Barra Funda the main reproductive period of the species is coincident with that area's rainy season, September through March, incidentally also the longest photo period of the year. The majority of the males and females, 98.3%, collected during the dry season, April through August, had undeveloped testes and ovaries, but 82.2% of the specimens of both sexes collected

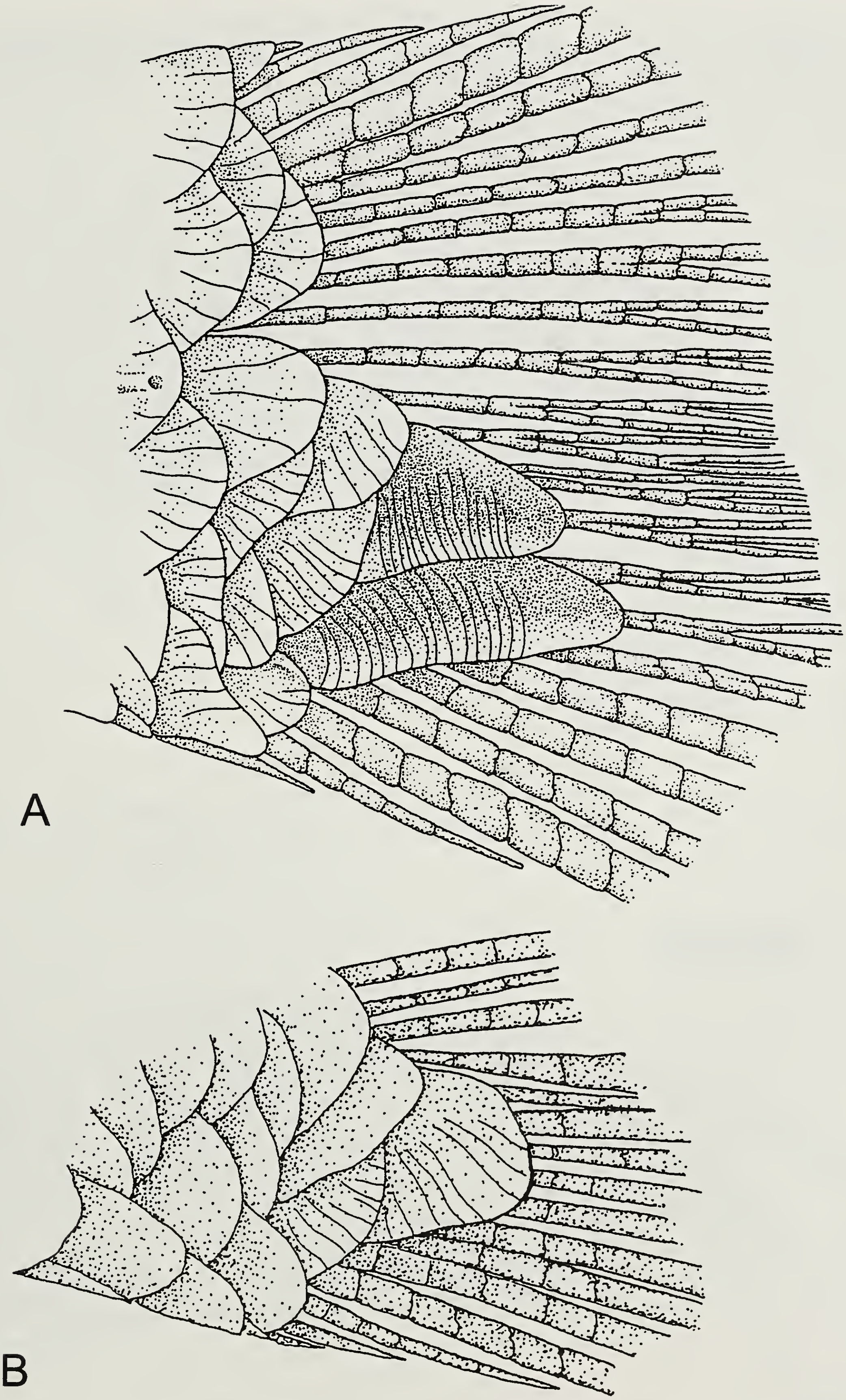

Fig. 33. *Planaltina britskii,* MZUSP62758, A, c&s, sexually active male, SL 35.1 mm. Caudal skeleton, lateral view, left side; B, sexually active female, SL 33.8 mm. Caudal skeleton, lateral view, left side.

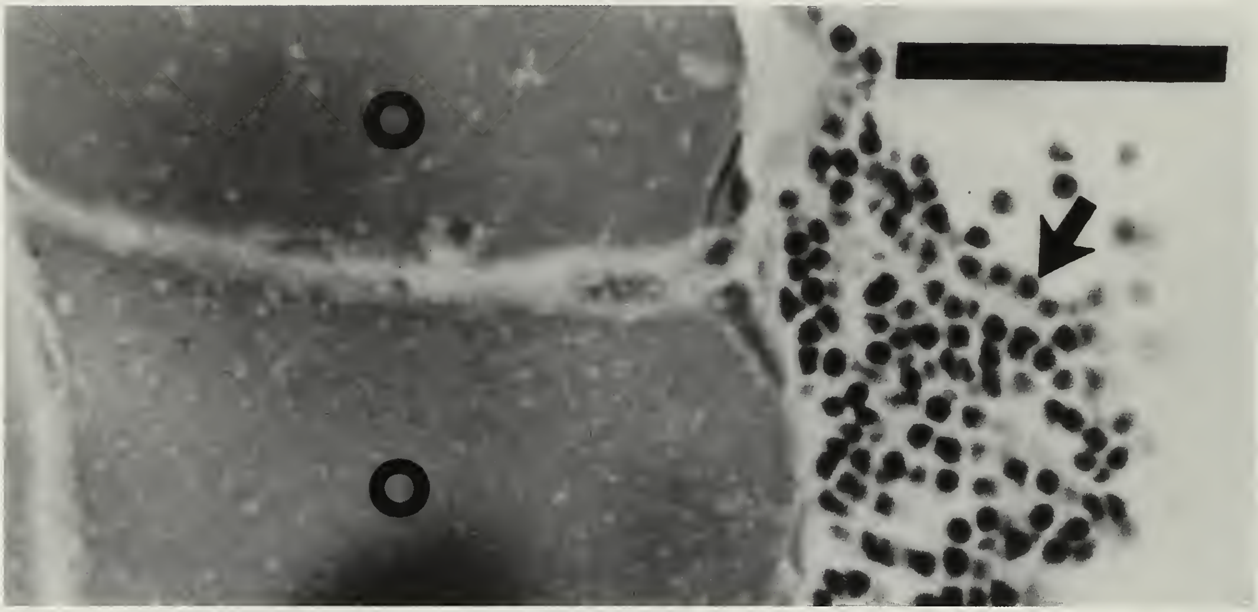

Fig. 34. *Planaltina britskii,* MZUSP 26911, histological section of ovary of an adult female SL 32.0 mm. Arrow indicates spermatozoa; O = oocyte cytoplasm. Bar = 20 μm.

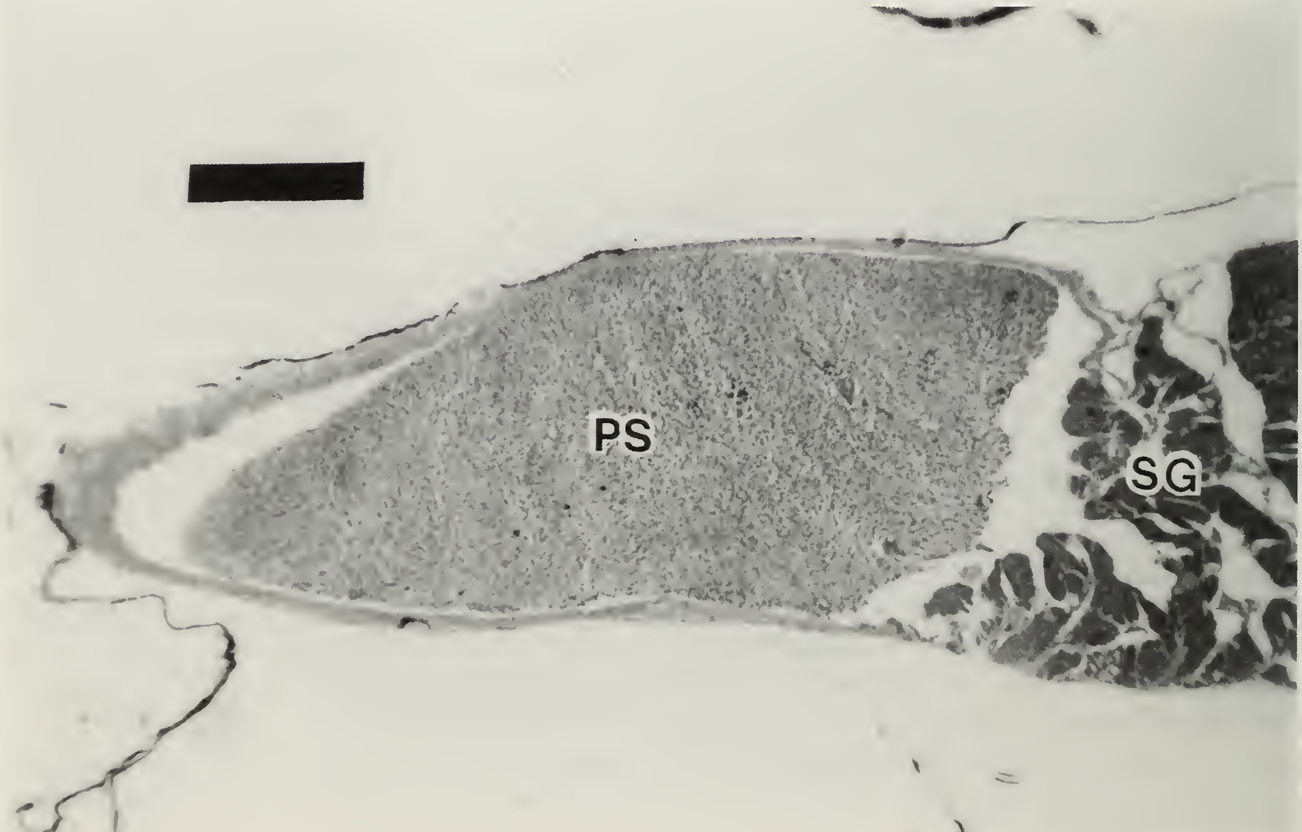

Fig. 35. *Planaltina britskii,* MZUSP 62757, holotype, SL 35.0 mm, mid-sagittal histology section through posterior testis showing more anterior spematogenic regions (SG) and posterior sperm storage region (PS). Bar = 200 μm.

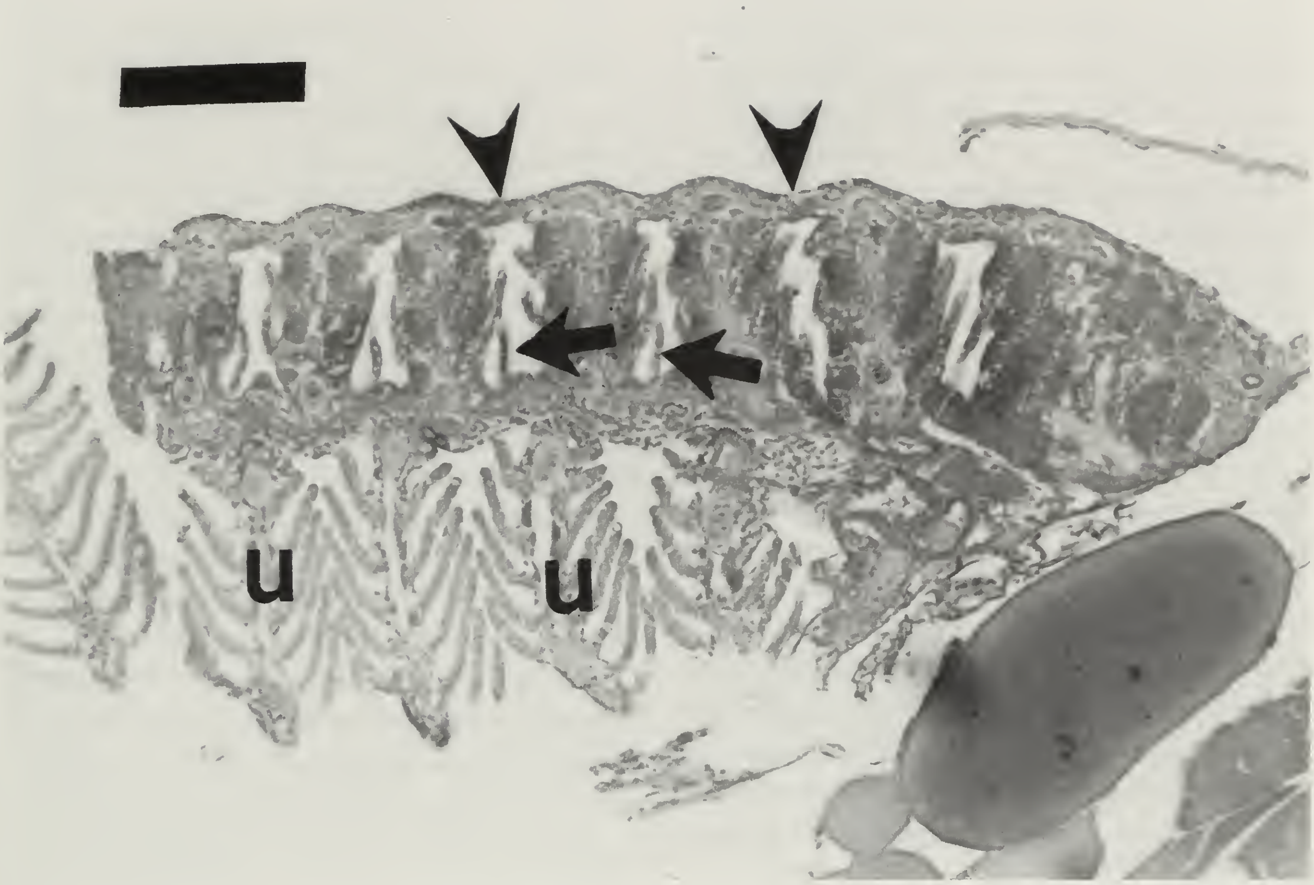

Fig. 36. *Planaltina britskii,* holotype MZUSP 62757, holotype, SL 35.0 mm, frontal histological section through anteriormost gills showing gill gland with its epithelial covering (arrowheads) and reduced secondary lamellae (arrows) within gill gland chambers which number nine. Unmodified gills (u) with secondary lamellae of usual length also shown. Bar = 100 μm.

during the rainy season were mature, the males having well-developed testes and the females well-developed oocytes. Garutti also found that the males reach larger sizes than the females.

Ecology.—The population sample from Córrego do Limoeiro, rio São José dos Dourados sub-basin (MZUSP 62760 and LIRP 2255) was collected in a fourth order stream running in gallery forest represented by old cerrado vegetation. The stream width varied from 2.3–3.2 meters and the water depth from 0.07–0.08 meters. Rapids and small pools were found along the stream and the bottom consisted mostly of sand. Marginal vegetation was mostly represented by palm trees (Arecaceae), ferns (Pteridophyta) and lichens. At the time of collecting activities the following data were taken: air temperature 35.5°C, water temperature 21.5°C, pH = 7.24, dissolved oxygen = 9.6 mg/l, and conductivity = 125.5 S/cm.

Other species taken at this site were: *Astyanax bimaculatus, Astyanax eigenmanniorum, Moenkhausia sanctaefilomenae, Piabina argentea, Characidium* sp., *Hypostomus ancistroides, Hypostomus* sp., *Sternopygus macrurus* and *Poecilia reticulata.*

The populations samples from córrego da Barra Funda, rio Preto sub-basin (MZUSP 62757, 62758, 62759, 26911, DZSJRP 647 and USNM 362134), were all collected near the mouth where this stream empties into a larger stream called ribeirão da Barra Grande at an altitude of about 440 meters. According to Garutti (1983) the collecting site included a circular pool approximately 8 meters in diameter with a maximum depth of 2 meters. The pool lacked marginal vegetation. Rapids occurred downstream from the pool and ran through a gallery forest to a pool of the ribeirão da Barra Grande. The maximum stream width along the rapids was two meters, the water depth varied from 0.4–1.5 meters and the marginal vegetation was grass.

During the period collections were made, from March 1980 through February 1982 the near surface water temperature varied between 19° and 30°C and the pH between 5.0 and 6.0. The water current in the gallery forest stream varied between 0.244 and 0.600 meters per second.

Other species at this collecting site were: *Serrapinnus piaba, Odontostilbe stenodon,* "*Cheirodon*" sp., *Astyanax bimaculatus, Astyanax fasciatus, Hemigrammus marginatus, Moenkhausia sanctaefilomenae, Piabina argentea, Serrasalmus spilopleura, Acestrorhynchus lacustris, Oligosarcus pintoi, Salminus hilarii, Characidium* sp., *Hoplias malabaricus, Pyrrhulina australis, Cyphocharax gilberti, Cyphocharax vanderi, Leporinus friderici, Leporinus octofasciatus, Leporinus striatus, Eigenmannia* sp., *Cetopsorhamdia iheringi, Nannorhamdia schubarti, Pimelodella* cf. *gracilis, Rhamdella minuta, Rhamdia hilarii, Aspidoras fuscoguttatus, Hypostomus ancistroides, Microlepidogaster francirochai, Poecilia reticulata, Cichlasoma portalegrense, Crenicichla britiskii, Tilapia* sp. and *Synbranchus marmoratus.*

Distribution.—This species is known to occur in the State of São Paulo in tributaries to rio Grande and rio Tietê, both tributaries of the upper rio Paraná basin.

Etymology.—The specific name, *britskii,* is a patronym for Dr. Heraldo A. Britski, ichthyologist at the Museu de Zoologia da Universidade de São Paulo, in recognition of his many contributions to the ichthyology of Brazil. Dr. Britski collected the first two known specimens and recognized that they represented a new species of glandulocaudine fish.

Discussion of generic and subfamily phylogenetic relationships.—Böhlke (1954: 265) placed *Planaltina* in the Glandulocaudinae and noted a physical similarity between *Planaltina* and *Bryconamericus.* However, he set aside the question of glandulocaudine relationships to other characid genera, suggesting that the Glandulocaudinae are probably polyphyletic and that perhaps its various component taxa had origins among several tetragonopterine genera. Böhlke (1958:43) and Géry (1977:35) also thought it likely that the Glandulocaudinae are polyphyletic. Weitzman et al. in Weitzman & Fink (1985:112–117) discussed the question of glandulocaudine monophyly versus polyphyly at some length and concluded that there was not enough information to settle the question. Weitzman & Menezes (1998:178–180) hypothesized the subfamily as monophyletic based on a phylogenetic analysis of the seven tribes of the Glandulocaudinae and used four unequivocal synapomorphies to unite the members of all of these tribes. Outgroup information relative to the Glandulocaudinae and its tribes, as well as the synapomorphies used to diagnose the subfamily, were based on what was then known about the absence or near absence of the distribution of these four features in species of the non-glandulocaudine genera of the Tetragonopterinae. Recently discovered information that some species of the tetragonopterine genus *Knodus* and all of the species of *Attonitus* and the related new genus and species are inseminating and that the anatomy of the primary and secondary sexual systems of these species display some to several of these same features used as synapomorphies for the Glandulocaudinae by Weitzman & Menezes (1998) suggest that the phylogenetic relationships of the tribes of the Glandulocaudinae need re-examination. We review at least some of the implications of this new information in our discussion below concerning the phylogenetic position of *Planaltina* and the other Diapomini. See also Weitzman et al. (2004) for a more detailed discussion of *Attonitus, Bryconamericus, Knodus* and the new genus and species regarding their possible relationships to the

Glandulocaudinae and other characids known to be inseminating.

The four synapomorphies for the Glandulocaudinae, each discussed at length by Weitzman & Menezes (1998:178), are as follows: 1) the presence of insemination, 2) the presence of a sperm storage area in the testes, 3) the presence of elongate sperm-cell-nuclei, and 4) the presence of an elongate cytoplasmic collar binding the flagellum to the sperm-cell nucleus in at least some stage of spermiogenesis (see Burns et al. 1998). So far as we know these characters remain valid for all species of the Glandulocaudinae with the exception of *Planaltina,* which differs by having essentially spherical sperm-cell nuclei and apparently lacks an elongate cytoplasmic collar binding the flagellum to the sperm-cell nucleus. However, their status as synapomorphies at the levels proposed by Weitzman & Menezes (1998) for most if not all glandulocaudines must now be reconsidered because Weitzman et al. (2004) found that these features are present in tetragonopterine species placed in *Attonitus,* some of the species currently placed in *Knodus,* the new genus and species and the species of a few other possibly related genera, for example *Brittanichthys* Géry and *Monotocheirodon.* However, all the species of these genera appear to lack the caudal-fin pheromone organ found in a variety of derived states, each characteristic for one of the various tribes of the Glandulocaudinae. It should be noted at this point that the putative homology of the caudal-gland cells among the glandulocaudine tribes remains to be investigated and therefore the homology of the caudal organs in the subfamily is a not a fully defended hypothesis.

It was recently discovered (Weitzman et al. 2004), that the species of these apparent glandulocaudine outgroup genera as well as at least some species of the Glandulocaudinae have pheromone organs and in some cases simple putative pheromone secretory cells on raised integumentary pads of the anal fin and sometimes the pelvic fins of mature, sexually active males. These features, when present, were also described and discussed above for the species of *Planaltina.* Until further research reveals the distribution of these primary and secondary sexual structures among the above discussed genera, and among other inseminating characids such as *Brittanichthys* and *Monotocheirodon,* we decline to discuss the phylogenetic significance of these features regarding the Glandulocaudinae as a whole. We suggest that new hypotheses concerning the phylogenetic relationships of the Glandulocaudinae to apparent outgroup taxa be held in abeyance until the distribution of the synapomorphies used by Weitzman & Menezes (1998) to diagnose the Glandulocaudinae can be delineated for the inseminating species currently placed in the non-glandulocaudine genera mentioned here. We further note that the inseminating characid genera of the cheirodontine tribe Compsurini, although inseminating, lack three of the four synapomorphies (numbers 2, 3 and 4 mentioned above) and have the sperm cell synapomorphies discussed for the Cheirodontinae by Malabarba (1998). Regarding synapomorphy number 3 of the glandulocaudines, their elongate sperm cell nuclei, it is true that the sperm nuclei of the species of the Compsurini are somewhat elongate, but they are never as elongate as in nearly all the glandulocaudine species and apparently the centrioles are located posterior to the nucleus rather than anterior to it as in most of the glandulocaudines. Thus nuclear elongation appears to occur through forward growth in the cheirodontines rather than backward growth in the glandulocaudines (Burns et al. 1998). However, these putative characteristics of the ultrastructure of glandulocaudine and compsurin cheirodontine sperm cells need confirmation in many species and genera of both groups.

Planaltina was considered by Weitzman & Menezes (1998:184) to belong in the glandulocaudine tribe Diapomini because *P. myersi* shares with the species of the other two genera of the tribe, *Acrobrycon* and

Diapoma, two unequivocal synapomorphies. 1) The male and female caudal organs are nearly equivalent in size. 2) A multiple series of caudal scales, at least three or more, occur immediately ventral to the lateral-line series and extend posteriorly to form the dorsal border of a pouch opening of the caudal gland.

Planaltina myersi is distinguished from the species of *Acrobrycon* and *Diapoma* by the possession of separate dorsal and ventral enlarged pouch scales and only three scales across the dorsal opening of the pouch (Weitzman & Menezes 1998:184, figs. 13–16 and Weitzman & Fink 1985:17, fig. 15). The two diapomin synapomorphies are shared with the two new species herein described (compare Figs. 19, 28, 33). However, the description of caudal-organ features separating *Planaltina* from the species of *Acrobrycon* and *Diapoma* need some modification based on the inclusion of the two new *Planaltina* species. 1) The species of *Planaltina* have between two and six scales forming the dorsal region of the pouch while the number of scales in the dorsal region of the pouch in *Acrobrycon* and *Diapoma* exceeds eight or nine. 2) The number of scales forming the dorsal border of the pouch is greater in *Acrobrycon* and *Diapoma* than in *Planaltina.* The species of *Planaltina* have one or two scales forming the dorsal border of the pouch while in the species of *Diapoma* the number varies between three and six. In *Acrobrycon* this number varies from four to at least seven. In *Planaltina* one of the scales forming the dorsal border of the pouch is elongate and forms most of that border while in *Acrobrycon* and *Diapoma,* even when one of the dorsal border scales is somewhat elongate or larger, its actual degree of entry into the pouch border is little longer than that of the other dorsal border scales. At this time we are not prepared to hypothesize with confidence which of the characters listed above to separate these diapomin genera are plesiomorphic or apomorphic relative to these three genera. In our view, the position and number of adnate scales on ventral lobe of the caudal fin of the inseminating or even non-inseminating species of *Knodus* (some of which may form an outgroup for the Diapomini) must be described and recorded before such hypotheses can be proposed. However, in view of the apparently more plesiomorphic nature of the sperm-cell nuclei of the species of *Planaltina* compared to those of *Acrobrycon* and *Diapoma,* as discussed here, we suggest that the species of *Acrobrycon* and *Diapoma* with a greater number of caudal scales may be the more derived and that a greater number of caudal scales may be a synapomorphy for *Acrobrycon* and *Diapoma.*

Histological examination and measurement of the sperm cell bodies of the three species of *Planaltina* recognized herein show that their sperm cells are aquasperm, but with sometimes a slight ellipsoid shape (see Appendix 1), while in *Diapoma speculiferum* and presumably the other species of *Diapoma,* the cell body is elongate and has the typical derived ultrastructure of glandulocaudine sperm cell with a cytoplasmic collar surrounding the flagellum as it parallels the side of the elongate sperm cell body (Burns et al. 1995:133, table 3, Burns et al. 1998:237, fig. 2). Although we have no information on the ultrastructure of the sperm cell of *Acrobrycon,* it has a cell body somewhat more elongate than that of the species of *Diapoma.* Thus in this respect, the three species of *Planaltina* appear plesiomorphic relative to the species of *Diapoma* and *Acrobrycon.* Although this information is useful for suggesting a hypothesis of the phylogeny of the genera and species of the Diapomini, confirmation of such relationships among all diapomin species and their relationships to outgroup inseminating species currently in *Knodus* must await detailed research on species of the latter genus in order to obtain a greater knowledge of the characids that apparently form an outgroup or outgroups to the glandulocaudine tribes as diagnosed by Weitzman & Menezes (1998). See also Weitzman et al. (2004) for a more complete discussion of this problem.

One interesting undescribed species needs to be mentioned in regard to the statement just given above. Burns et al. (1995:133, table 3) recorded spherical sperm cell nuclei, aquasperm, in *Planaltina myersi,* USNM 278989, and in *Planaltina* sp. (this latter sample should have been listed as USNM 362836 but was also listed as USNM 278989 in the table by error). See Appendix 2 for field data and in Weitzman et al. (2004) for sexual characteristics. Both of these taxa have aquasperm and are inseminating. At this time we would place the population sample called *Planaltina* sp. in Burns et al. (1995) in *Knodus* because it has adnate scales on the lower caudal-fin lobe and therefore no caudal pouch. However, it is an inseminating species, and the type species of *Knodus, K. meridae* Eigenmann, although it too has adnate caudal scales and aquasperm, is apparently not an inseminating species according to our histological examination based on the specimens listed in Appendix 2 of Weitzman et al. (2004). The inseminating species currently in *Knodus* may belong to a series of species of that form a sister group to the Diapomini. However, the histological and ultrastructure characteristics of the primary sexual organs in those species up to the present referred to *Bryconamericus* and *Knodus* is complex and mostly unexplored. See Weitzman et al. (2004) for further discussion of these fishes. In our opinion the species traditionally referred to *Bryconamericus* and *Knodus* need a thorough phylogenetic study in order to better hypothesize possible relationships among the genera and species of the Diapomini.

Phylogenetic relationships among the three species of Planaltina.—The phylogenetic relationships among the species of *Planaltina* cannot be solved without better outgroup information than is currently available. There are over a dozen characters that provide information for distinguishing species; see especially the distinguishing characters under the title "*Definition*" for each of the three species above and Figs. 3–13, 19, 28, 33. However, reliable outgroup information for many of these characters is unavailable and some of the characters that might be hypothesized to be derived compared to those found in characids usually considered members of the Tetragonopterinae support contradictory hypotheses of phylogenetic relationships within the species of *Planaltina.* For example, *P. myersi* and *P. glandipedis* share the number of scale rows between the dorsal-fin origin and the lateral line, the number of scale rows between the anal-fin origin and the lateral line, the least number of scale rows around the caudal peduncle, and the number of vertebrae. We cannot at this time polarize any of these characters without appropriate outgroup information. Species in *Acrobrycon* and *Diapoma,* some undescribed in both genera, are not well known enough to be a source of outgroup information and some of the undescribed inseminating species currently referred to *Knodus* may in fact be the closest outgroup of the species of *Planaltina.* The species of *Acrobrycon* and *Diapoma* may be more derived diapomins than the species of *Planaltina* based on their more elongate sperm nuclei (in those so far investigated). Alternatively, if the less elongate and more numerous caudal organ scales of the species of *Acrobrycon* and *Diapoma* are considered plesiomorphic for the Diapomini and more like the caudal squamation in some of the inseminating species of *Knodus,* then we arrive at a different hypothesis. Parsimony ultimately must be used to settle these problems, but the available data is still insufficient for that purpose.

There is some evidence that *P. glandipedis* is a paedomorphic relative to *P. myersi* and *P. britskii.* It is smaller in size, has no adipose fin, and has fewer cusps on its jaw teeth than the other two species, all reductions common in relatively small characiform fishes (see Weitzman & Vari 1988, and Buckup 1993). On the other hand *P.*

glandipedis has a slightly greater number of scale rows around the caudal peduncle and more predorsal scales. In our view an analysis of the phylogenetic relationships among the species of *Planaltina* must await detailed descriptions of the characters of all diapomins so far described and yet to be described as well as a complete study of the inseminating species that are currently assigned to *Knodus*.

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Literature Cited

Anonymous (Corrêa e Castro, R. M.). 2000. Os peixes escondidos do Alto Paraná. FAPESP Pesquisa, São Paulo, Brazil, 58:44–47.

Böhlke, J. E. 1954. Studies on fishes of the family Characidae. No. 7, A new genus and species of glandulocaudine characids from central Brazil.—Stanford Ichthyological Bulletin 4(4):265–274.

———. 1958. Studies of fishes of the family Characidae, No. 14: a report on several extensive recent collections from Ecuador.—Proceedings of the Academy of Natural Sciences of Philadelphia 110:1–121.

Buckup, P. A. 1993. Phylogenetic relationships and reductive evolution in neotropical characidiin fishes (Characiformes, Ostariophysi).—Cladistics 9:305–341.

Burns, J. R., & S. H. Weitzman. 1996. Novel gill-derived gland in the male swordtail Characin, *Corynopoma riisei* (Teleostei: Characidae: Glandulocaudinae).—Copeia 1996:627–633.

———, S. H. Weitzman, H. J. Grier, & N. A. Menezes. 1995. Internal fertilization, testis and sperm morphology in glandulocaudine fishes (Teleostei: Characidae: Glandulocaudinae).—Journal of Morphology 224:131–145.

———, ———, K. R. Lange, & L. R. Malabarba. 1998. Sperm ultrastructure in characid fishes (Teleostei: Ostariophysi). Pp. 235–244 *in* L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena and C. A. S. Lucena, eds., Phylogeny and Classification of Neotropical Fishes. Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil, Edipucrs, 603 pp.

———, S. H. Weitzman, & L. R. Malabarba. 1997.

Insemination in eight species of cheirodontine fishes (Teleostei: Characidae: Cheirodontinae).—Copeia 1997:433–438.

Bushmann, P. J., J. R. Burns, & S. H. Weitzman. 2002. Gill-derived glands in glandulocaudine fishes (Teleostei: Characidae: Glandulocaudinae).—Journal of Morphology 253:187–195.

Garutti, V. 1983. Distribuição longitudinal da ictiofauna do Córrego da Barra Funda, bacia do rio Paraná. Unpublished Ph.D. dissertation, Instituto de Biociências, Universidade de São Paulo, 172 pp.

Glantz, S. A., & B. K. Slinker. 1990. Primer of applied regression and analysis of variance. McGraw-Hill, Health Professions Division, New York, xviii+777.

Géry, J. 1977. Characoids of the World. T. F. H. Publications, Neptune City, New Jersey, 1–672.

Malabarba, L. R. 1998. Monophyly of the Cheirodontinae, characters and major clades (Ostariophysi: Characidae). Pp. 193–233 *in* L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena and C. A. S. Lucena, eds., Phylogeny and Classification of Neotropical Fishes. Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil, Edipucrs, 603 pp.

Menezes, N. A., & S. H. Weitzman. 1990. Two new species of *Mimagoniates* (Teleostei: Characidae: Glandulocaudinae), their phylogeny and biogeography and a key to the glandulocaudine fishes of Brazil and Paraguay.—Proceedings of the Biological Society of Washington 103:380–426.

Pfeiffer, W. 1967. Schreckreaktion und Schreckstoffzellen bei Ostariophysi und Gonorhynchiformes. Zeitschrift für vergleichende Physiologie 56:380–396.

———. 1977. The distribution of the fright reaction and alarm substance cells in fishes.—Copeia 1977:653–665.

Quintero-Hunter, I., H. Grier, & M. Muscato. 1991. Enhancement of histological detail using Metanil yellow as a counterstain in periodic acid Schiff hematoxylin staining of glycol methacrylate tissue sections. Biotechnology and Histochemistry 66:169–172.

Schriebman, M. P. 1964. Studies of the pituitary gland of *Xiphophorus maculatus* (the Platyfish).—Zoologica 49:217–234.

Weitzman, S. H., & S. V. Fink. 1985. Xenurobryconin phylogeny and putative pheromone pumps in glandulocaudine fishes (Teleostei: Characidae).—Smithsonian Contributions to Zoology 421:1–121.

———, ———, A. Machado-Allison, & R. Royero L. 1994. A new genus and species of Glandulocaudinae (Teleostei: Characidae) from Southern Venezuela.—Ichthyological Exploration of Freshwaters 5:45–64.

———, & L. R. Malabarba. 1999. Systematics of *Spintherobolus* (Teleostei: Characidae: Cheirodontinae) from eastern Brazil.—Ichthyological Exploration of Freshwaters 10(1):1–43.

———, & N. A. Menezes. 1998. Relationships of the tribes and genera of the Glandulocaudinae (Ostariophysi: Characiformes: Characidae) with a description of a new genus, *Chrysobrycon*). Pp. 171–192 *in* L. R. Malabarba, R. E. Reis, R. P. Vari, Z. M. S. Lucena and C. A. S. Lucena, eds., Phylogeny and Classification of Neotropical Fishes. Museu de Ciências e Tecnologia, PUCRS, Porto Alegre, Brazil, Edipucrs, 603 pp.

———, ———, J. R. Burns, & H.-G. Evers. 2004. A new genus and species of inseminating characid fish from the upper rio Xingu and rio Tapajós, Brazil, (Teleostei: Characiformes: Characidae) with comments on relationships among inseminating characids. Neotropical Ichthyology, Porto Alegre, Brasil.

———, & L. Palmer. 1979. A new species of *Hyphessobrycon* (Teleostei: Characidae) from the Neblina region of Venezuela and Brazil, with comments on the putative 'rosy tetra clade.'—Ichthyological Exploration of Freshwaters 7(3): 209–242.

———, & R. Vari. 1988. Miniaturization in South American freshwater fishes; an overview and discussion.—Proceedings of the Biological Society of Washington 101:444–465.

Appendix 1

Sperm-cell dimensions for three species of Planaltina.—The following measurements were taken of sperm nuclei that exhibited a slightly non-spherical shape. These cells were clearly in the minority, but may give a more accurate assessment of the nuclear shape. Most views of the sperm nuclei were spherical. The cells measured varied from slightly ovoid, to pear shaped, to indented, to slightly elongate. The differences in measurements among the three species may be real or, alternatively, be due to variable shrinkage of cells having been treated differently in the past. For example separate collections may have been fixed in different concentrations of formalin. They may also have been slowly transferred to 70% ethyl alcohol by intermediate stages causing little or no shrinkage or, on the other hand, transferred from formalin fixative directly to 70% ethyl alcohol preservative, causing cell shrinkage.

Measurements were taken directly under oil immersion (100× lens) using an ocular micrometer or from photographic enlargements of negatives taken with a photomicroscope using an oil immersion (100×) lens. For each species, 20 cells were measured. Means ± standard deviations ($n - 1$ weighting) are given.

1. *Planaltina myersi*:
   USNM 278989: Male 37.4 mm SL, female 35.0. mm SL.
   n = 20:
   Male SZ nuclear length: 1.73 ± 0.12 μm
   Female SZ nuclear width: 1.16 ± 0.11 μm
2. *Planaltina glandipedis*:
   USNM 362136: Paratype, male 26.3 mm SL, paratype, female 27.0. mm SL.
   n = 20:
   Male SZ nuclear length: 1.97 ± 0.14 μm
   Female SZ nuclear width: 1.51 ± 0.12 μm
3. *Planaltina britskii*:
   MZUSP 62757: Holotype, male 35.0 mm SL, MZUSP 62757: paratype, female 36.5 mm SL.
   n = 20:
   Male SZ nuclear length: 1.89 ± 0.11 μm
   Female SZ nuclear width: 1.48 ± 0.11 μm

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On a new species of tree-climbing crab of the genus *Labuanium* (Crustacea: Decapoda: Brachyura: Sesarmidae) from Taiwan

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Abstract.—Specimens of a tree-climbing sesarmid crab from Taiwan previously referred to *Labuanium rotundatum* (Hess, 1865) are here shown to belong to a new species, *L. scandens.* The new species differs from *L. rotundatum* s. s. in having a less prominently granulated carapace, the outer surface of the chela covered with numerous small and closely arranged granules, and a differently structured male first pleopod.

The genus *Labuanium* Serène & Soh, 1970, currently contains 10 species from the Indo-West Pacific (Serène & Soh 1970). Of these, one of the more often reported species is *L. rotundatum* (Hess, 1865), a taxon that has been reported from many parts of the Indo-West Pacific, although apparently, it is not a very abundant species, and not many specimens are known. Tesch (1917:193–198), in a detailed discussion on the taxonomy of this species provided a long list of junior synonyms for this species, viz. *Sesarma dentifrons* A. Milne-Edwards, 1869, *Sesarma oceanica* De Man, 1889, *Sesarma gardineri* Borradaile, 1900, *Sesarma* (*Episesarma*) *rotundata papuomalesiaca* Nobili, 1899, and *Sarmatium faxoni* Rathbun, 1906.

Labuanium rotundatum was first reported from East Asia by Sakai (1939) on the basis of a male specimen collected from Tansui in northern Taiwan, and although cited by subsequent authors (Sakai 1940, 1976; Dai et al. 1986, Dai & Yang 1991, Cai et al. 1994), no further material was forthcoming until Liu (1999) recorded this species from southern Taiwan. Ng et al. (2001) subsequently added some notes on this species from Taiwan. In 1999, through the courtesy of Lu Eldredge of the Bernice P. Bishop Museum, the first author examined some specimens of *L. rotundatum* from some Pacific islands that appeared to differ in several respects from the Taiwanese material. But because there was a lack of material from Taiwan and other parts of the Pacific, not much else could be done. Between 2000 and 2001, we obtained an excellent series of specimens from Guam and Taiwan, and the study of this material confirmed our suspicion of the existence of two separate species, one of which is undescribed. The description of the new species forms the basis of the present paper.

Material examined is deposited in the Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A. (BPBM); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Taiwan National Museum, Taipei, Taiwan (TMCD); Institute of Zoology, Academia Sinica, Nankang, Taipei, Taiwan (ASIZ); National Museum of Marine Biology and Aquarium, Pingtung, Taiwan (NMMBA); and Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC). The abbreviations G1 and G2 are used for the male first and second pleopods respectively. The measurements are cited as: cw (carapace width) × cl (carapace length). The terminology essentially follows that used by Ng (1988). The length of the ambulatory legs were obtained by adding the maximum lengths of the merus, carpus, propodus and dactylus.

Labuanium scandens, new species
Figs. 1–4

Sesarma (*Sesarma*) *rotundatum*.—Sakai 1939:687, pl. 110 fig. 4, 1940:32. (Not *Sesarma rotundatum* Hess, 1865.)

Labuanium rotundatum.—Sakai 1976:663, text fig. 362, Dai et al. 1986:486, Dai & Yang 1991:532, Cai et al. 1994:597, Liu 1999:88, Ng et al. 2001:42. (Not *Sesarma rotundatum* Hess, 1865.)

Material examined.—All localities in Taiwan. Holotype male, 42.3 × 41.2 mm, TMCD 3290, Hsiang-Chiao-Wan, Hengchun, Pingtung County, coll. H.-C. Liu, 24 Jan 2002. Paratypes: 3 males, 38.5 × 37.5 mm, 31.8 × 30.3 mm, 14.6 × 14.4 mm, 1 female, 23.2 × 21.8 mm, ZRC 2002.444, Hsiang-Chiao-Wan, Hengchun, Pingtung County, coll. H.-C. Liu, 24 Jan 2002; 1 male, 16.3 × 15.8 mm, 1 female, 38.4 × 37.2 mm, TMCD 3291, Hsiang-Chiao-Wan, Hengchun, Pingtung County, coll. H.-C. Liu, 15 Dec 1999; 1 female, 27.1 × 27.0 mm, NMMBA 2002-01, Hsiang-Chiao-Wan, Hengchun, Pingtung County, coll. P.-H. Ho, 3 Oct 2001; 1 male, 36.1 × 35.8 mm, 2 females, 36.8 × 36.3 mm, 32.3 × 31.6 mm, IZAS 72860, Hsiang-Chiao-Wan, Hengchun, Pingtung County, coll. H.-C. Liu, 22 Dec 2001; 2 males, 35.5 × 34.2 mm, 19.1 × 18.7 mm, 3 females, 28.1 × 26.8 mm, 28.1 × 27.1 mm, 21.5 × 20.3 mm, ZRC 2001.29, Hsiang-Chiao-Wan, Hengchun, Pingtung County, coll. P. K. L. Ng, 7 Nov 2000; 1 female, 40.2 × 39.7 mm, ZRC 1998.447, Hsiang-Chiao-Wan, Hengchun, Pingtung County, coll. H.-C. Liu, 20 May 1998.

Diagnosis.—Carapace slightly wider than long, dorsal surfaces finely granular; posterolateral regions with finely granular oblique striae; outer surface of chela with numerous small, uniformly arranged rounded granules, dorsal margin with a distinct granulated but non-pectinated ridge on outer edge with 26–32 relatively longitudinally elongate granules, dorsal surface of dactylus with numerous granules; outer surface of ambulatory meri rugose, dorsal margin gently serrated; lateral margins of male segment 6 with distal part convex, proximal part almost straight; G1 relatively stout, almost straight; distal part bent 90° from vertical, distal chitinous part gently upcurved.

Description of male holotype.—Carapace rounded, slightly wider than long, broadest at median part of carapace, dorsal surfaces finely granular, regions well defined, gastric and branchial regions swollen; posterolateral regions with finely granular oblique striae (Fig. 1A, B). Frontal margin deflexed, sinuous from dorsal view, vaguely divided into 2 low lobes by broad U-shaped cleft, margin relatively entire; postfrontal cristae distinct, sharp, separated into 4 parts, median parts larger, wider, sharper, positioned more anteriorly than lateral parts, separated from lateral parts by short fissure, lateral parts adjacent to low inner supraorbital angle; frontal region prominently concave (Fig. 1A, B). Supraorbital margin smooth, with small cleft before external orbital tooth (Fig. 1B, C). Anterolateral margin strongly convex, gently curving into posterolateral margin, junction not discernible; external orbital tooth well developed, triangular, outer margin convex, directed anteriorly, outer margin distinctly convex, separated from rest of anterolateral margin by deep V-shaped cleft, rest of margin with 2 relatively low teeth; posterolateral margin gently convex, converging to almost straight posterior carapace margin (Fig. 1A, B).

Merus of third maxilliped longitudinally ovate, anterior part widest, posterior part tapering sharply to ischium (Fig. 1C), distinctly longer than ischium; ischium with shallow median sulcus; exopod slender, reaching to mid-length of merus, flagellum long, reaching across width of merus.

Male chelipeds subequal (Fig. 1A, B);

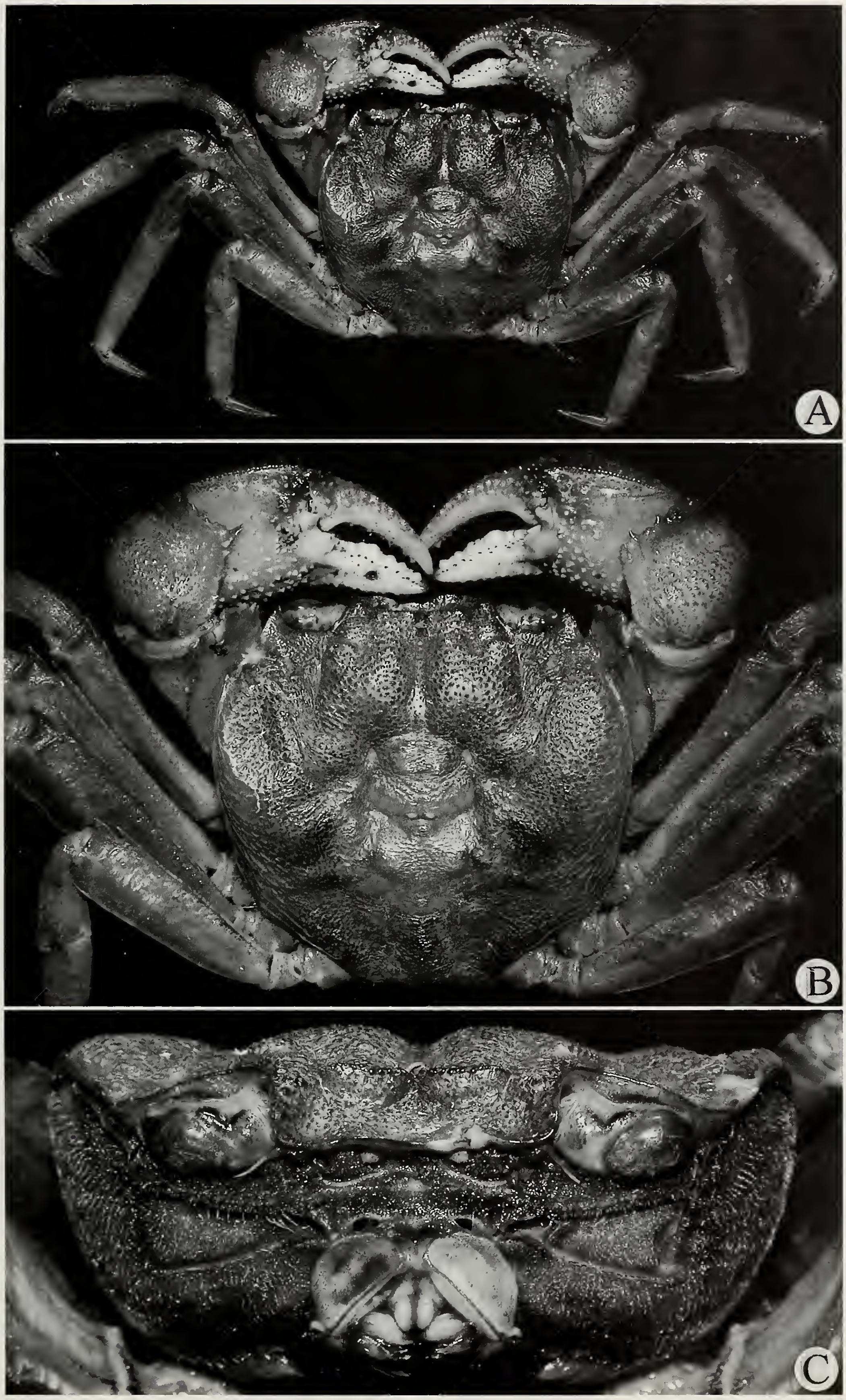

Fig. 1. *Labuanium scandens,* new species. Holotype male, 42.5 × 40.5 mm, TMCD 3290, Taiwan. A, overall view; B, carapace and chelipeds; C, frontal view.

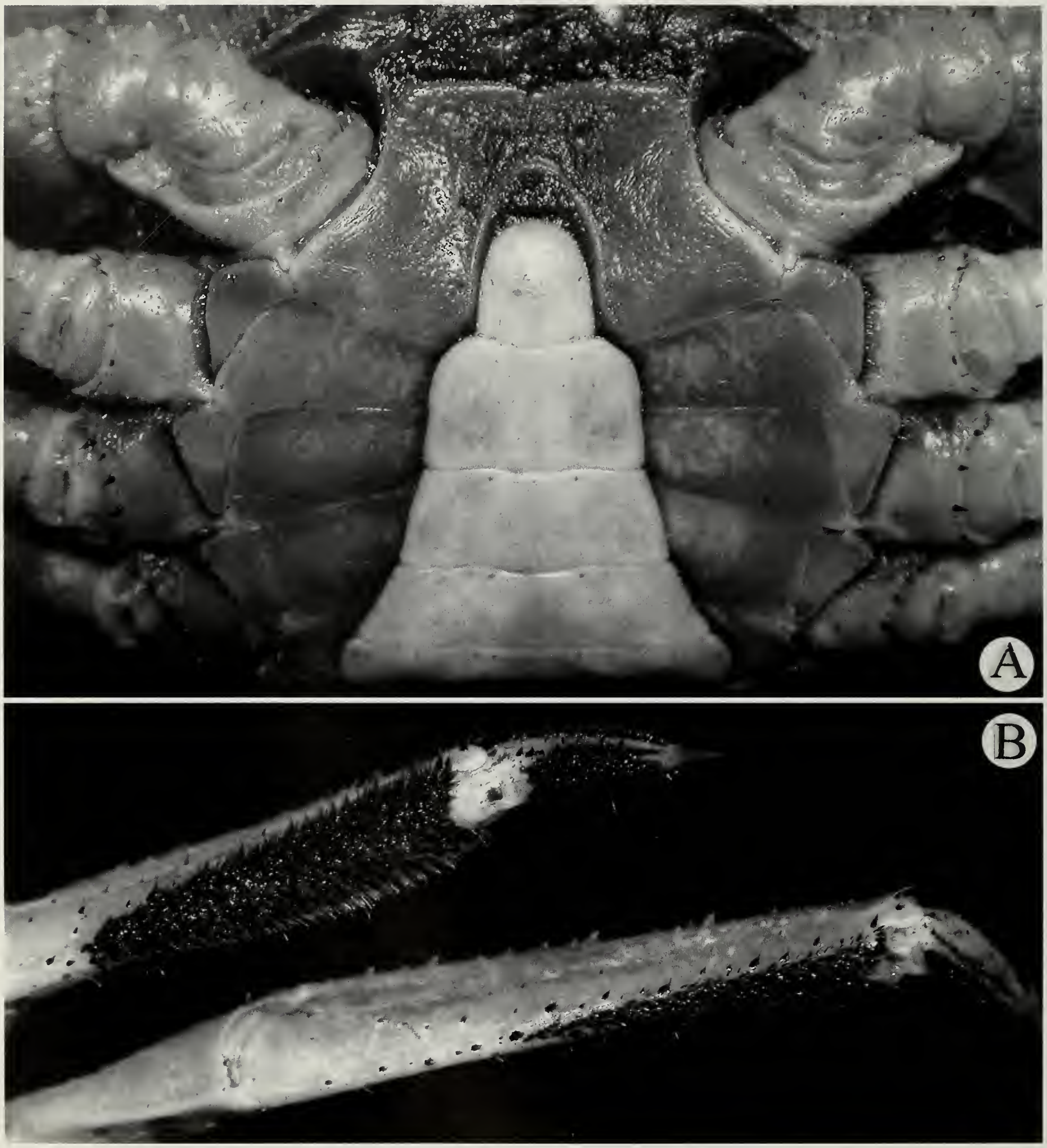

Fig. 2. *Labuanium scandens,* new species. Holotype male, 42.5 × 40.5 mm, TMCD 3290, Taiwan. A, anterior thoracic sternum and abdomen, ventral view; B, propodi and dactyli of first two ambulatory legs.

outer surface with numerous small, uniformly arranged rounded granules (Fig. 3A). Ventral surface of ischium with 2 short rows of tubercles, distal ones more prominent; ventral surface of basis granulated. Outer surface of merus with numerous rounded granules on outer surface, with low but discernible longitudinal median granulated ridge; inner margins prominently serrated, dorso-distal part dilated to form sublamelliform structure that is just visible from dorsal view. Outer surface of carpus finely granulated; slightly longer than broad; inner distal angle with long sharp tooth, distal and proximal margins serrated with some spines larger (Fig. 1B). Palm inflated, outer, dorsal and inner surfaces with numerous small, uniformly arranged round-

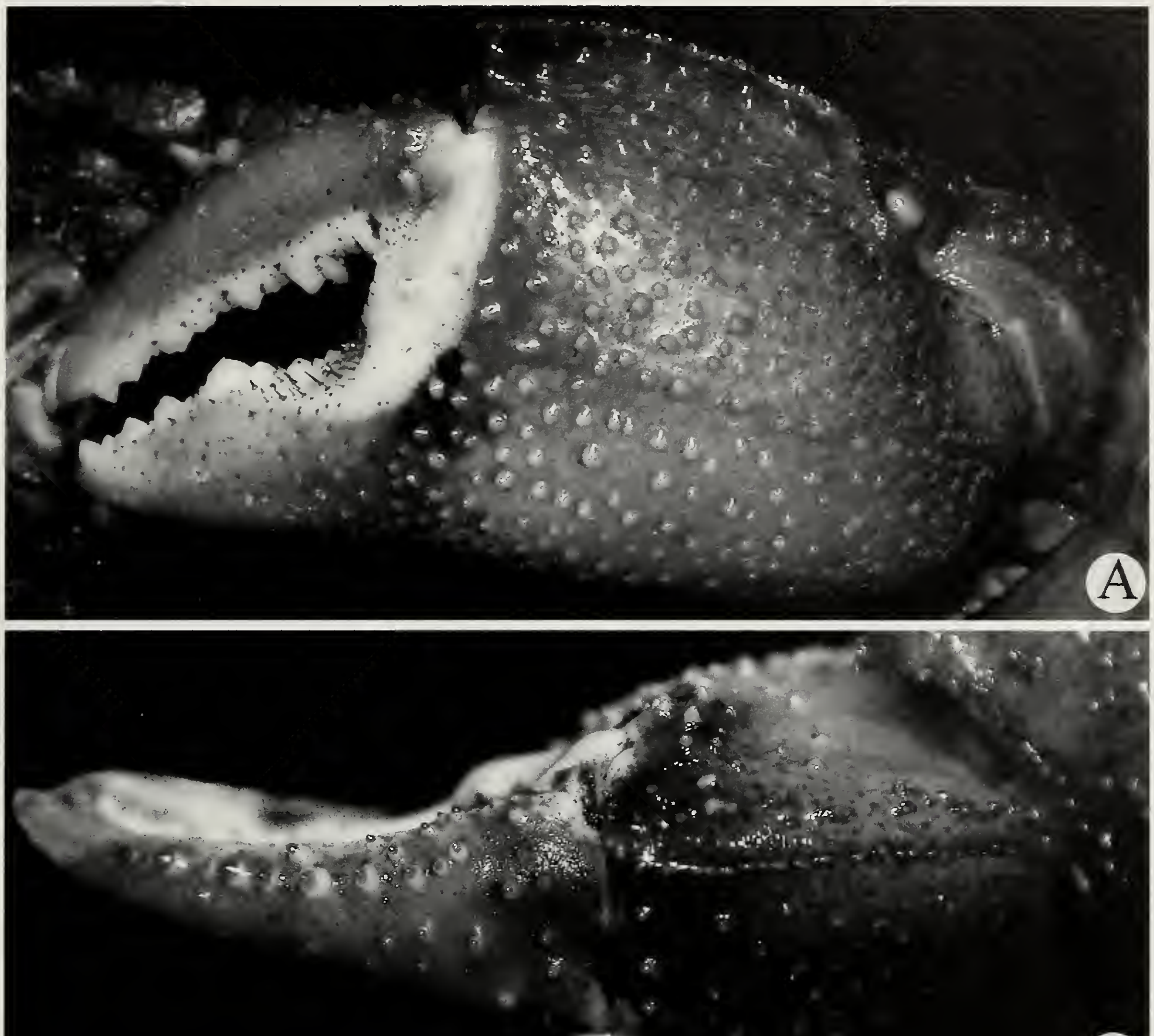

Fig. 3. *Labuanium scandens,* new species. Holotype male, 42.5 × 40.5 mm, TMCD 3290, Taiwan. Left chela. A, outer view; B, dorsal view; C, inner view.

ed granules (Fig. 3A); dorsal margin with a main, always distinct granulated but nonpectinated ridge on outer edge with 27 or 29 relatively more longitudinally elongate closely arranged granules, joining another less well defined (sometimes barely discernible) granulated ridge which extends from proximal edge of palm and curving along inward surface and gradually disappearing as it reaches median part (Fig. 3B, C); ventral margin (including pollex) with small sharp granules. Fingers shorter than palm, forming basal proximal gape when closed (Fig. 3A); dorsal surface of dactylus with numerous granules, most of which have a corneous tip, proximal 8–11 granules relatively smaller, scattered, subsequent 8 or 9 granules relatively larger, arranged in uneven row (Fig. 3B, C); cutting edges of dactylus and pollex with numerous prominent teeth (Fig. 3A).

Third ambulatory legs longest (Fig. 1A). Carpus of all legs with 2 subparallel low ridges on outer surface (Fig. 1A). Outer surface of propodus with short curved low ridge on proximal part. Meri of all legs relatively slender; surfaces rugose, dorsal margin gently serrated, subdistal tooth prominent (Fig. 1A). Dorsal and ventral margins of all dactyli with densely packed short setae forming brush-like structures; prominent brush-like setae present on distal half of ventral margins of first and second propodus, that on second propodus relatively less extensive; distoventral margins of propodi of other legs with tufts of short black setae, but not as dense or continuous, not distinctly brush-like (Fig. 2B).

Surfaces of thoracic sternites gently rugose; sternites 3 and 4 separated by almost straight, setae-lined ridge; abdominal cavity reaching to median part of sternite 4 (Fig. 2A). Abdomen triangular (Fig. 2A); telson shorter than segment 6, lateral margins gently convex on distal part but almost straight proximally, tip rounded; segment 6 with distal part of lateral margins convex, proximal part almost straight; segments 3–5 increasingly trapezoidal; lateral margins of segment 5 gently convex, that of segment 4 gently concave, that of segment 3 gently convex (Fig. 2A). Segments 1 and 2 transversely narrow.

G1 relatively stout, almost straight; distal surface strongly setose, obscuring margins, distal part sharply bent 90° from vertical, distal chitinous part gently upcurved from lateral view (Fig. 4). G2 short.

Etymology.—The name is derived from the Latin "scansus" for climb, alluding to the habits of this species. The name is used as a noun in apposition.

Distribution.—Known for certain only from Taiwan thus far.

Variation.—The holotype is the largest specimen of *L. scandens* available, and other than having its left branchial region slightly depressed (probably because of injury shortly after it molted), it is in excellent condition. Differences between sexes in this species are not substantial, most obvious being the proportionately more slender chela of females. The general forms of the male and female chelae are similar. Smaller specimens of *L. scandens* tend to be more squarish, with the lateral carapace margins almost straight or only gently convex; and the dorsal surface is relatively flatter. In larger specimens, the lateral carapace margins become prominently more convex and the dorsal surface is relatively more swollen. This is also true of *L. rotundatum.* In the series of specimens of *L. rotundatum* examined, the frontal margin of females may be more denticulate, appearing weakly serrated, although this is not always the case, with even a few of the smaller males also having a denticulate margin. The frontal margin of *L. scandens* is usually entire, although in some specimens, appears uneven; with only three or four individuals having distinct denticles. Based on the specimens of *L. rotundatum* examined, the presence of denticles along the frontal margin does not appear to be correlated with sex or size.

The strength of the anterolateral teeth of *L. scandens* varies. In smaller specimens,

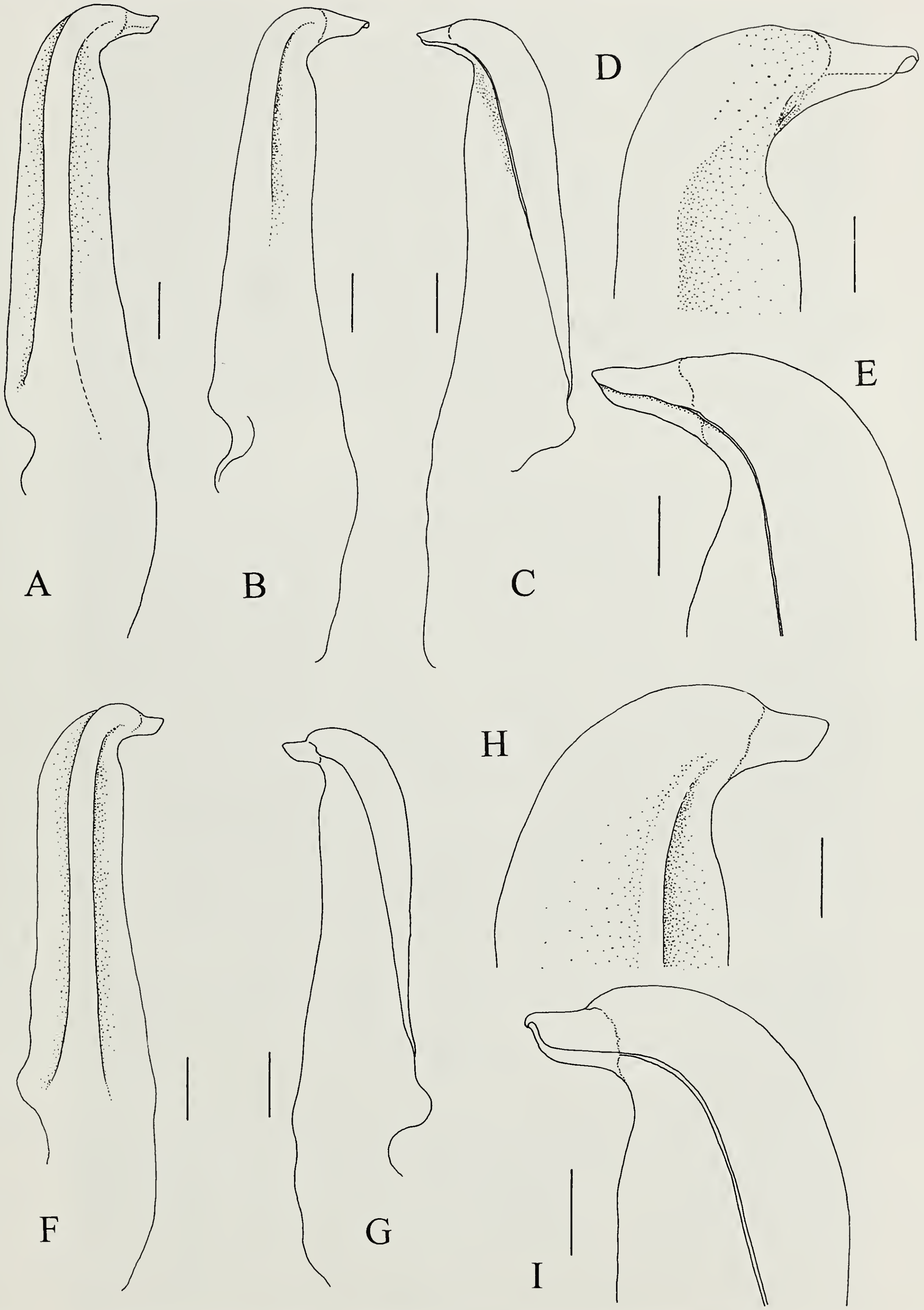

Fig. 4. *Labuanium scandens,* new species. Left G1s (denuded). A–E, holotype male, 42.5 × 40.5 mm, TMCD 3290, Taiwan; F–I, paratype male, 35.5 × 34.2 mm, ZRC 2001.29, Taiwan. A, F, dorsal (sternal) views; B, marginal view; C, G, ventral (abdominal) views; D, H, distal part, dorsal (sternal) views; E, I, distal part, ventral (abdominal) views. Scales equal 1.0 mm (A–C, F, G), and 5.0 mm (D, E, H, I).

the two teeth are usually more pronounced and sharper, and in larger specimens, the second tooth is invariably low, sometimes barely discernible. The cleft on the supraorbital margin is usually absent, with the margin appearing entire being present only on the holotype and a few other specimens. The strength of the inner dorsal granulated ridge of the palm varies a great deal, and in some specimens it is almost absent. The outer ridge on the other hand, is always distinct, although the number of granules varies from 26 to 32. The density and extent of the brush-like setae on the ambulatory propodi and dactyli does not differ substantially between the sexes, but smaller specimens invariably have less setae, with the ventral margins of the propodus being often almost glabrous. These observations are also valid for *L. rotundatum.*

Remarks.—It is rather surprising that none of the five junior synonyms of *L. rotundatum* are conspecific with the present material from Taiwan. Still, those taxa had all been described, often from limited material, from various parts of the south and southwest Pacific, and Hawaii, with one record from Nias in the eastern Indian Ocean, viz. *Sesarma dentifrons* A. Milne-Edwards, 1869 (one female, type locality Samoa), *Sesarma oceanica* De Man, 1889 (one male, one female, type locality Ponape Island), *Sesarma* (*Episesarma*) *rotundata papuomalesiaca* Nobili, 1899 (two males, one female, type localities Nias Islands [western Sumatra, Indonesia], New Guinea), *Sesarma gardineri* Borradaile, 1900 (six males, four females, type locality Funafuti, Rotuma Islands), and *Sarmatium faxoni* Rathbun, 1906 (three males, four females, Marshall Islands and type locality Oahu [Hawaii]). *Sesarma rotundatum* Hess, 1865, s. str. was described from one male, ostensibly from Sydney, Australia, but this data is likely to be incorrect (see "Remarks" for *L. rotundatum*). De Man (1891, 1896) and Tesch (1917) provide compelling arguments to show that *S. dentifrons, S. oceanicum, S. gardineri, S. rotundata papuomalesiaca* and *S. faxoni* are all junior synonyms of *L. rotundatum.*

Although we have not examined the type material for most of these species, fortunately, Hess (1865), A. Milne-Edwards (1869), De Man (1889), Nobili (1899), Borradaile (1900), Rathbun (1906) all provided good figures and/or sufficiently detailed descriptions for their species (supplemented by the detailed comments by Man 1891, 1896; Tesch 1917), and we are confident their taxa are conspecific with the excellent series of specimens of *L. rotundatum* we have from Guam and elsewhere. All these specimens are characterized by their carapaces being prominently striated on the lateral surfaces, the median surface is strongly granulated, the regions are not well indicated and the gastric and branchial regions are not prominently swollen (Fig. 5), the outer and inner surfaces of the chelipedal carpus and chela having relatively few but larger and well spaced large conical or rounded granules, with the areas between them smooth (Fig. 7); the dorsal margin of the male chela possessing a outer ridge which has 10 to 14 relatively large granules (Fig. 7B); and the lateral margins of adult male abdominal segment 6 gradually diverging posteriorly (Fig. 6A). The carapaces of males tend to have smoother frontal margins (often more denticulate in females, see "Variations") and there is a clear tendency for the carapace to become proportionately wider with size, especially in males.

Comparisons of the excellent series of specimens from Guam and Taiwan reveal numerous differences that confirm that we are dealing with two different species. Compared to *L. rotundatum, L. scandens* has the carapace granules and striae distinctly smaller and lower (but more numerous), with the regions more prominent, the gastric and branchial regions distinctly swollen and the groove separating them broader and deeper (Fig. 1); the outer and inner surfaces of the chela has smaller but far more granules, the entire surface ap-

Fig. 5. *Labuanium rotundatum* (Hess, 1865). Male, 42.9 × 39.7 mm, ZRC 2002.454a, Faifai Beach, Guam. A, overall view; B, carapace and chelipeds; C, frontal view.

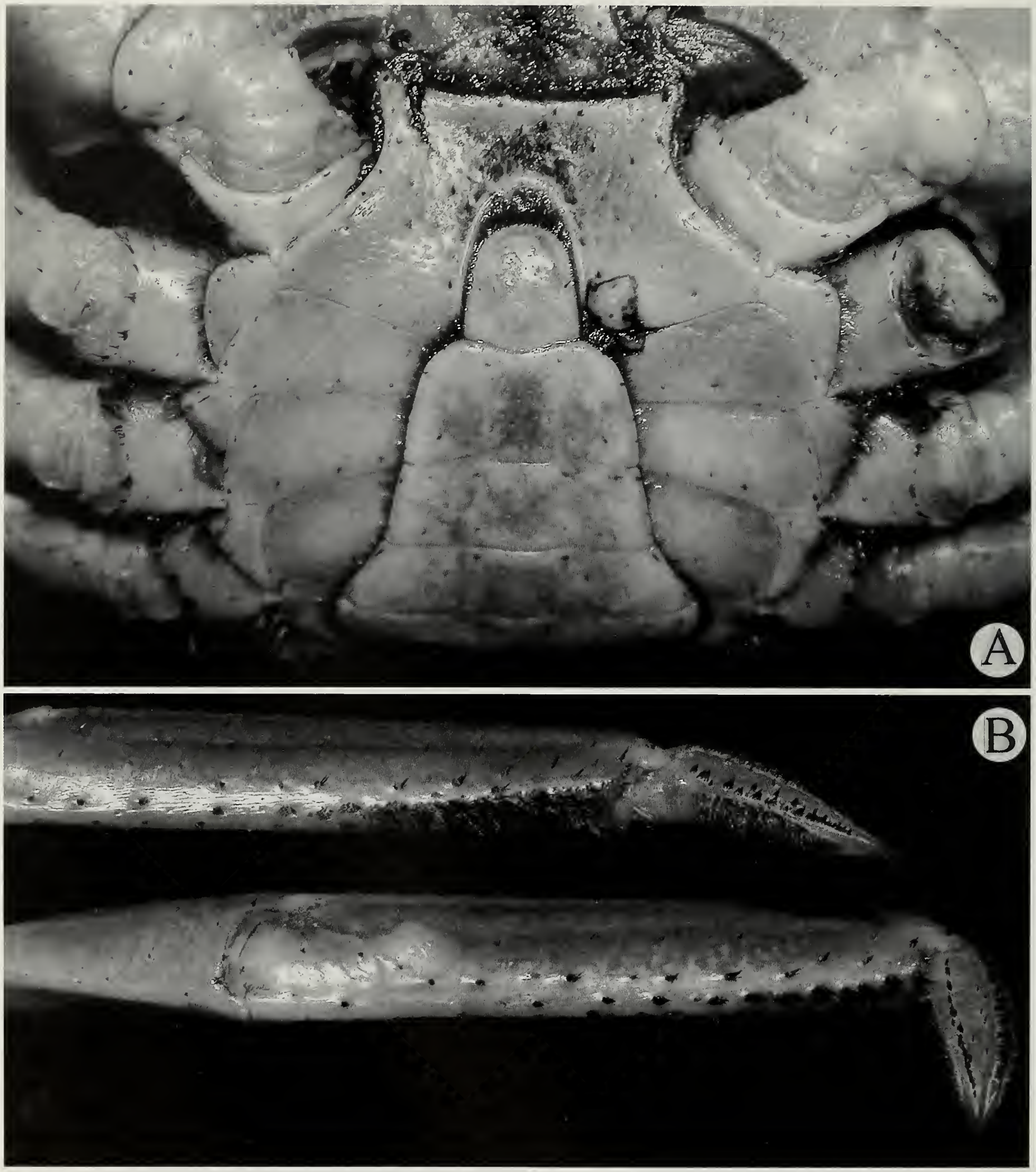

Fig. 6. *Labuanium rotundatum* (Hess, 1865). Male, 42.9 × 39.7 mm, ZRC 2002.454a, Faifai Beach, Guam. A, anterior thoracic sternum and abdomen, ventral view; B, propodi and dactyli of first two ambulatory legs.

pearing granular (Fig. 3); the dorsal margin of the male chela has an outer ridge with more (26–32) relatively smaller granules (Fig. 3B); and the lateral margins of adult male abdominal segment 6 are subparallel (Fig. 2A). These differences are apparent even for smaller male specimens for both species. The G1s of the two species also differ, with that of *L. scandens* being relatively more slender with the chitinous distal part relatively longer and bent at an angle of 90° (vs. relatively shorter and bent slightly upwards) (Fig. 4 vs. Fig. 8A–D, H, I). The G1 structure is slightly variable within

Fig. 7. *Labuanium rotundatum* (Hess, 1865). Male, 42.9 × 39.7 mm, ZRC 2002.454a, Faifai Beach, Guam. Left chela. A, outer view; B, dorsal view; C, inner view.

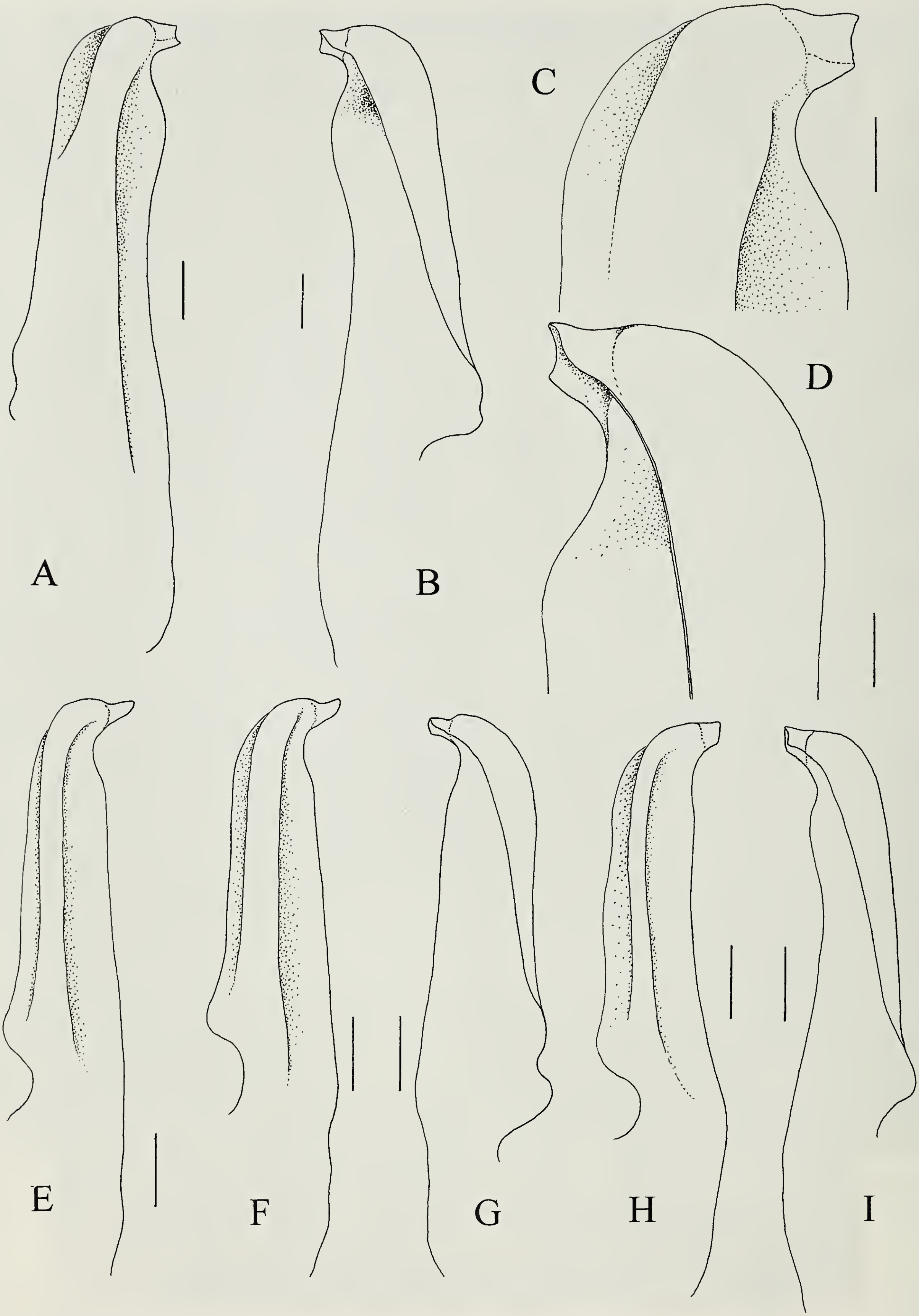

Fig. 8. *Labuanium rotundatum* (Hess, 1865). Left G1s (denuded). A–D, male, 42.9 × 39.7 mm, ZRC 2002.454a, Faifai Beach, Guam; E–G, male, 28.0 × 29.1 mm, BPBM 4191, Swain's Island; H, I, male, 27.9 × 17.0 mm, ZRC, Haputo Beach, Guam. A, E, F, H, dorsal (sternal) views; B, G, I, ventral (abdominal) views; C, distal part, dorsal (sternal) view; D, distal part, ventral (abdominal) view. Scales equal 1.0 mm (A, B, E–I), and 0.5 mm (C, D).

each species, but when specimens of equivalent or similar sizes are compared, the differences are marked.

The specimens of *L. rotundatum* from Swain Island in Samoa (BPBM 4191) are rather problematic in that their carapace is somewhat less granular compared to those from Guam (but still more so than in *L. scandens*), and their G1s appear to be more slender (Fig. 8E–G). In fact, the overall form of the G1 of these specimens is more similar to that of *L. scandens,* although the distal chitinous part is gently bent upwards like in *L. rotundatum* rather than at 90°. Also notable is that the carapaces of both males from Samoa are longer than broad. No other specimens of *L. rotundatum* examined so far from elsewhere have such proportions, their carapaces always being broader than long. The form of their chelae, however, is typical for *L. rotundatum.* Nevertheless, in lieu of more specimens, it seems best to refer these specimens to *L. rotundatum* for the time being. However, it is quite possible that there is more than one species belonging to what is here identified as *L. rotundatum,* and some of the synonyms may be shown to be valid in the future. But the G1s of more specimens from throughout the Pacific must be examined before more can be said. In any case, there is no doubt that the Taiwan specimens are very different from *L. rotundatum* and all the other taxa now synonymized with it.

Labuanium scandens is known only from southern Taiwan thus far. Although Sakai (1939) recorded *L. rotundatum* from Tansui in northern Taiwan, we have not yet found it there. The coastal areas of northern Taiwan have been heavily developed in recent years and pristine habitats are no longer extant there. Sakai's (1939: pl. 110 fig. 4, 1976: text fig. 362) figure of *L. rotundatum* leave little doubt that his specimen is conspecific with *L. scandens.*

Color.—The color of *L. scandens* varies somewhat with age. Smaller specimens are usually darker brown and mottled with light brown to white blotches and dark specks. Larger specimens are usually of a more uniform darker brown. The chela of larger males and females are mainly dirty white, with the dactylus purplish. In sharp contrast, adult *L. rotundatum* are usually a more uniform grey to dark greyish-brown, although smaller ones have a blotchy carapace. In general, the color of *L. rotundatum* is darker than *L. scandens.* The chelae of *L. rotundatum* are also uniformly white to dirty-white.

Notes on habits.—*Labuanium scandens* is a phytotelmic tree-climbing species. Its presence is closely associated with the presence of closed forest canopy and the availability of water-filled tree-holes. Tree species where the crabs have been recorded from are *Hernandia sonora, Barringtonia asiatica* and *Aglaia elliptifolia.* The tree cavities in which *L. scandens* live can sometimes be deep, occasionally over 50 cm. The tree holes collect rain-water, and the pools vary in depth from several centimeters to over 40 cm, depending on the season. The phytotelm water ranges from clear to dark-brown and turbid with a lot of sediment. The tree holes in which the crabs are found are always sheltered from direct sunlight. *Labuanium scandens* not only uses these holes as refuges, but also molts there, under the water. In the several cases when *L. scandens* was observed molting in the wild, the exuviae were not eaten soon after, disappearing only after a few days, although it is not certain if the crab itself is responsible. In three cases, the crab molted in captivity, and the exuviae were consumed by the crab shortly after it had hardened. *Labuanium scandens* has been found to inhabit holes between 0.5 to 4 m from the ground, but have been observed climbing over 5 m high in trees. It is primarily nocturnal, hiding in tree-holes during the day. Of the over 52 specimens of *L. scandens* observed (not all collected), the only time they were found on the ground is when they are ovigerous and are making their way to the sea. Ovigerous females can be found from July to October. The eggs are small and hatch out into pelagic, free-swimming larvae. The release of larvae seems correlated with the lunar cycle, with females making their way to the sea during the full moon period.

Not much is known about their diet. Specimens have been observed to scrape algae or lichens off the tree bark, as well as feed on dried leaves and flowers. The chelae of *L. scandens* are not particularly adapted to scrape algae off trees like in many other known tree climbing sesarmid crabs (Sivasothi et al. 1993, Lim et al. 1999), suggesting that this species has a more varied diet, probably including animal matter.

Labuanium rotundatum (Hess, 1865)

Figs. 5–8

Sesarma rotundata Hess, 1865:149, pl. 6 fig. 9 (type locality ostensibly Sydney, Australia, but see "Remarks").

Sesarma dentifrons A. Milne-Edwards, 1869:31 (type locality Samoa).

Sesarma oceanica De Man, 1889:429, pl. 10 fig. 9 (type locality Ponape Island).

Sesarma (*Episesarma*) *rotundata* var. *papuo-malesiaca* Nobili, 1899:268 (type localities Nias Islands [western Sumatra, Indonesia], New Guinea).

Sesarma gardineri Borradaile, 1900:593, pl. 42 fig. 8 (type locality Funafuti, Rotuma Islands).

Sarmatium faxoni Rathbun, 1906:841, pl. 7 fig. 1 (type locality Oahu, Hawaii).

Labuanium rotundatum—Serène & Soh 1970:401; Davie, 2002:221.

(For complete synonymy, see Tesch 1917: 193)

Material examined.—7 males, 16.4 × 15.9 mm, 31.6 × 30.8 mm, 34.4 × 32.1 mm, 36.8 × 35.6 mm, 39.3 × 39.2 mm, 42.9 × 39.7 mm, 43.7 × 41.2 mm, 3 females, 15.1 × 14.8 mm, 28.1 × 27.3 mm, 42.5 × 39.7 mm, ZRC 2002.454, in forest, Faifai Beach, near Gun Beach, Tumon Bay, Guam, coll. H.-C. Liu & P. K. L. Ng, 28 Jul–01 Aug 2001; 2 males, 22.2 × 21.1 mm, 22.5 × 21.2 mm, ZRC 2002.457, Ritidian Point, northern Guam, coll. H.-C. Liu & P. K. L. Ng, 31 Aug 2001; 2 males, 27.9 × 17.0 mm, 19.1 × 18.6 mm, 1 female, 11.9 × 11.6 mm, ZRC 2002.456, Haputo Beach forest, Guam, coll. P. K. L. Ng, 3 Aug 2001; 1 ex-ovigerous female, 31.6 × 30.4 mm, ZRC 2002.455, with first zoeae, hatched 4 Aug 2001, Haputo Beach forest, Guam, coll. P. K. L. Ng, 3 Aug 2001; 1 male, post-molt, carapace soft, deformed, ca. 37.9 × 35.7 mm, BPBM 4354, Puka-Puka Island, northern group of Cook Islands, coll. R. D. Frisbe, 1936; 1 male, 28.0 × 29.1 mm, 1 female, 35.2 × 34.5 mm, BPBM 4191, 1 male, 24.0 × 24.5 mm, ZRC 2002.453, Swain's Island, American Samoa, coll. Itasca Expedition, Mar 1936; 1 male, 23.5 × 23.8 mm, 1 female, 36.5 × 35.6 mm, BPBM S10701, Arno Atoll, Marshall Islands, no other data. 1 female, 37.0 × 34.4 mm, USNM 22837, holotype of *Sarmatium faxoni* Rathbun, 1906, Oahu, Hawaii.

Distribution.—Nias Islands (western Sumatra, Indonesia), Java, Samoa, Ponape Island, Nias Islands (western Sumatra, Indonesia), New Guinea, Guam, Puka-Puka Island (Cook Islands), Funafuti (Rotuma Islands), Marshall Islands, Oahu (Hawaii).

Remarks.—In describing *Sesarma rotundata,* Hess (1865) noted that he only had one specimen measuring 45 by 45 mm from "Sydney". The specimen was supposed to be deposited in the Zoological Museum of Göttingen (Germany). The specimens of Hess have since been transferred to the Senckenberg Museum (Frankfurt am Main). Andreas Allspach, who compiled a list of the extant Hess material for Peter Davie, could not locate the type of *Sesarma rotundata,* and the specimen is almost certainly no longer extant (P. Davie, pers. comm.). In addition, Davie (2002:221) comments that "The type locality of 'Sydney' [for *Sesarma rotundata*] is certainly erroneous; extensive field collecting across northern Australia has so far failed to rediscover the existence of *L. rotundatum*; it is most likely that it was collected from the islands of the south-west Pacific and sent to Hess via Sydney". The selection of a neotype for *Sesarma rotundata* Hess, 1865, would be necessary if it is later shown that what is now called *L. rotundatum* is composed of more than one cryptic species. But this should only be done when all the types of the putative synonyms are also re-examined. As things are now, *L. scandens* is so different from *L. rotundatum* as it is now understood that there is no need for a neotype for the latter species.

Other aspects of the taxonomy of *L. rotundatum* have been discussed earlier under the "Remarks" for *L. scandens.*

Color.—The carapace of adult *L. rotundatum* is usually uniform grey to dark greyish-brown, with smaller specimens having more light and dark colored blotches. The chelae are always uniform white to dirty-white, without any bright colors.

Notes on habits.—It is also useful to make some notes about the ecology of *L. rotundatum* in Guam. In general, the habits of *L. rotundatum* parallel those of *L. scandens.* On Guam, we have found them on coconut trees some 20–30 m from the sea, as well as on large *Pandanus.* Specimens were observed at heights of up to 4 m from the ground. Smaller specimens have also been found on near-vertical rocks at the base of large trees. They are more active during rain. Specimens were mostly observed moving about only at night.

Acknowledgments

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Literature Cited

Borradaile, L. A. 1900. On some Crustaceans from the South Pacific. Part IV. The Crabs.—Proceedings of the Zoological Society of London 1900:568–596, pls. 40–42.

Cai, E.-X., Z.-G. Huang, A.-Y. Dai, H.-L. Chen, & S.-L. Yang. 1994. Brachyura. Pp. 576–600 *in* Z.-G. Huang, ed., Marine species and their distributions in China's Seas. Department of Ocean Management and Monitoring State Oceanic Administration. China Ocean Press, Beijing.

Dai, A.-Y., & S.-L. Yang. 1991. Crabs of the China Seas. China Ocean Press, Beijing & Springer-Verlag, Berlin, pp. 21+608, figs. 1–295, pls. 1–74.

———, ———, Y.-Z. Song, & G.-X. Chen. 1986. Crabs of the China Seas. China Ocean Press, Beijing, 11+642 pp. (in Chinese)

Davie, P. J. F. 2002. Crustacea: Malacostraca. Eucarida (Part 2). Decapoda—Anomura, Brachyura. Zoological Catalogue of Australia. 19.3B. CSIRO Publications, 641 pp.

Hess, W. 1865. Beiträge zur Kenntnis der Decapoden-Krebse Ost-Australiens.—Archiv für Naturgeschichte 36:127–173, pls. 1, 2.

Lim, K. K. P., D. H. Murphy, N. Sivasothi, P. K. L. Ng, & K. S. Tan. 1999. Animals. Pp. 4–158 *in* P. K. L. Ng & N. Sivasothi, eds., A guide to the mangroves of Singapore. II. Animal diversity. Singapore Science Centre.

Liu, H.-C. 1999. Tales of Taiwanese land crabs.—Taiwan Natural Science 63:76–90. (in Chinese)

Man, J. G. De. 1889. Ueber einige neue oder seltene indopacifische Brachyuren.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 4:409–452, pls. 9, 10.

———. 1891. Carcinological studies in the Leyden Museum. No. 5.—Notes of the Leyden Museum 13:1–61, pls. 1–4.

———. 1896. Ueber neue und wenig bekannte Brachyuren des Hamburger und Pariser Museums.—Mitteilungen aus dem Naturhistorischen Museum zu Hamburg 13:75–118, 3 pls.

Milne-Edwards, A. 1869. Notes sur quelques nouvelles espèces du genre *Sesarma* (Say).—Nouvelles Archives du Muséum d'Histoire Naturelle, Paris 5:25–31.

Ng, P. K. L. 1988. The Freshwater Crabs of Peninsular Malaysia and Singapore. Department of Zoology, National University of Singapore, Shinglee Press, Singapore, pp. i–viii, 1–156, 4 color pls.

———, C.-H. Wang, P.-H. Ho, & H.-T. Shih. 2001.

An annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda).—National Taiwan Museum Special Publication Series, Taipei 11:1–86, 8 color pls.

Nobili, G. 1899. Contribuzioni alla conoscienza della fauna carcinologica della Papuasia, delle Molucche e dell'Australia.—Annali dei Museo Civico di Storia Naturale di Genova (2)20:230–282.

Rathbun, M. J. 1906. The Brachyura and Macura of the Hawaiian Islands.—United States Commission Bulletin for 1903, part 3:827–930, i–viii (index), pls. 1–24.

Sakai, T. 1939. Studies on the crabs of Japan. IV. Brachygnatha. Brachyrhyncha. Pp. 365–741, pls. 42–104. Yokendo Ltd., Tokyo.

———. 1940. Bio-geographic review on the distribution of crabs in Japanese waters.—Records of Oceanographic Works, Japan 11:27–63.

———. 1976. Crabs of Japan and the adjacent seas. In three volumes: (1) English Text, pp. xxix+773 pp.; (2) plates vol., pp. 1–16, plates 1–251; (3) Japanese text, pp. 1–461. Kodansha Ltd., Tokyo.

Serène, R., & C. L. Soh. 1970. New Indo-Pacific genera allied to *Sesarma* Say, 1877 (Brachyura, Decapoda, Crustacea).—Treubia 27(4):387–416.

Sivasothi, N., D. H. Murphy, & P. K. L. Ng. 1993. Tree-climbing and herbivory of crabs in the Singapore mangroves. Pp. 220–237 *in* A. Sasekumar, ed., Mangrove Fisheries and Connections. ASEAN-Australia Marine Science Project: Living Resources (Malaysia). Kuala Lumpur, Malaysia.

Tesch, J. J. 1917. Synopsis of the genera *Sesarma, Metasesarma, Sarmatium* and *Clistocoeloma,* with a key to the determination of the Indo-Pacific species.—Zoologische Mededelingen, Leiden 3: 127–260, pls. 15–17.

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Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 3: The genus *Narella* Gray, 1870

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Abstract.—The seven species of *Narella* known from the North Atlantic are described and illustrated, often with the aid of stereo SEM photomicrographs in order to show the shape and relationships of the body wall sclerites. Two species are described as new: *N. alvinae* and *N. spectabilis,* the former the deepest known representative of this genus. Two keys, tabular and dichotomous, are provided for the seven species. The types of all but one of the species were examined; only photographs of the syntype were studied of *N. bellissima.* New material is reported for all but one species, based primarily on collections housed at the USNM and MCZ.

Like many primnoid genera, species of the genus *Narella* have very conspicuous polyps composed of a discrete number of large sclerites (scales), which are often delicately sculptured and arranged in a definite pattern and number. In most species there are only 16–18 sclerites in each polyp (exclusive of tentacular sclerites), which are always arranged in pairs. Even the eight opercular scales are paired across the sagittal axis. Species of *Narella* live exclusively in deep water (146–3419 m) and are found worldwide, including off Antarctica. One of the Atlantic species, *N. alvinae,* is the deepest known for this genus and the second deepest collected primnoid. Twenty-seven species of *Narella* are known: seven occurring in the Atlantic, 14 from the western Pacific, three from the Hawaiian Islands, one from the southwest Indian Ocean, one from the Galápagos, and one from off Antarctica.

Material and Methods

Most of the new specimens reported in the paper were collected by vessels operated by the University of Miami (*Columbus Iselin, Pillsbury, Gerda*) and later deposited to the USNM. Other specimens were obtained from the MCZ (*Atlantis*) and ROM (*Alvin*).

Designation of polyp scales follows the terminology employed by Versluys (1906) as amplified by Bayer et al. (1983). Synonymies for all species are purported to be complete. The SEM photomicrographs were taken by the authors on a variety of SEM microscopes both at the University of Miami and the Smithsonian. Unprefaced SEM stub numbers pertain to the series of Bayer, those prefaced with a C, to the series of Cairns.

The following abbreviations are used: *Alb*—USFWS *Albatross*; *Atl*—*Atlantis* and R/V *Atlantis II BL*—U.S. Coast Survey Steamer *Blake*; BM—British Museum (now The Natural History Museum, London); *CI*—R/V *Colombus Iselin*; *G*—R/V *Gerda*; H:W—height to maximum width of an opercular scale; JS—Johnson-Smithsonian Deep Sea Expedition; *JSL-II*—R/V *Johnson Sea-Link II*; MCZ—Museum of Comparative Zoology, Harvard, Cambridge; MOM—Museum Oceanographique, Monaco; *O*—M/V, R/V *Oregon*; *P*—R/V *Pills-*

bury; ROM—Royal Ontario Museum, Ontario; *SB*—M/V, R/V *Silver Bay*; SEM—Scanning Electron Microscope stub number; USNM—United States National Museum (now the National Museum of Natural History, Washington, D.C.).

Subclass Octocorallia
Order Alcyonacea
Suborder Calcaxonia
Family Primnoidae Gray, 1858
Genus *Narella* Gray, 1870

Narella Gray, 1870:49 [type-species: *Primnoa regularis* Duchassaing & Michelotti, 1860, by monotypy].

Stachyodes Wright & Studer in Studer, 1887:49 [no species originally included; type-species: *Stachyodes regularis* Wright & Studer, 1889 (not Duchassaing & Michelotti, 1860), =*Stachyodes studeri* Versluys, 1906, by subsequent monotypy (Wright & Studer, 1889:54)].

Calypterinus Wright & Studer in Studer, 1887:49 [no species originally included; type-species: *Calypterinus allmani* Wright & Studer, 1889, by subsequent monotypy (Wright & Studer, 1889:53)].

Diagnosis.—Colonies of moderate size (up to about 50 cm), dichotomously branched in one plane or unbranched; polyps facing downward in whorls or pairs, rarely isolated; 3 or 4 pairs of large abaxial body scales, adaxial scales reduced to 1 well-developed buccal in each row, sometimes with 1 or 2 more below it; operculum consisting of 8 generally triangular scales each with a more or less distinct longitudinal keel on inner surface and corresponding trough on outer; tentacles usually with numerous flat rodlets; coenenchymal sclerites as scales, generally elongated, sometimes with raised external crests; axis heavily calcified, longitudinally grooved, with a discoidal basal holdfast attached to solid objects.

Remarks.—Versluys (1906) divided the species of *Narella* (as *Stachyodes*) into two groups, one with the sclerites of the basal pair meeting at the adaxial (lower) side of the polyp to form a complete ring, the other not. However, as some of the specimens investigated for the present account have some polyps with "closed" basal scales and others with "open" basals, even on a single branch, it appears that this character is not reliable even at the specific level. It has therefore been omitted as a basis for classification.

One of the most diagnostic features at the species level among the Atlantic *Narella,* and perhaps among all the species of this genus, is the shape and sculpture of the body wall sclerites, especially the basal sclerites, each species having a unique architecture (shape) and surface texture (crests and/or granulation). But, this feature is difficult to determine, often requiring *SEM* or various staining techniques to see. Thus, the dichotomous key, designed for ease of use, does not emphasize that character, rather the grosser characters such as the branched or unbranched nature of the colony. Unfortunately, branching characteristics can be misleading, in that long branches of a branched colony are often collected separated from the main colony, falsely suggesting that such a detached branch is an unbranched colony. Thus, we recommend favoring the tabular key (Table 1) for identification purposes, which gives a suite of characters for every species, including aspects of the basal sclerite architecture and texture.

The four pairs of opercular sclerites of all species of *Narella* appear to follow a similar pattern of size and shape. Sclerites of the adaxial pair are always the smallest in height and width (usually at least twice as tall as the basal width, shaped like an isosceles triangle) and are symmetrical in shape. The scales of the inner- and outer-lateral pairs are progressively taller and wider and asymmetrical, the adaxial side of each scale produced as a "shoulder" that overlaps the edge of the scale to its adaxial side. The abaxial operculars are invariably the largest of the operculars, both in height and width, the widest part occurring at about mid-height (often resembling the playing card spade) and are symmetrical, having projecting shoulders on both edges. The triangular shape of the operculars invariably changes in the ad- to abaxial direction, such that the ratio of height to maximum width decreases, essentially changing form isosceles to almost equilateral triangular. This ratio of height to maximum width is often species specific and thus the term H:W is introduced herein to define this shape for the opercular scales.

Key to the Seven Atlantic Species of *Narella*

1. Polyps with 3 pairs of large body scales 2
1′. Polyps with 4 pairs of large body scales 6
2. Colonies unbranched .... *N. versluysi* (Hickson, 1909)
2′. Colonies branched, sometimes sparingly so 3
3. Colonies dichotomous branched in a lyriform pattern; opercular scales covered in abaxial view .... *N. bellissima* (Kükenthal, 1915)
3′. Colonies dichotomous branched, but not in a lyriform pattern; opercular scales visible 4
4. Distal margin of upper (i.e., "abaxial") part of basal scales projecting conspicuously as a pair of broad, flat, truncated or rounded lobes standing approximately normal to axis; lateral part of basal scales abruptly meeting upper ("abaxial") part at about 90°, ridged; sparingly branched .... *N. alvinae,* n. sp.
4′. Distal margin of basal scales projecting only as a pair of short, rounded lobes, oriented downward to axis; lateral part of basal scales meeting as smooth curve, not a 90° angle and not ridged; regularly and profusely branched 5
5. Whorls of polyps closely placed, 10–12 in 3 cm of axial length; 5 or more polyps per whorl; outer surface of large body scales rough, closely covered by small, sharp granules .... *N. regularis* (Duchassaing & Michelotti, 1860)
5′. Whorls of polyps more distantly spaced, 7–9 in 3 cm of axial length; usually 3 (2–4) polyps per whorl; outer surface of large body scales smooth except for more or less conspicuous radial wrinkles ..... *N. pauciflora* Deichmann, 1936
6. Colonies sparingly branched dichotomously in one plan; polyps in whorls of 3–5, with 5–7 whorls in 3 cm of axial length; body scales without longitudinal crests .... *N. laxa* Deichmann, 1936
6′. Colonies apparently unbranched; polyps in whorls of 4, with 8 whorls in 3 cm of axial length; body scales with longitudinal crests .... *N. spectabilis,* n. sp.

Narella bellissima (Kükenthal, 1915)

Figs. 1A, 2A–C, 3A–D, 14

Not *Primnoa trilepis* Pourtalès, 1868:130.
Stachyodes trilepis.—Studer, 1901:41–42, pl. 5, pl. 11, figs. 3, 6, 7.
Stachyodes sp.—Versluys, 1906:123–124.
Stachyodes bellissima Kükenthal, 1915: 154; 1919:457; 1924:310.
Stachyodes regularis.—Kükenthal, 1919: 466–467 (specimen from St. Vincent at 88 fms, *BL*-232).
Stachyodes Allmani.—Thomson, 1927:29.
Narella regularis.—Deichmann, 1936:169, pl. 26, fig. 3.—Tixier-Durivault & d'Hondt, 1974:1412.—Grasshoff, 1982a: 738, map 3; 1982b:947, figs. 15–17.
Narella bellissima.—Grasshoff & Zibrowius, 1983: in part, 122–123, pl. 4, figs. 17–18 (not page 120, pl. 2, fig. 8).—Carpine & Grasshoff, 1985:33.—Grasshoff, 1986:26–27.

Material examined.—Mona Passage: 18°12′N, 67°42′W, 515 m, *O*-2644, 5 Oct 1959, 3 colonies almost complete save for holdfast, USNM 52776 (*SEM* 378, 1734, unnumbered stub made in 1971, C1031).

Off St. Vincent: 13°20′N, 61°02.5′W, 576–823 m, *P*-881, 6 Jul 1969, one small colony almost complete but lacking holdfast, USNM 52777 (*SEM* 380, 1723).

West of Puerto Rico: 18°03′45″N, 67°48′10″W, 439–549 m, JS-43, 11 Feb

Table 1.—Distinguishing characteristics of the seven Atlantic species of *Narella*.

	Pairs of body scales	Branching	Number of whorls/ 3 cm	Number of polyps/ whorl	Polyp size (mm)	Distal margin of basal scale	Ring of adaxial basal scales	Body wall scales: texture; ridging
N. bellissima	3	Dichotomous (lyriform)	10–13	3–$\underline{5}$–8	2.0–2.2	Prominent lobes, projecting perpendicular to axis	Closed	Smooth (low radiating granulation); basals slightly ridged at corners
N. regularis	3	Dichotomous (not lyriform)	11–13	4–$\underline{5}$	2.0–2.3	Inconspicuous lobes, inclined downward 60°	Open	Coarsely granular; all body wall scales longitudinally ridged
N. pauciflora	3	Dichotomous (not lyriform)	6–$\underline{7}$–9	2–$\underline{3}$–5	2.6–2.8	Inconspicuous lobes, inclined downward 70°	Open	Smooth; prominent radially arranged ridges
N. alvinae	3	Dichotomous, but sparingly branched	7	4	2.7–3.1	Prominent lobes, perpendicular	Open	Smooth; basals prominently ridged at corners
N. versluysi	3	Unbranched	8–10	4–7*	3.2–3.7	Prominent lobes, inclined downward 60° to perpendicular	Open	Granular; no external ridges
N. laxa	4	Dichotomous, but sparingly branched	5–7	3–5	3.0	Inconspicuous lobes, perpendicular	Open	Coarsely granular; no external ridges
N. spectabilis	4	Unbranched (?)	8	4	3.5	Inconspicuous lobes, perpendicular	Closed	Granular; prominent longitudinal ridges at corners of all body wall scales

Table 1.—Continued.

	Opercular visible in adaxial view	H:W of abaxial opercular	Pairs of adaxial buccal scales	Other distinctive characters	Distribution and depth
N. bellissima	No	0.81–1.0	1+	Buccal scales quite long; abaxial operculars quite short	Amphi-Atlantic; 161–1968 m
N. regularis	Yes	1.45–1.55	1		Lesser Antilles, Bahamas; 366–792 m
N. pauciflora	Yes	1.3–2.0	1–2 (ridged)	Operculars deeply creased longitudinally	Antilles, Bahamas; 738–1473 m
N. alvinae	Yes	1.25–1.45	1	coenosteal scales prominently ridged	Bermuda; 3419 m
N. versluysi	Yes	1.2–1.3	1+	Basal scales ridged interiorly	Amphi-Atlantic; 550-3100 m
N. laxa	Yes	1.8–1.9	2–3	Opercular scales flat in basal region	Amphi-Atlantic: 2980–3186 m
N. spectabilis	Yes	2.1–2.6	2	Abaxial operculars sometimes multi-tipped	Tongue of the Ocean, Bahamas; 1485 m

* 9–14 in eastern Atlantic types.

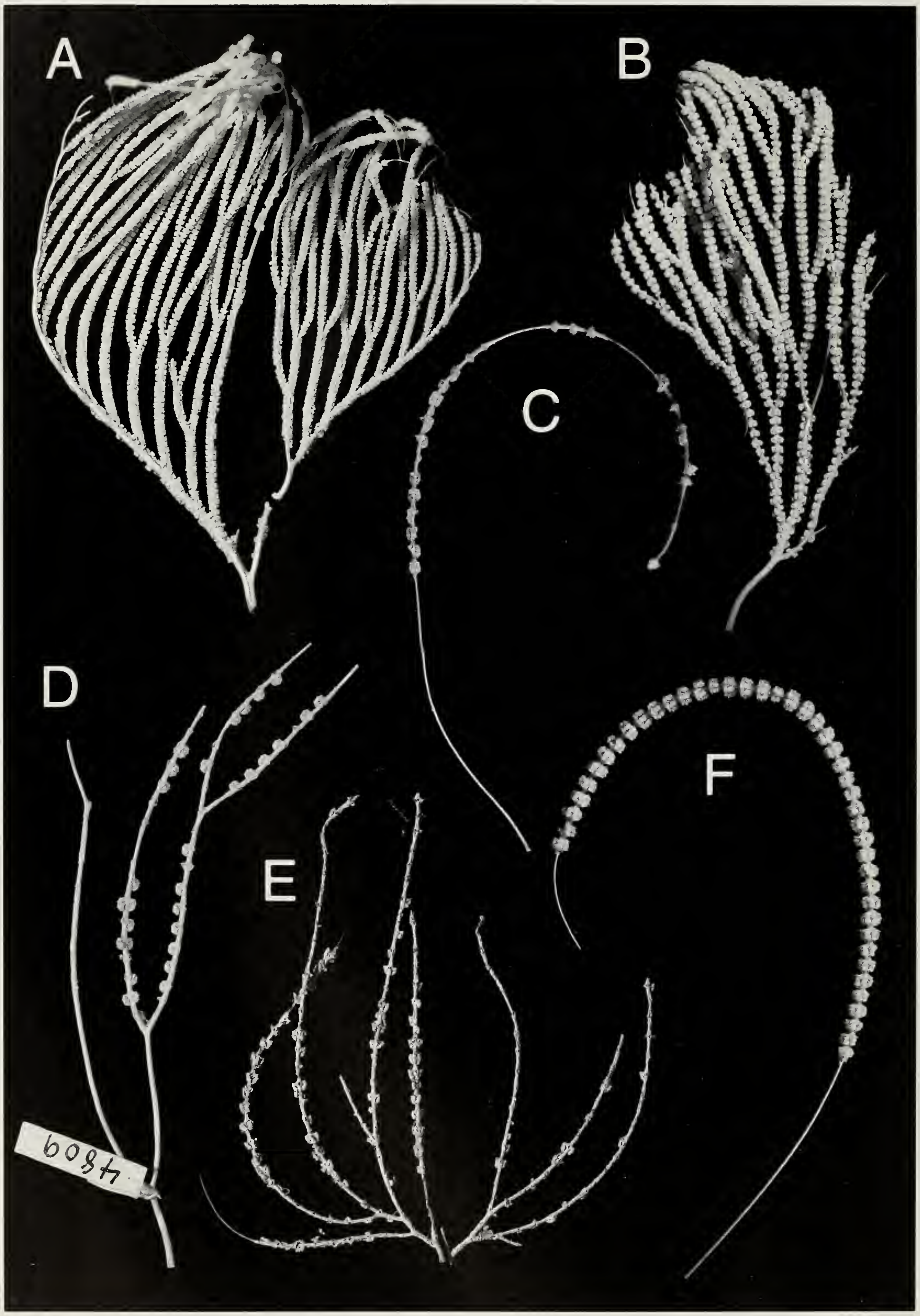

Fig. 1. A, *Narella bellissima, O*-2644, USNM 52776, colony in two pieces, ×0.33; B, *N. regularis, Alb*-2752, USNM 49385, colony, ×0.50; C, *N. spectabilis,* holotype, USNM 57578, ×0.67; D, *N. pauciflora,* holotype, MCZ 4809, ×0.80; E, *N. laxa,* holotype in two pieces, USNM 11853, ×0.55; F, *N. versluysi, CI*-140, USNM 57570, ×0.55.

1933, 3 dichotomous branches, the tallest 15.5 cm, USNM 54281 (*SEM* 412).

West of Puerto Rico: 18°17′05″N, 67°24′45″W, 512–622 m, JS-47, 13 Feb 1933, one nearly complete small colony with part of calcareous holdfast, and 6 detached branches, USNM 57444 (*SEM* 1726)

Bahamas, off Egg Island, Eleuthera: 25°30.85′N, 76°55.10′W, 790 m, *JSL-II*-813, 12 Apr 1984, branches cut from a large colony, USNM 1004869 (*SEM* 1727).

Bahamas, off Chub Cay, Berry Islands: 25°23.40′N, 77°55.25′W, 792 m, *JSL-II*-815, 13 Apr 1984, branches cut from a large colony, USNM 1004866 (*SEM* 1709, 1711).

Straits of Florida between Delray Beach, Florida, and Grand Bahama Island: 26°24′N, 79°36′W, 738 m, *CI-140,* 28 Sep 1973, one branch 14 cm tall, USNM 57568 (*SEM* 1733).

Off Northwestern Spain, Bay of Biscay: 44°11′N, 8°40′W, 450–500 m, *Thalassa* V807, 28 Oct 1968, 2 branches, USNM 94560 and 94561 (*SEM* 894, 1712–1716) (reported by Grasshoff, 1982b).

Lesser Antilles: *BL*-232, MCZ 4807, several colony and branch fragments now separated into 8 lots, alcohol and dry, previously reported as *N. regularis* by Deichmann (1936).

Lesser Antilles: *BL*-233, MCZ 4808, several branches now separated into two lots, alcohol, previously reported as *N. regularis* by Deichmann (1936).

Photographs of syntypes (MOM).

Types.—Four syntypes are deposited at the MOM, one in alcohol and three dry (Carpine & Grasshoff 1985), cataloged as 12 0011. Type Locality: *Hirondelle* station 105: 38°23′45″N, 30°51′30″W (off Azores), 927 m.

Description.—Colonies have a short, stout main stem, which bifurcates into 2 subsidiary branches, the angle between these two branches being 100°–110°, each of which give rise to a series of regularly spaced (every 12–15 mm) branches on their facing sides, altogether forming a uniplanar, lyriform colony shape. The largest specimen examined (*O*-2644) has a main stem 2 cm in height and 5 mm in axial diameter, a total colony height of 43 cm, and approximately 14 branches that originate from each of the subsidiary branches. The branches originating from the two subsidiary branches are up to 28 cm in length, most of which bifurcate only once, some of which bifurcate twice, and several of which are unbranched. The axis is strongly calcified, fairly stiff, and golden-yellow in color; it bears fine longitudinal grooves. Polyps are arranged in whorls of 3–8 (average 5), the lower number characteristic of whorls at the ends of branches, the higher number found on larger-diameter basal branches. Whorls and polyps are so closely spaced that the branch coenenchyme cannot be seen, 10–13 whorls occurring in 3 cm branch length, the tips of the opercular scales almost touching the basal scales of the adjacent proximal polyp and the sides of each polyps touching their adjacent polyp in the same whorl. As is characteristic for the genus, the polyps point downward; the length of a polyp, as measured parallel to the axis from basal scale to the tip of the operculars, is 2.0–2.2 mm.

Each polyp is protected by three pairs of large abaxial body scales and a pair of small adaxial buccal scales. The pair of basal scales are quite prominent, standing perpendicular to the axis up to 1.8 mm in height, the upper half of each of these scales projecting above the medial scales as a tall, broad, rounded lobe. The sides of these basal scales curve around the base of the polyp and meet on the adaxial side in a ring structure, but do not fuse. At the point of curvature from the abaxial to lateral edges, there is usually a low longitudinal ridge on the lower half of the sclerite. The pair of medials are much smaller sclerites (0.7–0.8 mm in length), roughly square, and slightly creased transversely, resulting in a slight distal flare; they do not meet on the adaxial side. The pair of abaxial buccals are quite large (up to 1.3 mm in length and 0.90 mm

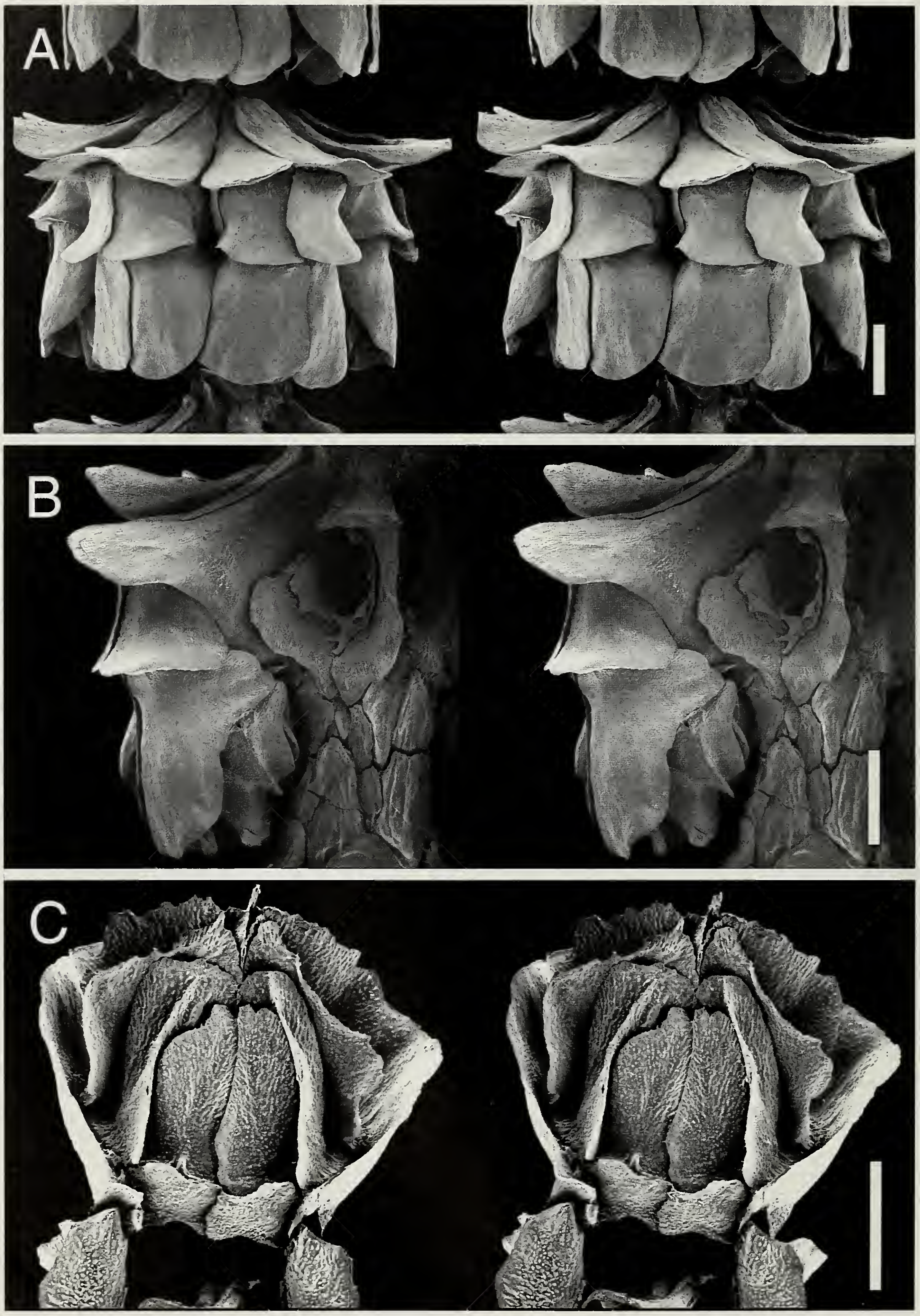

Fig. 2. *Narella bellissima*: A, B, *JS*-47, USNM 57444, a complete polyp whorl and lateral view of a polyp; C, *JSL-II* 815, USNM 1004866, adaxial view. Stereo views. All scale bars are 0.5 mm.

in width), and, although they do not meet on the adaxial side, form a protective cone enveloping the distal polyp and opercular scales, such that only the tips of the opercular scales can be seen from side or abaxial view. The distal edges of these buccals are quite thin and delicate, appearing translucent for the distal 0.1 mm because of a lack of tubercles on their inner surface of this region. The three pairs of large abaxial scales overlap each other slightly on the sagittal line and are covered by very small granules arranged in lines that radiate from a central point on each scale about ⅓ the distance up from its base; however, the granulation is so fine that these scales appear smooth. A pair of quadrate-shaped adaxial buccal scales also occurs just beneath the adaxial operculars, these scales measuring about 0.3 mm in greater width. Their inner surface is tuberculate, the outer granular, and their distal edges finely serrate, the serrations being 2–6 μm in width. Rarely, one can observe in some specimens 10–12 pairs of vestigial adaxial scales that are elliptical in shape and only about 0.1 mm in greater diameter.

The adaxial operculars are elongate-triangular and symmetrical, up to 0.7 mm in height and 0.31 mm in basal width (H:W = 2.1–2.9). They are longitudinally concave, sometimes bearing a short medial ridge within this concavity, and also bearing a prominent medial keel on the distal half of its under surface. The inner- and outer-lateral and abaxial opercular scales are only slightly taller and wider (up to 0.75 mm tall and 0.47 mm wide: H:W about 1.3–16) and asymmetrical, such that there is a slight shoulder on the adaxial side, making the interior keel appear off-center. The abaxial operculars are only slightly taller but much wider than the laterals, sometimes wider than tall (e.g., 0.78 mm tall and 0.80 mm wide: H:W = 0.81–1.0) and symmetrical, bearing shoulders on each side at mid height, making the longitudinal interior keel centrally placed. The opercular scales have a progressively deeper longitudinal groove exteriorly and a more prominent keel on their inner surfaces in the ad- to abaxial gradient. At first glance, in situ, it would appear that the operculars are flat with a medial ridge, but when disarticulated, it can be seen that these sclerites are deeply longitudinally grooved with a keel on lower face. When closed, the opercular scales form a tight, somewhat overlapping crown around the polyp, which is also protected by the abaxial buccals, all of which are directed toward the branch axis. The tentacles contain small (80 μm length), granulated, slightly curved spindles. The coenenchymal scales are elongate and irregular in shape, arranged in one layer, up to 1.2 mm in length, and usually longitudinally ridged. The inner surfaces of all sclerites are tuberculate, except for the distal edges of the body wall scales. The tubercles are roughly 10 μm in diameter and spiny, the individual spines being about 1 μm in diameter.

Comparisons.—*Narella bellissima* is the only Atlantic species in the genus to have dichotomous branching that results in a lyriform colony. Based on Table 1, it is most similar to *N. alvinae,* both species having prominent lobate basal scales, but *N. bellissima* differs in having smaller polyps and consequently more whorls per cm, less prominent ridging on the body wall scales, proportionately longer buccal scales and smaller operculars resulting in the operculars being almost completely hidden from view, and occurs at a shallower depth.

Distribution.—Eastern Atlantic: Bay of Biscay off France and NW Spain (Grasshoff 1982b, 1986); off Portugal (Grasshoff 1986); Azores (Studer 1901, Tixier-Durivault & d'Hondt 1974); Madeira (Thomson 1927, Grasshoff 1982a); Canary Islands (Grasshoff & Zibrowius 1983); Cape Verde Islands (Grasshoff 1986); ?Dakar (Grasshoff & Zibrowius 1983); 225–1968 m. Western Atlantic: Lesser Antilles and Bahamas (Fig. 14); 161–792 m.

Remarks.—Studer (1901) was the first to describe and beautifully illustrate a speci-

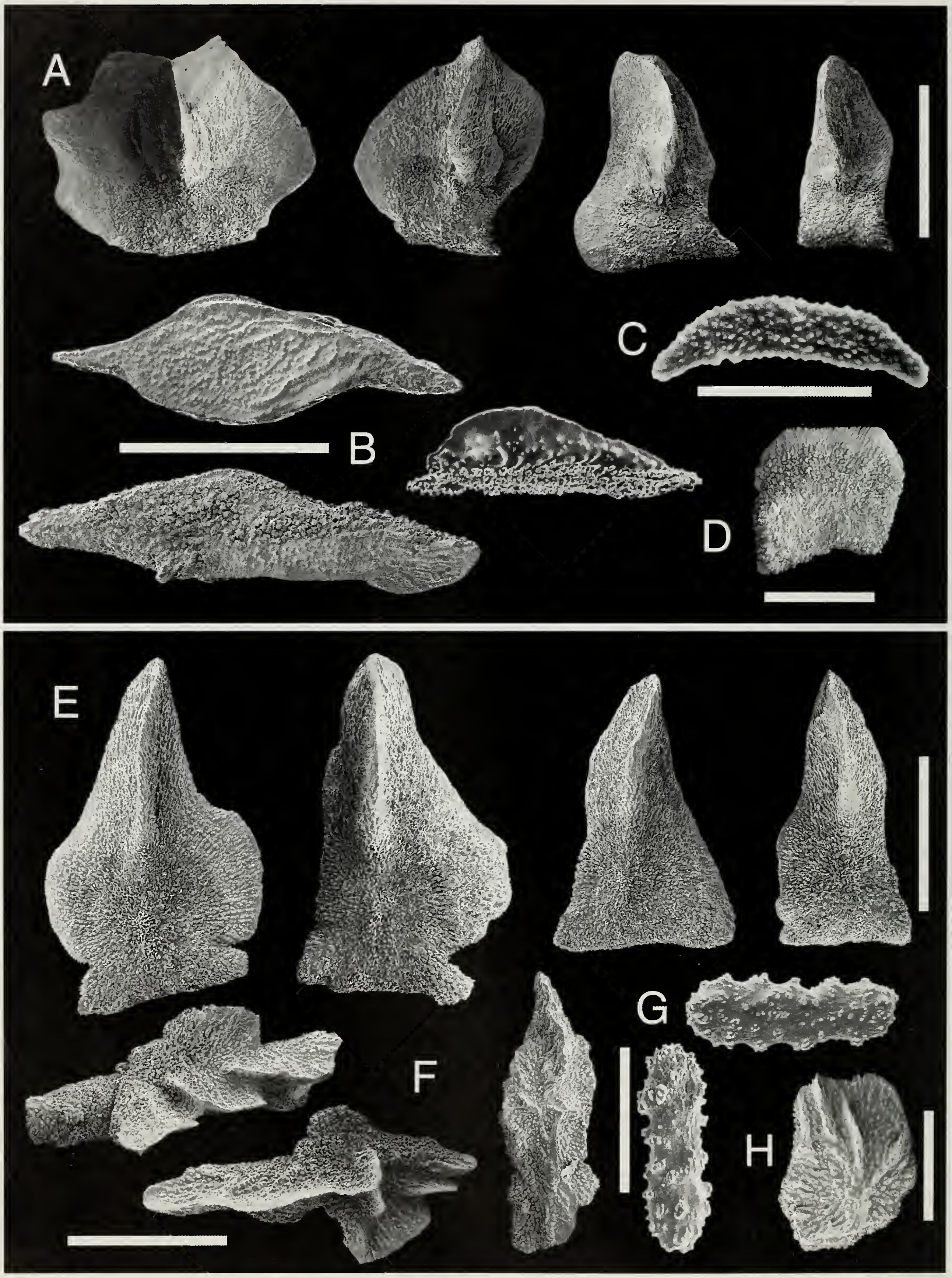

Fig. 3. A–D, *Narella bellissima* (A, B, D, *O*-2644, USNM 52776; C, P-881, USNM 52777): A, underside of abaxial, outer-lateral, inner-lateral, and adaxial opercular scales; B, three coenenchymal scales; C, a tentacular scale; D, an adaxial buccal scale. E–H, *Narella regularis* from *Alb*-2752, USNM 49385: E, underside of abaxial, outer-lateral, inner-lateral, and adaxial opercular scales; F, three coenenchymal scales; G, two tentacular scales; H, an adaxial buccal scale. Scale bars: A, B, E, F = 0.5 mm; C, G = 0.05 mm; D, H = 0.25 mm.

men of this species, but incorrectly identified it as *Stachyodes trilepis* (see Bayer, 2001). Versluys (1906) examined Studer's specimens, recognized the mistake, but, having examined only a small fragment of the type, declined to name it. He did note, and we concur, that Studer's illustration (Studer 1901:pl. 5) of the larger syntype, which was purportedly drawn at natural size, depicts the polyps at almost twice their normal size, and thus results in only half as many whorls per cm. Finally, Kükenthal (1915), in one line and one additional couplet in a key, provided the name *S. bellissima* for this taxon. He (Kükenthal 1919) later redescribed the species, but incorrectly reported the depth of capture as 1700 m, apparently misinterpreting the depth given by Studer in meters as fathoms. In the same paper, Kükenthal (1919) also reported *S. regularis* from St. Vincent, but examination of this specimen shows it to be typical *N. bellissima.* Likewise, examination of all the specimens reported as *N. regularis* by Deichmann (1936), which includes Kükenthal's specimen, shows them to be *N. bellissima.* Although widespread in the eastern Atlantic (see Distribution), these are the first correctly identified records of *N. bellissima* from the western Atlantic.

Histological sections prepared from samples of USNM 52772 specially fixed in Bouin's fixative confirm Studer's observation (1901:pl. 11, figs. 3, 6) on *Stachyodes trilepis* (=*Narella bellissima*) that the sulcal side of the polyps is abaxial. The longitudinal muscles of the mesenteries are very well developed, as would be expected in polyps capable of strong contraction and adaxial flexion, as illustrated by Studer (1901:pl. 11).

Narella regularis (Duchassaing & Michelotti, 1860)
Figs. 1B, 3E–H, 4A–C, 7

Primnoa regularis Duchassaing & Michelotti, 1860:17, pl. 1, fig. 12, 13.—Kölliker, 1865:135, pl. 17, fig. 13.—Duchassaing, 1870:13 (listed).—Wright & Studer, 1889:56.

Not *Stachyodes regularis* Wright & Studer, 1889:55 (junior secondary homonym, replacement name: *S. studeri* Versluys, 1906).—Kükenthal, 1919:466–467 (=*N. bellissima*).

Stachyodes regularis.—Versluys, 1906: 96.—Kükenthal, 1924:316.

Not *Narella regularis.*—Deichmann, 1936: 169.—Tixier-Durivault & d'Hondt, 1974: 1412.—Grasshoff, 1982a:738, map 3; 1982b:947 (all = *N. bellissima*).

Narella regularis.—Bayer, 1956:F222, fig. 159,5.

Material examined.—Bahamas, off Chub Cay, Berry Islands: 25°23.40′N, 77°55.25′W, 792 m, *JSL-II*-815, 13 Apr 1984, 10 branches cut from a large colony, USNM 1004861 (SEM 1728).

Off northwestern Cuba: 23°10′N, 81°28′W, 366 m, *Atl*-3480, 11 May 1939, 1 branch 6 cm long, MCZ 3674.

Off northwestern Cuba: 23°12′N, 81°22′W, 777 m, *Atl*-3469, 9 May 1939, 2 large colonies (one 45 cm tall and 11 mm in basal stem diameter), MCZ 3601.

Off St. Vincent: 13°34′00″N, 61°04′00″W, 514 m, bottom temperature 8.4°C, *Alb*-2752, 4 Dec 1887, 4 nearly complete colonies and 4 detached branches, USNM 49385 (SEM 381, 376, C1032).

Holotype (see below).

Types.—The holotype of *P. regularis* is deposited at the Museo Regionale di Scienze Naturali, Turin (Coel. 275), but all polyps had fallen from the axis, making it difficult to characterize the species. Type Locality: Guadeloupe, Lesser Antilles, depth unknown.

Description.—Colonies have a short main stem, above which they are equally and dichotomously branched at approximate intervals of 15–25 mm, resulting in a uniplanar (not lyrate) fan. The largest colony examined (*Alb*-2752) has a main stem of at least 3.5 cm (but is broken from the substrate) and 2.7 mm in axial diameter, a

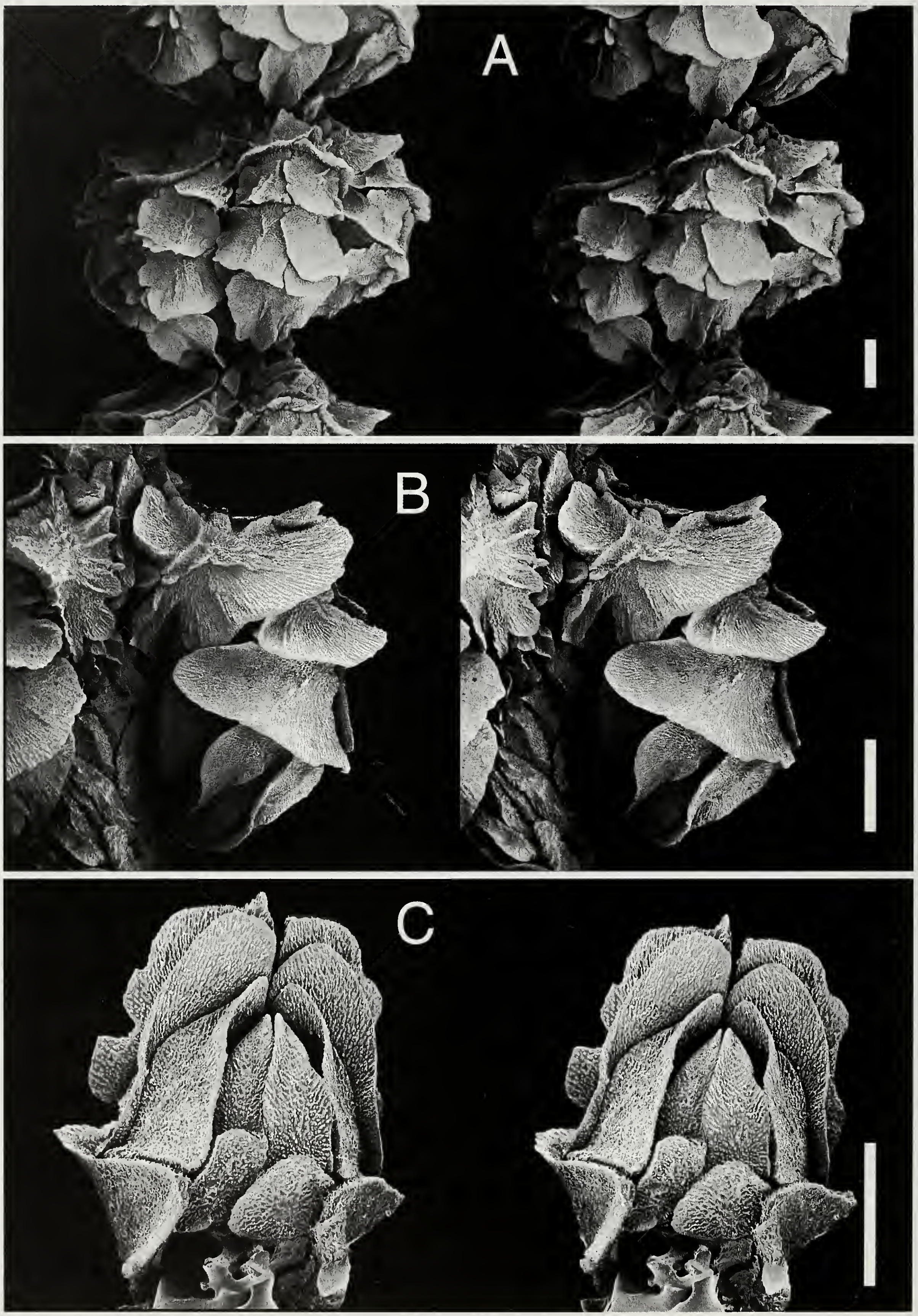

Fig. 4. *Narella regularis* from *Alb*-2752, USNM 49385: A, a complete polyp whorl; B, polyp in lateral view; C, polyp in adaxial view. Stereo views. All scale bars are 0.5 mm.

total colony height of 19 cm, and 37 terminal branchlets, the longest branchlet the result of 7 bifurcations. The axis is heavily calcified, fairly stiff and golden-yellow in color. Polyps are arranged in whorls of 4 or 5, the predominant number being 5. Whorls of polyps are fairly closely spaced, such that 11–13 whorls occur in 3 cm branch length, the tips of the opercular scales separated by about 0.45 mm from the basal scale of the adjacent polyp. The sides of each polyp do not touch each other, but are separated by 0.1–0.2 mm. The downward pointed polyps measure 2.0–2.3 mm in length parallel to the axis.

Each polyp is protected by 3 pairs of large abaxial body scales and a pair of smaller adaxial buccals. The sclerites of the basal pair project at a downward angle of about 60° from the axis and are about 1.25 mm in height, only the distal 0.1–0.2 mm extending beyond the junction with the medials. The basal scales curve around the body of the polyp but do not meet on the adaxial side. The pair of medials are much smaller (e.g., 0.50–0.65 mm long) and narrower, projecting at a downward angle of about 45° from the axis and having a distal outwardly flared margin. The abaxial buccals are slightly more elongate (e.g., 0.70–0.80 mm) and much broader, oriented essentially parallel to the branch axis and forming a cone that encircles only the very base of the opercular scales. The outer surface of the sclerites is distinctly roughened by close-set, sharp granules which impart a rough, shagreen-like appearance, and the inner surface where in contact with the mesogloea, by crowded, complex tubercles. The basal pair of body scales is ornamented by several sharply raised irregular ridges radiating from the depositional center or "nucleus," and similar, but less conspicuous, ridges mark the outer surface of the medial and buccal scales as well. The pair of small adaxial buccals are rhomboidal in shape, about 0.40 mm in greater diameter, and have a finely serrate distal edge.

The adaxial operculars are symmetrical isosceles triangles, varying in height from 0.6 to 0.9 mm and up to 0.45 mm in basal width (H:W = 2.0–2.2). The inner- and outer-lateral operculars are larger (up to 1.0 mm tall and 0.65 mm wide: H:W = 1.5–1.7) and asymmetrical, a bearing a slight shoulder on their adaxial side. The largest (i.e., abaxial) operculars are symmetrical, up to 1.1 mm in height and about 0.75 mm wide (H:W = 1.45–1.55). They are slightly notched basally, thus resembling certain Indian arrowheads. Thus all operculars, although differing in size and symmetry, have roughly the same H:W ratio, and all bear a longitudinal groove on their exterior surface and a prominent keel on their interior surface. All of the opercular scales are easily seen in side view, except for the very base, which is protected by the abaxial buccals. The tentacles contain small (65–75 μm long and about 20 μm wide), straight, granular rodlets. Coenenchymal scales are elongate and somewhat irregular in shape, arranged in one layer, up to 0.75 mm in length, and ridged, the ridges sometimes anastomosing on the surface.

Comparisons.—In addition to those characters mentioned in Table 1, *N. regularis* differs from *N. bellissima* in having larger, consistently triangular opercular scales (H:W always >1.5), which are largely unprotected by the abaxial buccal scales; a curved polyp, instead of one that is parallel to the branch axis; a smaller ratio in length of their buccal scales in relation their medial scales; lacking a distal translucent region; basal scales that do not meet on the adaxial side; and more highly ridged body wall and coenenchymal scales, the ridges of the latter sometimes anastomose.

Distribution.—Lesser Antilles, Bahamas, off Cuba (Fig. 7); 366–792 m.

Remarks.—Eliminating the misidentifications and simple listings of this species, as indicated in the synonymy, these are the first legitimate records of *N. regularis* subsequent to its description.

Narella pauciflora Deichmann, 1936
Figs. 1D, 5A–C, 6A–D, 7

Narella pauciflora Deichmann, 1936:170, pl. 25, fig. 3, pl. 26, fig. 2.

Material examined.—Off Morro Light, Cuba: 1473 m, *BL*-2, date, 3 branches, MCZ 4807?.

Off Campeche Bank, Mexico: 23°52′N, 88°58′W, 1473 m, *BL*-35, date, 1 complete colony and several branches, MCZ 4814, 4814a.

NW of Cardenas, Cuba: 23°54′N, 81°27′W, 1153–1190 m, *G*-375, 17 Sep 1964, several badly damaged branches retaining only a few polyps, USNM 52771.

Off northwestern Cuba: 23°24′N, 81°00′W, 676–1106 m, *Atl*-2995, 16 Mar 1938, 3 colony fragments, MCZ 3872.

Off northwestern Cuba: 23°22′N, 81°05′W, 859–1216 m, *Atl*-2996, 16 Mar 1938, 3 colony fragments, MCZ 3831.

South of Cay Sal Bank: 23°51.9′N, 80°42.7′W, 1079–1089 m, *G*-1111, 30 Apr 1969, 9 branches, the largest 19 cm tall, USNM 52772 (SEM 377, 377A, C1013).

N of Cardenas, Cuba: 23°51′N, 81°02′W, 1107–1162 m, *G*-372, 16 Sep 1964, 2 branches, the larger 12 cm tall, with one bifurcation, the other unbranched and partly denuded, USNM 52773.

NE of Havana, Cuba: 23°45′N, 81°49′W, 1400–1395 m, *G*-965, 1 Feb 1968, 5 broken branches, the largest 21 cm tall, with ophiuroids attached, cortex and polyps rubbed off in several places, USNM 52774.

Off St. Lucia: 14°17′N, 60°45.2′W, 1280 m, *P*-892, 7 Jul 1969, 3 branches, the largest 27 cm tall with several bifurcations, apparently about half of a colony, without holdfast, severely damaged, with attached ophiuroids, USNM 52775 (SEM 1729).

Tongue of the Ocean, Great Bahama Bank: 24°02′N, 77°17′W, 1335 m, *CI*-19, 6 Jul 1972, one nearly complete colony with part of calcareous holdfast, 31 cm tall, terminal branchlets broken off, ophiuroid attached, dry, USNM 57571 (SEM 1704); 5 branches, the largest 22 cm tall, and smaller fragments more or less damaged, with ophiuroid attached, USNM 57572.

Tongue of the Ocean, Great Bahama Bank: 23°29′N, 77°05′W, 1234 m, *CI*-46, 24 Feb 1973, several badly broken fragments, the largest about 18 cm tall, with ophiuroids attached, in alcohol, USNM 57573 (SEM 406, 1730).

Tongue of the Ocean, Great Bahama Bank: 23°40′N, 77°08′W, 1372 m, *CI*-47, 24 Feb 1973, one badly damaged branch about 10 cm tall, most polyps lost, USNM 57574.

Straits of Florida between Delray Beach, Florida, and Grand Bahama Island: 26°24′N, 79°36′W, 738 m, *CI*-140, 28 Sep 1973, 6 broken branches severely decorticated, the largest 23 cm tall, USNM 57575.

NE of San Juan, Puerto Rico: 18°40′N, 65°58′W, 1446–1510 m, *P*-830, 4 Feb 1969, several broken branches, the largest 12 cm tall, and decorticated fragments, with ophiuroids attached, USNM 57577.

Locality unknown: unknown *Blake* station, 3 branches, MCZ 4813.

Types (see below).

Types.—The holotype (*BL*-124, MCZ 4809) consists of one branch 13 cm long and several smaller branches preserved in alcohol. The paratypes (BL-227, MCZ 4810 and 4810a) consist of one broken colony and several branches, also preserved in alcohol. Type Locality: 17°47′30″N, 64°53′45″W (off St. Croix), 1061 m.

Description.—Colonies have a stout main stem that is entirely calcified (white) and which bifurcates repeatedly in a fairly regular fashion (dichotomous branching) resulting in a uniplanar colony. The largest specimen (*CI*-19) is 31 cm tall, having a calcified basal stem 13 mm in diameter and 24 mm in height. Branching is fairly sparse, branch segments between branching nodes are 10–50 mm in length, and the longest terminal branch is 14 cm, the distal most branch being the result of 6 successive bifurcations. The angle between branches is only 25°–30°. Above the calcified base, branches are fairly stiff, golden-yellow in

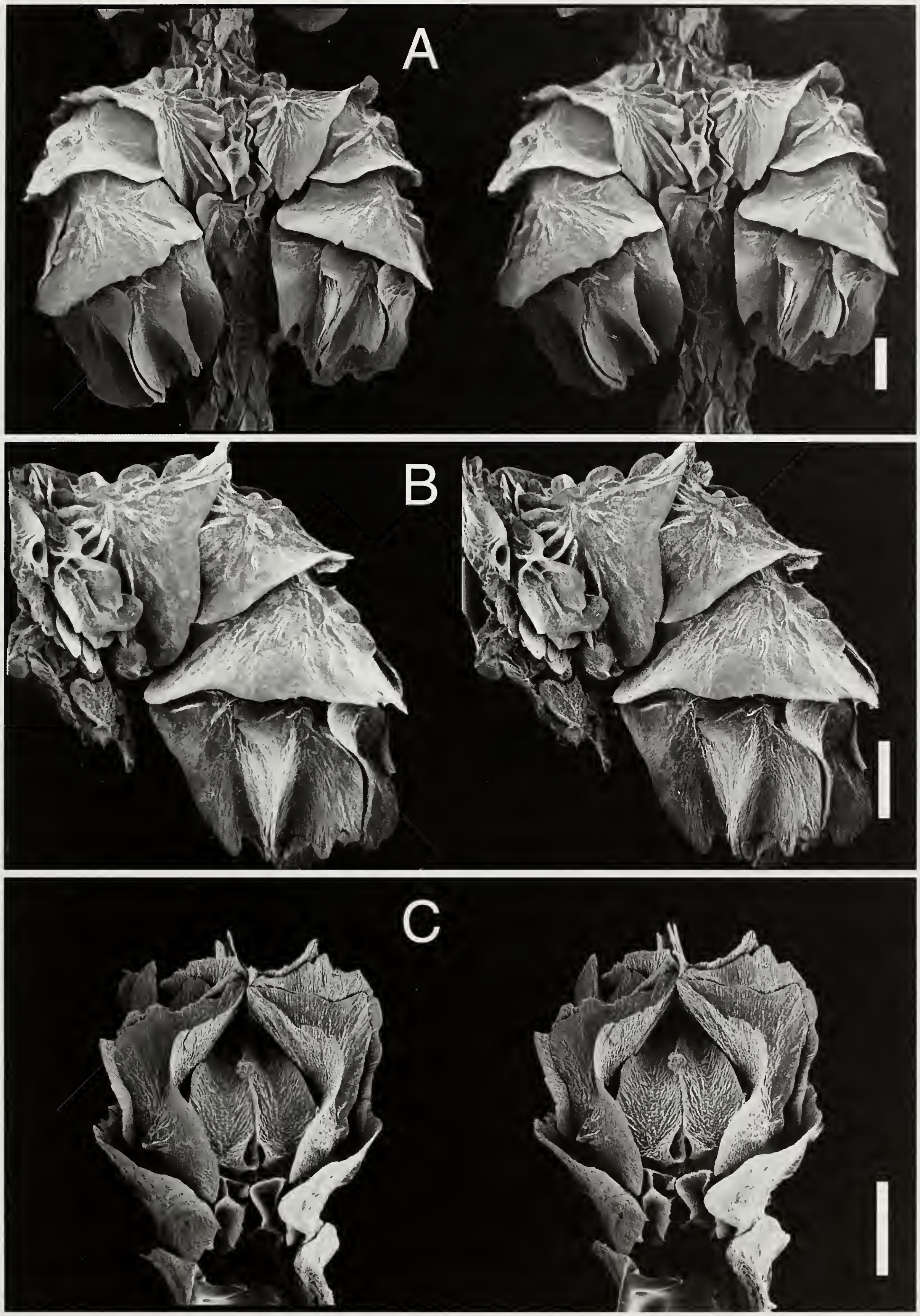

Fig. 5. *Narella pauciflora* from G-1111, USNM 52772: A, a complete polyp whorl; B, polyp in lateral view; C, polyp in adaxial view. Stereo views. All scale bars are 0.5 mm.

color, and longitudinally grooved. Polyps are fairly well separated, arranged in whorls of 2–5 (usually 3) and only 6–9 (usually 7) whorls occurring in 3 cm. Thus, the lateral edges of each polyp in a whorl are separated from its adjacent polyps in that whorl by approximately the width of a polyp, and whorls are separated from one another by about 1.5 mm. As is characteristic for the genus, the polyps are pointed downward, measuring 2.6–2.8 mm in length.

Each polyp is protected by 3 pairs of large abaxial body scales and 1–2 pairs of much smaller adaxial buccal scales. The sclerites of the basal pair project at a downward angle of about 70° from the axis, and are about 1.1–1.3 mm in height, only the distal 0.2 mm extending beyond the junction with the medials. The basal scales curve around the body of the polyp but do not meet on the adaxial side. The medials are smaller (about 1.0 mm), projecting at a downward angle of about 25° from the axis. The abaxial buccals are of intermediate size (about 1.15 mm) and much broader than the medials, oriented parallel to the axis or at a slight angle from it, forming a cone that encircles only the very bases of the eight opercular scales. Although somewhat variable, the surfaces of the 3 pairs of large abaxial sclerites are ornamented with prominent ridges, these ridges radiating from a center in the basal third of each sclerite. Otherwise, the outer surface of these sclerites is fairly smooth. The pair of adaxial buccals are square to slightly rectangular in shape and about 0.7 mm in width. They are usually highly ridged, the ridges sometimes reticulate, and have a finely serrate upper edge. Often there is another pair of smaller scales about half the size of the adaxial buccals that are directly proximal to the adaxial buccals, which are also ridged.

The adaxial operculars are tall symmetrical triangles, and are by far the smallest opercular scales, about 1.15 mm in height and 0.35 mm in width (H:W of 2.9–3.3). The inner-lateral operculars have a broad base, which is asymmetrically elongated on the adaxial side to partially cover the adaxial operculars. These sclerties are up to 1.5 mm in height and 1.0 mm broad at the base (H:W = 1.4–1.5). Outer-lateral and abaxial operculars are even taller (up to 2.0 mm) and about 0.75 mm in width, resulting in H:W of about 1.5–2.0, these sclerites sometimes having 2 or 3 pointed tips. All opercular sclerites are deeply creased medially, edges of adjacent sclerites almost parallel with one another, the crease corresponding to a thick medial keel on the interior surface of the sclerite. Opercular sclerites also bear low, radiating ridges on their outer surfaces, and each adaxial opercular often bears a small (0.15 mm in diameter), short tube on its lower adaxial margin (Fig. 5C) of unknown function. The tentacles contain small, straight granular rodlets 65–90 μm in length and about 15 μm in width. Coenenchymal scales are elongate (up to 1.9 mm), irregular in shape, and ridged, the ridges often radiating from a central point, sometimes longitudinal, and sometimes quite high and reticulate, the latter case most common on those coenenchymal scales adjacent to the basal scales.

Comparisons.—*Narella pauciflora* is perhaps closest morphologically to *N. regularis* (see Table 1), but can be distinguished by its larger polyps, fewer polyps per whorl, fewer polyps per unit distance on a branch, and in often having two pairs of highly ridged adaxial buccal scales.

Distribution.—Antilles and Bahamas (Fig. 7); 738–1473 m.

Remarks.—This is the first report of this species since its original description.

Narella alvinae, new species
Figs. 6E–I, 7, 8A–D

"delicate coral" Calder, 1993:1, 26–27 (color figures).

Material examined/holotype.—25 km NW of Bermuda: 32°35′N, 64°55′W, 3419 m, *Alvin*-2566, 17 Mar 1993: main colony now fragmented into 47 fragments, the largest 27 cm in height with 6 terminal branch-

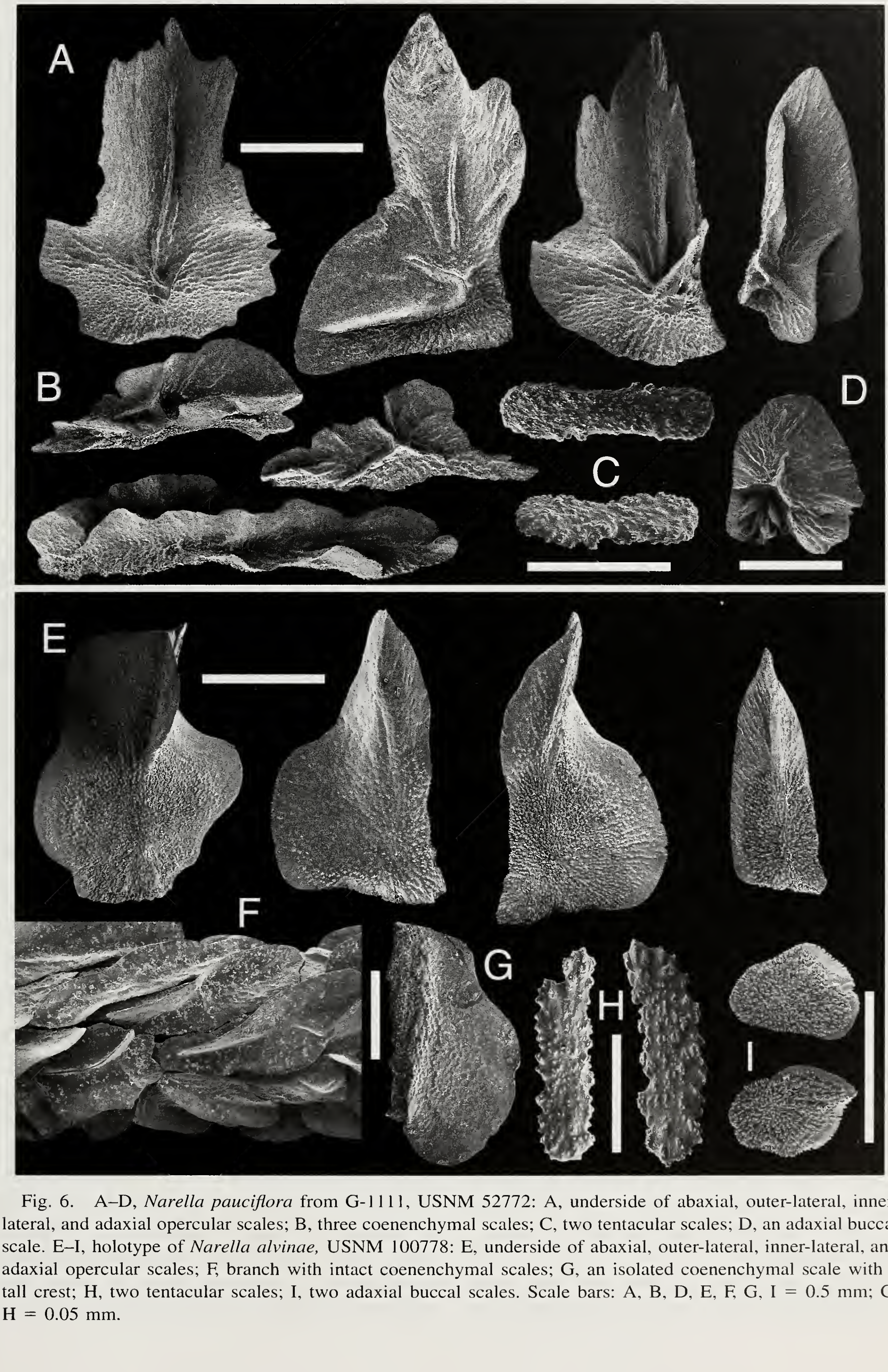

Fig. 6. A–D, *Narella pauciflora* from G-1111, USNM 52772: A, underside of abaxial, outer-lateral, inner-lateral, and adaxial opercular scales; B, three coenenchymal scales; C, two tentacular scales; D, an adaxial buccal scale. E–I, holotype of *Narella alvinae,* USNM 100778: E, underside of abaxial, outer-lateral, inner-lateral, and adaxial opercular scales; F, branch with intact coenenchymal scales; G, an isolated coenenchymal scale with a tall crest; H, two tentacular scales; I, two adaxial buccal scales. Scale bars: A, B, D, E, F, G, I = 0.5 mm; C, H = 0.05 mm.

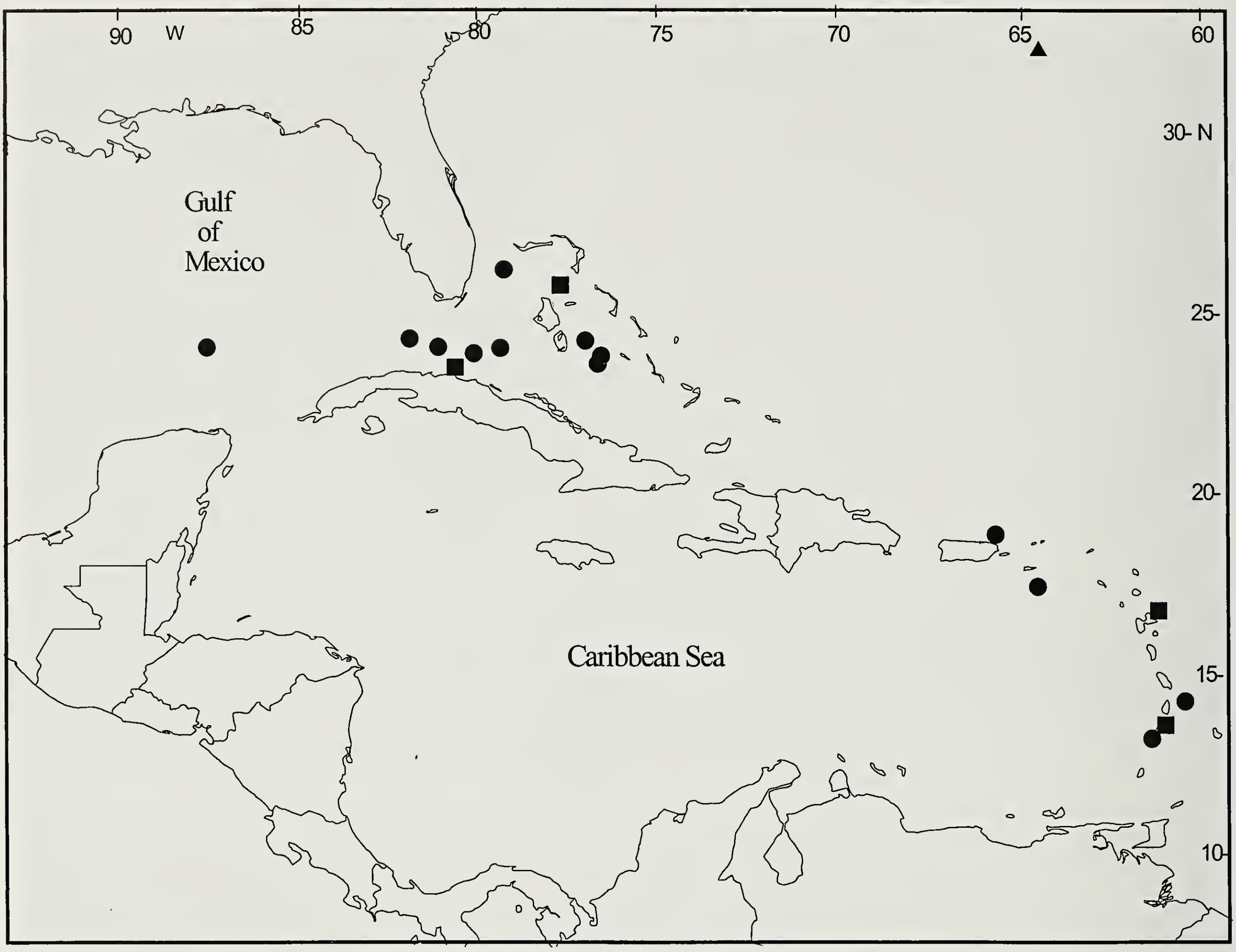

Fig. 7. Distribution of *Narella pauciflora* (circles), *N. regularis* (squares), and *N. alvinae* (triangle).

es, ROMIZ B3521; 12 branches and hundreds of separate polyps, USNM 100778 (*SEM* C1023-26, 1030), all from the same colony and considered to be holotypic. Type Locality: as stated above.

Description.—The holotypic colony is sparingly and dichotomously branched in one plane, resulting in 26 rather long terminal branches 10–13 cm long. Most of these branches have been broken from the main colony, but the entire colony is figured in situ by Calder (1993). The thickest branch axis is only 0.9 mm in diameter, fairly rigid, smooth, and golden-yellow in color. Polyps whorls are spaced 1.2–1.7 mm apart. There are 4 polyps within each whorl and about 7 whorls occur in 3 cm of branch length. Fully developed polyps are 2.7–3.1 mm in length.

The polyps are covered by 3 pairs of large abaxial scales and 1 pair of adaxial marginals (buccals), sometimes with a few much smaller adaxials in a more proximal position on the polyp. The sclerites of the abaxial basal pair project perpendicular to the axis and are about 1.7 mm in height, the distal 0.6 mm projecting beyond the junction with the adjacent medials as a prominent lobe, the 2 of which together form a collar around the base of the polyp. Each basal sclerite bears a prominent longitudinal crest up to 0.45 mm in height at the point of curvature from the abaxial to lateral edges of the scale; these scales do not form a complete ring and thus do not touch or fuse on the adaxial side. In fact, the lower proximal edge of each basal sclerite is often slightly notched, the notch fitted to a slightly apically indented coenenchymal scale. Furthermore, the coenenchyme between the basals of 2 adjacent polyps consists of 2 characteristically long (up to

1.8 mm) coenenchymal sclerites that bear unusually tall crests (up to 0.48 mm). The structure and position of the coenenchymal sclerites that surround the basal sclerites is consistent and would appear to "lock in" or stabilize the basal sclerites into the coenenchymal sclerites, the interpolyp scales preventing lateral motion and those at the proximal ends of the basals preventing longitudinal movement, which might explain why in this species it is common for most of the polyps to be abraded from the axis but the basals remaining intact on the axis. The medial sclerites are 1.4–1.6 mm in length, not ridged, and have a thin, transparent, slightly upward curved distal edge. Buccal sclerites are similar to the medials but wider, overlapping only the basal region of the opercular scales. All abaxial scales are coarsely granular exteriorly. A pair of well-developed (0.45 mm in width), flat, rectangular adaxials occur contiguous to the adaxial operculars. In some specimens smaller (0.15 mm), elliptical adaxial sclerites occur lower on the polyp wall.

The adaxial operculars are the smallest of the operculars, symmetrically triangular, up to 1.05 mm in height and about 0.38 mm in greatest (basal) width (H:W = 2.5–2.7). The inner- and outer-lateral operculars are slightly larger (up to 1.4 mm and 0.70 mm in width: H:W = 1.8–2.2), and asymmetrical, the widest point being about a third of the distance from the base caused by a small lobe on the adaxial side of the sclerite. The abaxial operculars are symmetrical, up to 1.4 mm in height and 1.0 mm in width (H:W = 1.23–1.45), widest about a third up from the base cause by symmetrical lobes on either side of the sclerite, and bluntly tipped. All opercular sclerites are deeply longitudinally grooved externally, which corresponds to a prominent keel on their interior surface. The tentacular rodlets are flattened and granular, up to 97 μm in length and 24 μm in width. The coenenchymal scales are thin, slender (0.25 mm), elongate (1.2–2.0 mm) plates, imbricating on their edges, each plate having one thin, transparent, longitudinal ridge up to about 0.20 mm tall, which gives the branch axis a "frilly" aspect. As mentioned above, the coenenchymal sclerites adjacent to the basals have even taller ridges.

Etymology.—Named in honor of the collecting vessel, the R/V *Alvin.*

Comparisons.—Although similar to *N. laxa* in branching pattern, *N. alvinae* is morphologically most similar to *N. pauciflora* (see Table 1), both species having a similar number of polyps per whorl and whorls per cm, and polyp size; however, *N. alvinae* differs in having prominent lobes on its basal scales, sparse branching, and prominent crests only on the basal scales at the point of curvature from the abaxial to lateral edges. *N. alvinae* appears to be unique in having coenenchymal sclerites with prominent longitudinal crests.

Distribution.—Known only from the type locality off Bermuda (Fig. 7), 3419 m. This is the deepest known record of a *Narella* and one of the deepest collected primnoids on record.

Narella versluysi (Hickson, 1909)
Figs. 1F, 9A–C, 10A–D, 14

Calypterinus Allmanni (sic).—Roule, 1896: 303–304.—Versluys, 1906:93.

Stachyodes sp.—Versluys, 1906:93–94.

Stachyodes versluysi Hickson in Stephens, 1909:10–13.—Kükenthal, 1919:456–457; 1924:309.—Thomson, 1927:30–32, pl. 2, fig. 19, pl. 5, figs. 12–13 (in part: not station 970).—Stiasny, 1941:80–81.

Narella versluysi.—Deichmann, 1936: 171.—Grasshoff, 1982a:738, 747 (map 3); 1982b:946–947, figs. 13–14.—Carpine & Grasshoff, 1985:33.—Grasshoff, 1986:27.

Narella elegans Tixier-Durivault & Lafargue, 1968:622–626, figs. 3–4.

Material examined.—Straits of Florida, off St. Lucie Inlet, Florida: 27°06′N, 79°32′W, 677–659 m, *G*-170, 29 Jun 1963, one unbranched stem 35 cm long, lacking

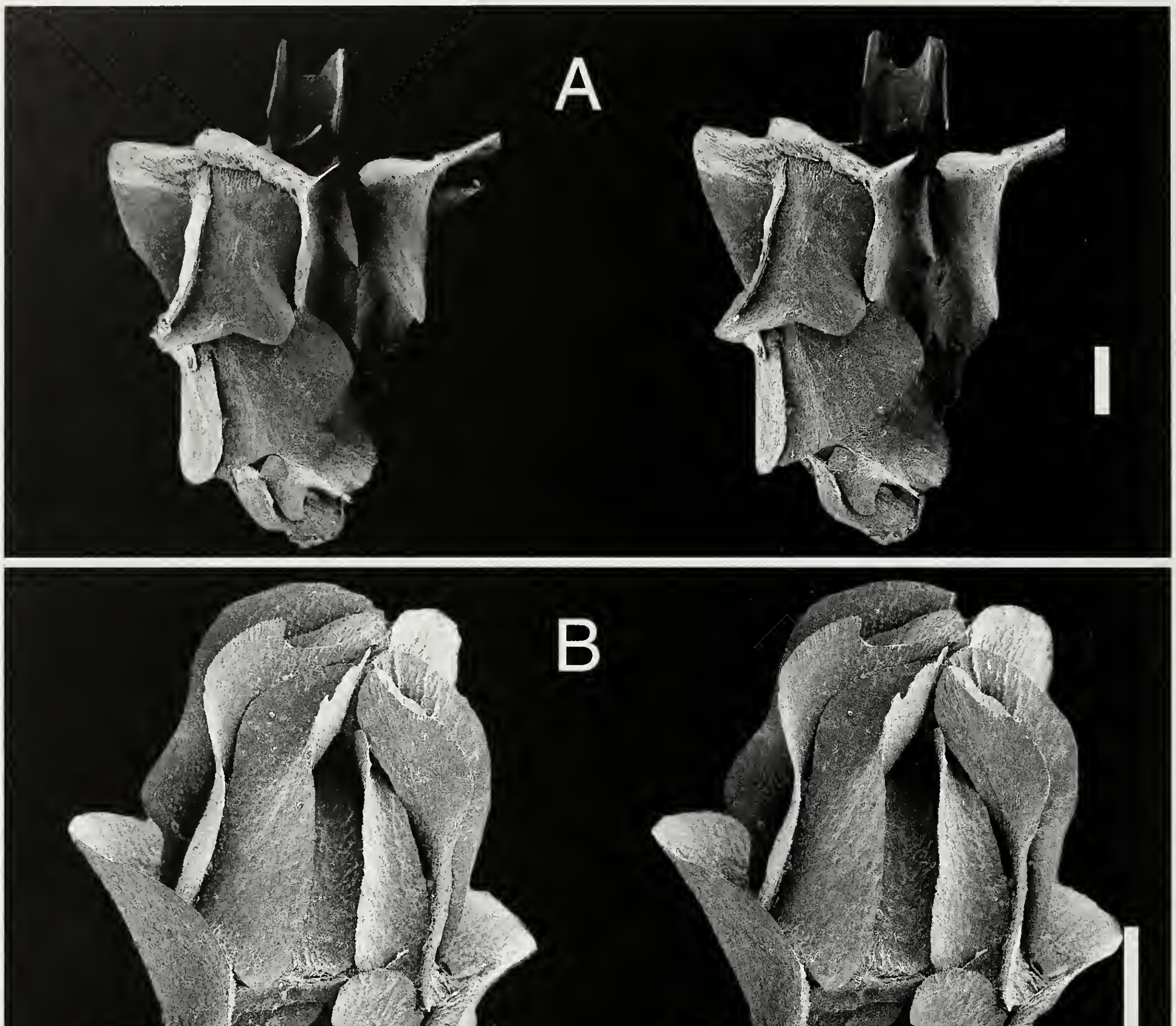

Fig. 8. *Narella alvinae,* holotype, USNM 100778: A, lateral view of polyp; B, polyp in adaxial view; C, lateral view of polyp; D, oral (opercular) view of polyp. A and B stereo views. All scale bars are 0.5 mm.

base and apex, USNM 52900 (unnumbered SEM stub).

Straits of Florida, between Palm Beach, Florida, and Settlement Point, Grand Bahama Island: 26°28′N, 79°33′W, 751 m, *G*-808, 13 Sep 1966, 2 pieces 5.5 and 12 cm long, probably of a single unbranched stem, lacking base and apex, USNM 52902.

Straits of Florida, off Delray Beach, Florida: 26°24′N, 79°36′W, 738 m, *CI*-140, 28 Sep 1973, 2 pieces 7 and 37 mm long, probably of a single unbranched stem, lacking base and apex, USNM 57570 (SEM 413, C1014–1015).

Straits of Florida off Delray Beach, Florida: 26°23′N, 79°37′W, 743–761 m, *CI*-246, 29 Oct 1974, 2 partly decorticated pieces 6 and 24 cm long, apparently part of one unbranched stem, lacking base and apex, USNM 57569.

Straits of Florida west of Riding Rock, Bahama Islands: 25°26′N, 79°23′W, 796 m, *G*-304, 23 May 1964, 3 unbranched stems, the largest 30 cm long, USNM 52901 (SEM 375).

Off northwestern Cuba: 23°18′N, 80°46′W, 896 m, *Atl*-3474, 10 May 1939, 2 branches the longest 17 cm, MCZ 3727 and 43647.

Off Bermuda: 32°14.47′N, 64°47.07′W, 900 m, "tangled in crab pot", 15 Nov 1990, one dry branch fragment 9 cm long, USNM 1004792; parent lot 76 cm long, dry, Bermuda Biological Research Station, uncataloged.

Types (see below).

Types.—Five syntypes are deposited at The Natural History Museum, London (1962.07.20.172) and an SEM stub (404) of one of these syntypes is at the USNM. Type Locality: off Ireland; 698–914 m.

Description (western Atlantic specimens).—Colonies evidently are unbranched, straight or nearly so, with a nearly uniform diameter of 5–7 mm (including polyps) and attaining a length up to 34.5 cm (*G*-170), although eastern Atlantic specimens are known to be as long as 78 cm (Hickson 1909). The axis is heavily calcified, brittle, and longitudinally grooved, with dull golden reflections, in the most robust specimen only 2.2 mm in axial diameter. In one specimen, the proximal part of the axis shows calcareous thickening of the kind present just above the holdfast of many other species. Polyps are fairly closely spaced, the lateral edges of polyps within a whorl touching each other, and the opercular scales of the zooids of one whorl touching (or nearly touching) the basal sclerites of the polyps of the next whorl. Polyps are arranged in whorls of 4–7, and 8–10 whorls occur in 3 cm of branch length. Polyps measure 3.2–3.7 mm in length, measured parallel to the axis from the basal part of the basal sclerites to the apex of the abaxial operculars.

Each polyp is protected by 3 pairs of large abaxial body scales and a variable number of smaller adaxial scales. The sclerites of the basal pair project perpendicular or at a downward angle of 60° from the axis and are about 2.1 mm in height, the distal 0.7–0.8 mm flared outward abaxially as a pair of rounded, smooth-edged, very thin, petal-like processes without marginal points or spines. The inner surface of one or both basal scales may have one or more prominent keels, which may be visible even in abaxial view and which articulate with a notch or groove on the lower side of the adjacent medial sclerite (Fig. 9A). The basal sclerites are smoothly curved around the base of the polyp but do not meet adaxially. The medials are the smallest of the large body wall scales, about 1.2 mm in length and fairly narrow, encircling only about half of the polyp. They also have a free, upturned distal edge that is very thin and delicate, oriented about 45° from the axis. The abaxial buccal scales are of intermediate size (about 1.7 mm in length), oriented parallel to the axis, and also concave in shape, their distal margins thin and flared outward as the other 2 pairs. These buccal scales form a prominent, open collar or cone that encircles only the basal region of the 8 operculars. Except for the internal

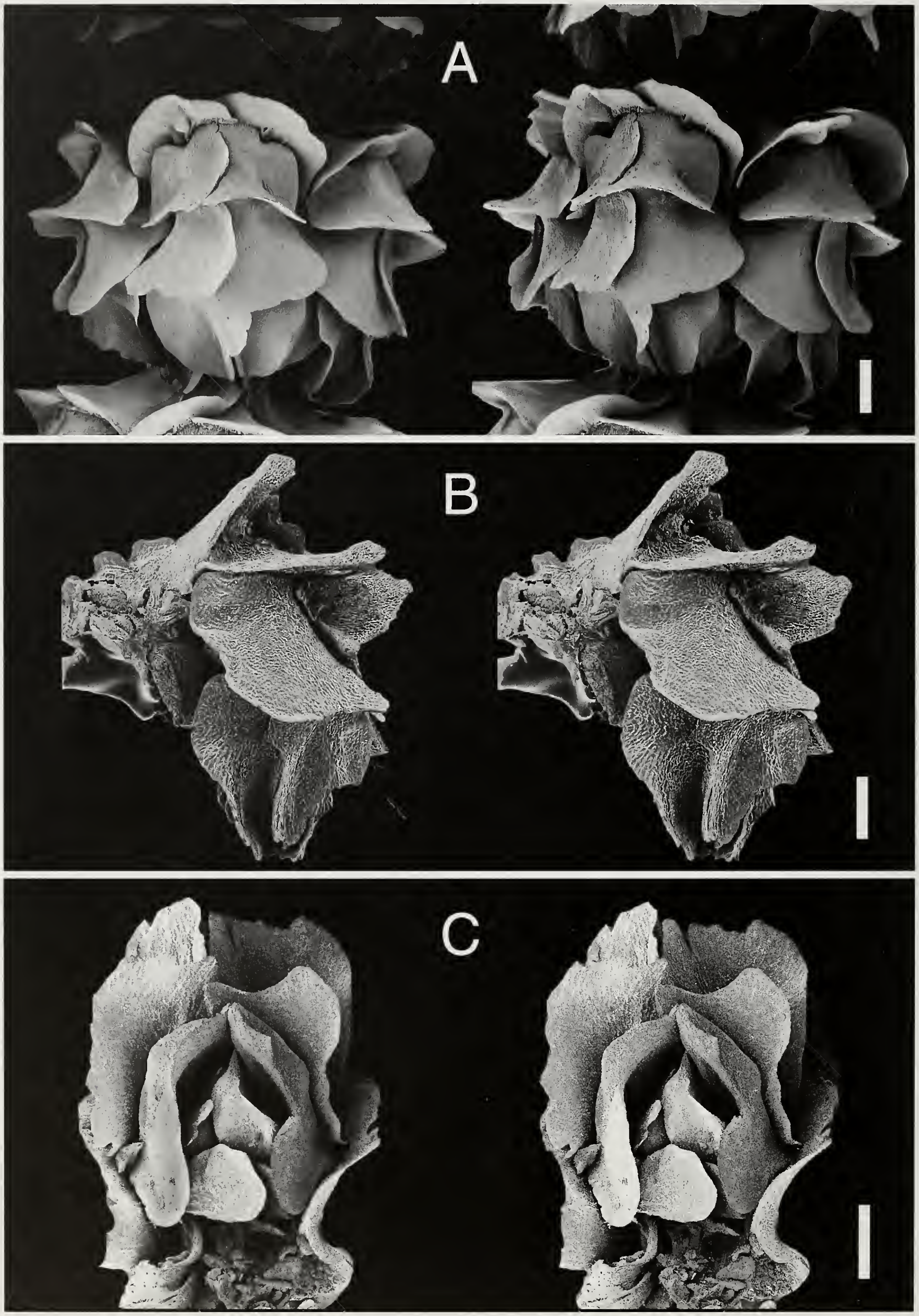

Fig. 9. *Narella versluysi*: A, *G*-304, USNM 52901, a complete polyp whorl; B, syntype, polyp in lateral view; C, *CI*-140, USNM 57570, polyp in adaxial view. Stereo views. All scale bars are 0.5 mm.

ridges of the basal scales, the exterior surfaces of the body scales are not ridged or keeled, but covered with a prominent granulation that seems to radiate from a central region of each scale. The adaxial side of each polyp is furnished with a pair of rather large marginal (buccal) scales, quadrate to tear-drop shaped, up to 0.40 mm in diameter, and having finely serrate edges. Additional pairs (up to 5 or 6) of smaller (0.14–0.30 mm width) adaxial scales occur proximal to these two marginal adaxial buccals, their distal margins becoming more coarsely serrate toward the base of the polyp.

As is typical in the genus, the adaxial operculars are the smallest of the opercular scales and shaped as isosceles triangles; they are about 1.0 mm in height and 0.30–0.50 mm in width (H:W = 2.1–3.3), often variable in width within the same polyp, one adaxial opercular being considerably wider than the other. The inner- and outer-lateral operculars are taller and broader, up to about 1.6 mm in height and 0.70–0.95 mm in width (H:W = 1.6–2.1). The abaxial operculars are of a similar height (1.5–1.6 mm), but are wider than the laterals at mid-height (resulting in a H:W of 1.2–1.3), and are blunt-tipped. All opercular scales bear a prominent ridge or keel on the distal half of their interior surface, the keel increasing in prominence in the ad- to adaxial direction, that of the abaxial opercular as much as 0.45 mm in height. The inner- and outer-lateral operculars are asymmetric in shape, each scale having a slightly broader shoulder on the adaxial side of the medial keel; the ad- and abaxial operculars are symmetric in shape. The tentacles are filled with thin, elongate (up to 80 μm long and 20 μm width), finely granular rodlets, some of which are curved to conform to the shape of the tentacle. Coenenchymal sclerites are thin and scale-like, up to 1.4 mm in length, and not closely fitted but commonly with one edge flared outward as a thin expansion projecting over neighboring scales and sometimes with a thin crest on the outer surface.

Comparisons.—Within the Atlantic, a branch fragment of *N. versluysi* could easily be confused with a terminal branch of *N. bellissima,* both species having prominent basal scales, body wall scales with thin distal edges, and a similar number of polyps per whorl (Table 1). But, *N. versluysi* differs in having larger polyps and larger-diameter branches; shorter buccal scales that expose most of the opercular scales; small, stellate adaxial scales; unridged basal scales; and fewer polyps per cm.

Distribution.—Eastern Atlantic: off Ireland, Bay of Biscay, Azores, off Portugal, off western Sahara (Grasshoff 1982a, 1982b); 550–3100 m. Western Atlantic: Bermuda; Straits of Florida (Fig. 14); 677–900 m. The record off Spitsbergen Bank, Arctic Ocean at 48 m (Thomson 1927) is an unlikely locality and depth; Carpine & Grasshoff (1985) implied that there might have been a labelling error associated with this record.

Remarks.—The present specimens agree in the main with Hickson's description of *Stachyodes versluysi* from off the west coast of Ireland. The two obvious differences may be superficial and of no taxonomic importance. First, in the present material, the smallest number of polyps in a whorl ranges from 4 to 7, whereas in the type material the smallest number reported is 9 and the largest "about 14." Although this could be no more than a reflection of colonial size, the diameter of Hickson's specimen at its distal end was not much larger than in the present material but there it had 9 polyps compared with 5 in the present specimens. In regard to number of polyps per whorl, the western Atlantic specimens are more similar to specimens reported by Thomson (1927) from the Azores, which have predominantly 7 or 8 (range 6–10) polyps per whorl or those described by Tixier-Durivault & Lafargue (1968) from the Bay of Biscay as *N. elegans,* which have 4–6 polyps per whorl; however, in the

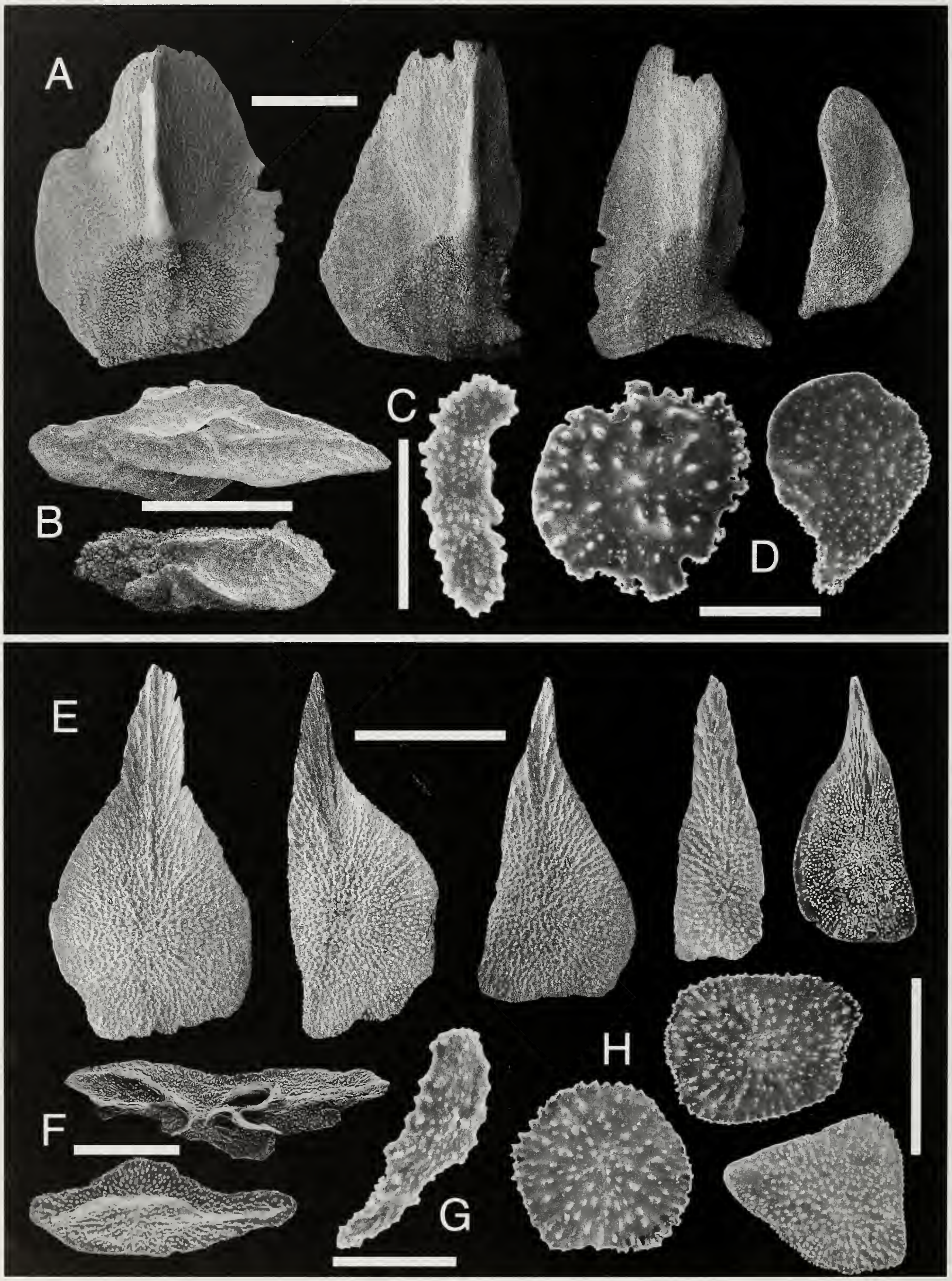

Fig. 10. A–D, *Narella versluysi* (A, B, CI-140, USNM 57570; C, D, G170, USNM 52900): A, underside of abaxial, outer-lateral, inner-lateral, and adaxial opercular scales; B, two coenenchymal scales; C, a tentacular scale; D, two adaxial buccal scales. E–H, holotype of *Narella laxa,* USNM 11853: E, upperside of abaxial, outer-lateral, inner-lateral, and two adaxial opercular scales; B, two coenenchymal scales; C, a tentacular scale; D, three adaxial buccal scales. Scale bars: A, B, E, F = 0.5 mm; C, G = 0.05 mm; D (right), H = 0.25 mm; D (left) = 0.09 mm.

latter case the polyps are also smaller, only 2.5 mm in length. But, Grasshoff (1982b) considered a polyp length range of 2.5–4.0 mm to be within the intraspecific range for this species. A second difference appears in the coenenchymal plates, which in *S. versluysi,* according to Hickson (1909:11), are large "compound" plates over 1 mm long, which break down into smaller "oblong, square, leaf-shaped, stellate and quite irregular" scales upon prolonged treatment with caustic potash. Perhaps by this drastic treatment (not used in the present study) Hickson was merely breaking up fully developed scales that may have been weakened by rough handling during collection.

J. A. Thomson's description (1927:30) of 18 specimens from the Josephine Bank and off the Azores also agrees in general both with Hickson's account and with the present western Atlantic material. However, the weak lateral crests on the basal scales described by Thomson but not evident in his beautifully drawn figure of an isolated polyp (1927:pl. 2, fig. 19), casts some doubt on the identification of his specimens as *Narella versluysi.* Two small pieces of Hickson's type specimen, which one of us (FMB) has examined in The Natural History Museum (London) through the kindness of Dr. P. F. S. Cornelius, show no trace of crests on the basal scales, although adjacent coenenchymal scales definitely have crests.

Previously known only from the eastern Atlantic, this is the first report of this species from the western Atlantic. Although generally assumed to be an unbranched species, some authors have qualified this description to include "slightly branched". Indeed, very few, if any, colonies have been collected intact including a holdfast, and thus the nature of its branching is difficult to verify.

Narella laxa Deichmann, 1936
Figs. 1E, 10E–H, 11A–C

Narella laxa Deichmann, 1936:170, pl. 26, fig. 1.—Grasshoff, 1985:305.

Material examined types.—South of Georges Bank: 40°34′18″N, 66°09′00″W, 3186 m, bottom temperature 3°C, *Alb*-2573, 2 Sep 1884: one dry colony 14 cm high and 6 cm wide, with a detached branch, USNM 11853 (holotype) (SEM 410, 411, C1027-28). Type locality: as stated above.

Same data: One fragment 1.5 cm long, with 4 whorls only, in alcohol. From the same haul as the holotype and probably a piece of it. The preservative has at some been slightly acid, as the sclerites are chalky in appearance and extremely fragile, USNM 49426.

Same data: one fragment 2.8 cm long, with 7 whorls; dry, glued to a piece of black cardboard. From same haul as holotype and undoubtedly a piece of it, MCZ 4811.

Description.—The large holotypic colony is sparingly branched in one plane, the short (5.4 mm tall and 1.6 mm in diameter) main stem dichotomously dividing, the remaining divisions all occurring within 15 mm of the first bifurcation, resulting in 9 undivided terminal branches 10–13 cm in length. The axis is stiff, brittle, smooth, light yellowish brown with scant indication of metallic luster in dry condition. Polyp whorls are fairly well spaced, a distance of about 2.5 mm separating each whorl, the polyps within a whorl touching laterally. Polyps are arranged in whorls of 3–5, of which 5–7 (or even 8 in places where whorls of young polyps are present between older ones) occur in 3 cm of branch length. Fully developed polyps are about 3 mm long, measured parallel to the axis; younger individuals are about 1.75 mm long.

The polyps are covered by 4 pairs of large abaxial body scales (1 pair of basals, 2 pairs of medials, and 1 pair of buccals), 2–3 pairs of smaller adaxial scales, and occasionally one or more inner-lateral buccal scales. The sclerites of the basal pair project perpendicular to the axis, and are about 1.4 mm in height, the distal 0.4 mm extending as short, rounded lobes beyond the junction with the first medial pair. The basal sclerites

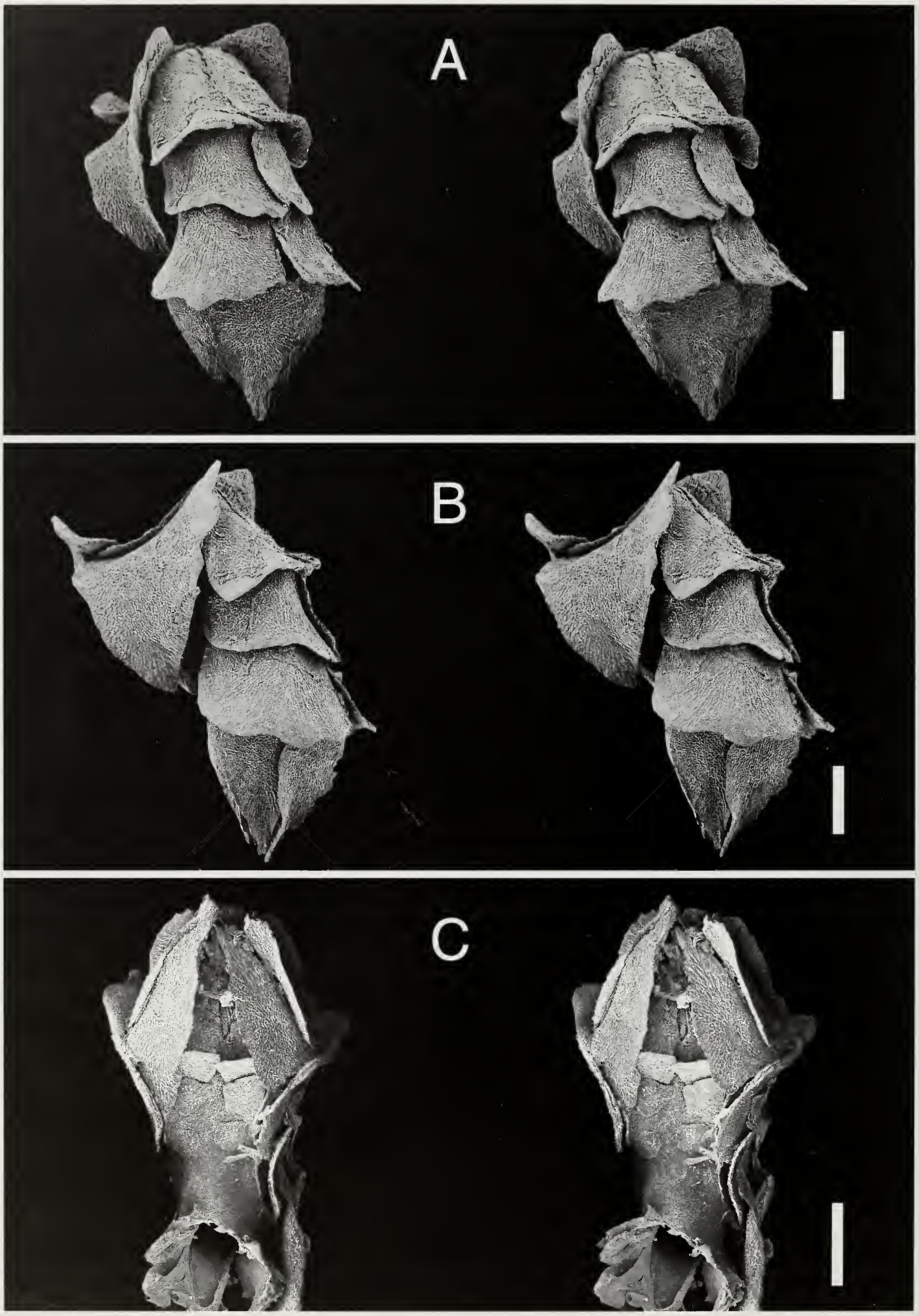

Fig. 11. *Narella laxa,* holotype, USNM 11853: A, abaxial polyp view; B, polyp in lateral view; C, polyp in adaxial view. Stereo views. All scale bars are 0.5 mm.

are smoothly curved around the base of the polyp, are not ridged, and do not meet adaxially. The 2 pairs of medial scales and the pair of abaxial buccals are progressively longer and wider toward the distal end of the polyp, the buccals almost encircling the polyp; however, in some polyps there are one or 2 medium-sized (0.35–0.43 mm in width) inner-lateral buccals that intercalate with the abaxial buccals and the adaxial buccals. The extra pair of medial scales allows for a slightly more flexible polyp than in most other species of *Narella,* the opercular scales usually directed straight toward the axis in a preserved polyp. The buccal scales cover only the basal-most region of the opercular scales. None of the larger body scales are ridged or crested, but all bear a coarse granulation that is arranged in lines radiating outward from the nucleus. Two or three pairs of well-developed, rectangular adaxial buccals lie below the adaxial operculars, those closest to the operculars about 0.30 mm in width, those more proximal, decreasing to about 0.15 mm in width. The distal edges of these scales are finely serrate.

The adaxial opercular scales are the smallest of the operculars, shaped as slender triangles 0.70–0.85 mm in height and 0.20–0.24 mm in basal diameter (H:W = 3.3–4.2). The inner- and outer-lateral operculars are larger, up to 1.1–1.2 mm in height and 0.51 mm in basal width (H:W = 2.1–2.5), the base asymmetrically extended on the adaxial side. The large abaxial operculars are symmetrical, about 1.0–1.3 mm in height and 0.65–0.70 mm in basal width (H:W = 1.8–1.9). The opercular scales are fairly flat becoming only slightly concave on their distal regions, which corresponds to but a weak keel on the internal side. The tentacles contain curved, granular rodlets up 0.105 mm in length. The coenenchymal scales are elongate (up to 1.10 mm in length), more or less imbricating, commonly with a prominent longitudinal crest.

Comparisons.—Only one other species of *Narella* at present known has 4 pairs of body scales, *N. spectabilis* n. sp., described below. It differs in the presence of distinct longitudinal crests on all the abaxial body scales, prominently keeled operculars, finer and smoother external sculpturing, and more elaborately crested coenenchymal scales (see also Table 1). *N. laxa* is also distinguished from all other western Atlantic species by having virtually flat opercular scales with rudimentary ventral keels, the opercular scales of all other species being strongly concave above.

Distribution.—Western Atlantic: known only from the type locality (see Material Examined) near Balanus Seamount, New England Seamount Chain, off Georges Bank; 3186 m. Eastern Atlantic: Shamrock Canyon, Bay of Biscay, 2980 m (Grasshoff, 1985).

Remarks.—Verrill, in his original manuscript on the Alcyonaria of the *Blake* and in the captions of his unpublished plates (Verrill, unpub.), generically separated *N. laxa* from the other species of *Narella,* which have only 3 pairs of large abaxial body scales. The discovery of another species with 4 pairs of scales lends support to that view, but clarification of this matter must await the study of a great deal more material than is available at present.

Narella spectabilis, new species

Figs. 1C, 12A–C, 13A–D, 14

Material examined/types.—Holotype: Tongue of the Ocean, Great Bahama Bank: 24°30′N, 77°22′W, 1485 m, *CI*-125, 25 Sep 1973, one unbranched stem partly decorticated and lacking distal tip and holdfast, USNM 57578 (*SEM* 407–409, 411, 416, C1029). Type Locality: as stated above.

Description.—The holotypic colony is 25 cm long and unbranched, but, because it is a fragment, it cannot be certain if this branch represents an unbranched species, like *N. versluysi,* or is an end branch of a sparingly branched species, such as *N. laxa.* The axis is 0.9 mm in diameter, stiff, brittle,

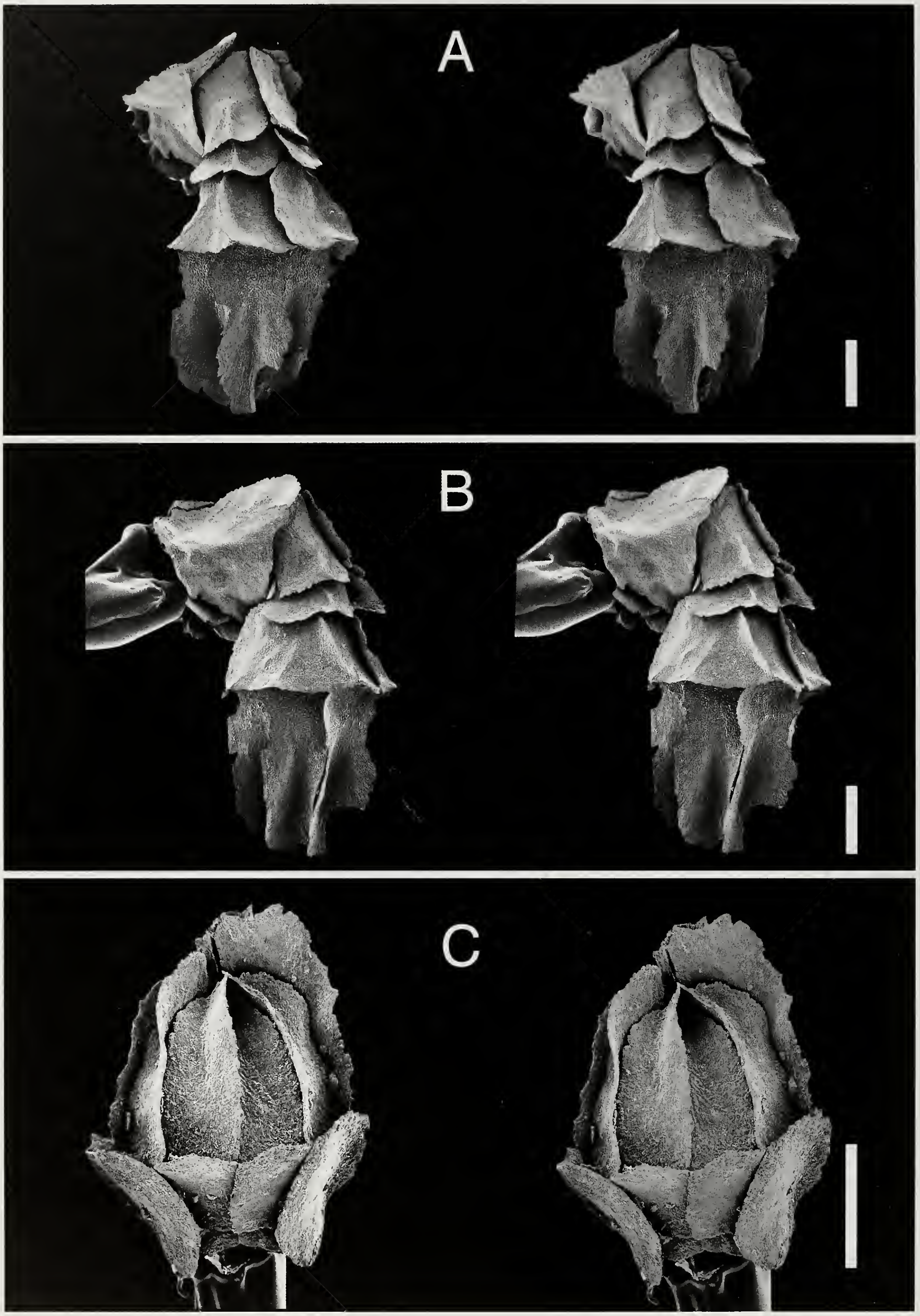

Fig. 12. *Narella spectabilis,* holotype, USNM 57578: A, polyp in abaxial view; B, polyp in lateral view; C, polyp in adaxial view. Stereo views. All scale bars are 0.5 mm.

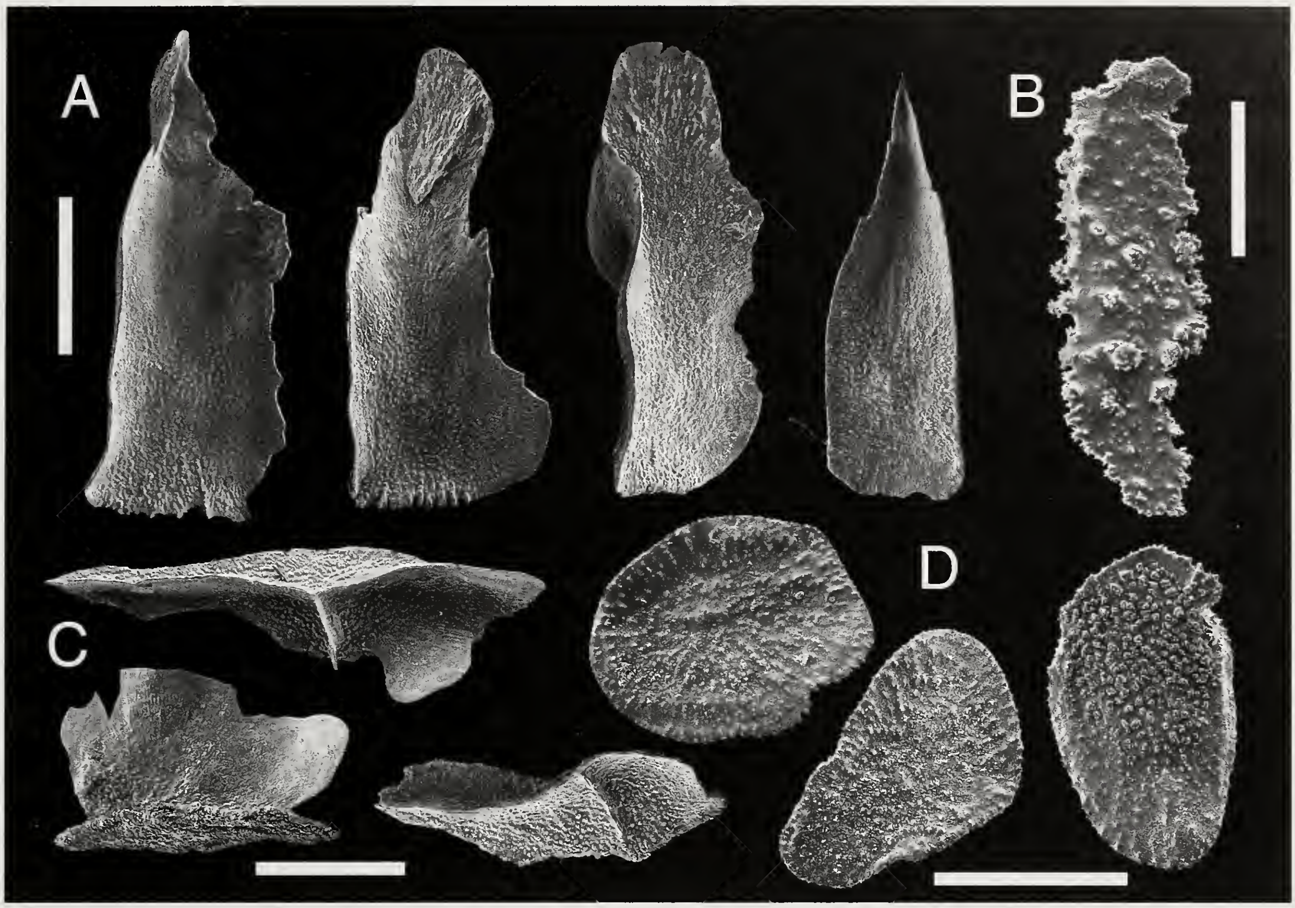

Fig. 13. A–D, holotype of *Narella spectabilis*, USNM 57578: A, upperside of abaxial, outer-lateral, inner-lateral, and adaxial opercular scales; B, a tentacular scale; C, three highly crested coenenchymal scales; D, three adaxial buccal scales. Scale bars: A, C = 0.5 mm; B, 0.05 mm; D = 0.25 mm.

yellowish white with pale golden reflections, and nearly smooth, with only the faintest suggestion of longitudinal grooving. Polyp whorls are not directly adjacent, but separated by about 0.5 mm from one another. Polyps are arranged in whorls of 4, of which 8 occur in 3 cm of branch length. Fully developed polyps are 3.5 mm in length.

The polyps are covered by 4 pairs of large abaxial body scales (1 pair of basals, 2 pairs of medials, and 1 pair of buccals) and 2 pairs of smaller adaxial buccals. The sclerites of the basal pair project perpendicular to the axis, and are about 1.15 mm in height, the distal 0.20 mm extending slightly beyond the junction with the proximal ends of the first medial pair. Each basal sclerite bears a prominent longitudinal crest up to 0.25 mm in height corresponding to the right angle curve it makes as it wraps around the lateral side of the polyp. The basal sclerites decrease in width toward the adaxial side where they meet to form a complete ring but do not fuse. The operculum is prominent, about ⅓ the length of the contracted polyp. The 2 pairs of medials and the abaxial buccal pair are about the same length (about 0.75 mm) but progressive wider toward the polyp tip, the buccals almost encircling the polyp. The second pair of medial sclerites is largely overlapped by the first (more proximal pair). Like the basals, these body wall sclerites are also longitudinally ridged along their midline, corresponding to the right angle curve around the lateral side of the polyp, but the ridges are much less prominent, and in the case of the buccals one or more shorter accessory ridges may be present. The buccal scales cover only the basal-most region of the large opercular scales. The longitudinal ridges and crests are aligned among the 4 pairs of body scales, all oc-

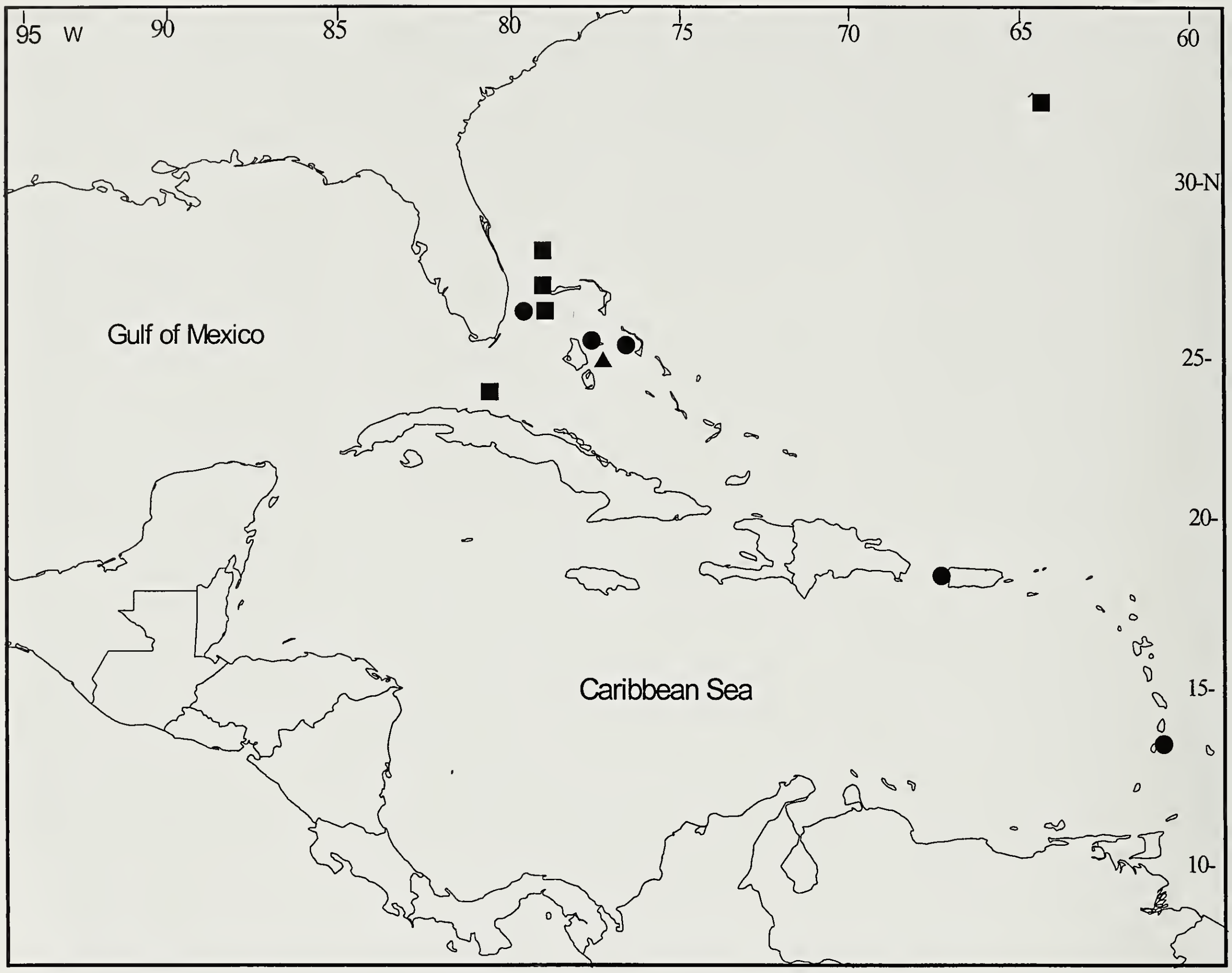

Fig. 14. Distribution of *Narella bellissima* (circles), *N. versluysi* (squares), and *N. spectabilis* (triangle).

curring at the right angle curve leading to the lateral side of the polyp wall, giving the polyp a polygonal shape in cross section. One might expect a corresponding linear depression on the underside of the sclerite which would align and allow the ridge of the more proximal sclerite to slid over it, but such depressions were not observed. All body scales are externally ornamented with fine, smoothly rounded granules arranged in lines radiating outward from a nucleus near the center of each sclerite. Two pairs of well-developed square to rectangular adaxial buccal scales are present, the marginal ones being quite large (up to 0.4 mm in width) the second pair about half this size, the distal edges of which are finely serrate.

The adaxial opercular scales are the smallest of the operculars, shaped as slender triangles but deeply concave exteriorly (essentially spoon-shaped), up to 0.85 mm in length and 0.35 mm in basal width (H:W = 2.4–3.2). Inner- and outer-lateral operculars are slightly longer (up to 1.3 mm in height and 0.50 mm in greatest width, H:W about 2.35) and are fairly symmetrical in shape, also highly concave but not spoon-shaped. Abaxial operculars are the largest opercular scales, up to 1.5 mm in length and unusually narrow (e.g., 0.6 mm, resulting in a high H:W of 2.1–2.6). The abaxial operculars sometimes have two additional apices in addition to the main apex (Fig. 13A). Thus, all opercular scales are roughly the same shape, but of increasing size in the ad- to abaxial direction. They all bear prominent longitudinal keels on their interior surfaces. The tentacles contain rotund granular rodlets up to 0.15 mm in length and 45 μm in diameter. The coenenchymal scales are thin, elongate, more or less imbricating, usually with a thin longitudinal crest, the crests of those coenenchymal scales adjacent to polyps being extremely tall (e.g., up to 0.45 mm).

Etymology.—Latin *spectabilis* = remarkable, notable.

Comparisons.—Only one other species of *Narella, N. laxa,* has four pairs of large body wall scales. *N. spectabilis* differs from that species in having longitudinal ridges on all body wall scales, a closed ring of basal scales, more slender and deeply concave opercular scales with a high H:W ratio, and would appear to be unbranched.

Although *N. spectabilis* appears to be related also to *N. studeri* (Versluys), *N. parva* (Versluys), and *N. bowersi* (Nutting), those species have only three pairs of body scales, with crests on only the basal pair.

Distribution.—Known only from the type locality of The Tongue of the Ocean, Bahamas (Fig. 14), 1485 m.

Acknowledgments

We wish to thank Ardis Johnson for the loan of *Narella* specimens deposited at the MCZ, and Dale Calder for the collection and loan of the type specimen of *N. alvinae.* We are also grateful to Manfred Grasshoff for valuable advice about the type deposition of various species, and we thank Linda Cole for her technical support.

Literature Cited

Bayer, F. M., 1956. Octocorallia. Pp. F166–189, 192–231 *in* R. C. Moore, ed., Treatise on invertebrate paleontology, University of Kansas Press, Lawrence.

———. 2001. New species of *Calyptrophora* (Coelenterata: Octocorallia: Primnoidae) from the western part of the Atlantic Ocean.—Proceedings of the Biological Society of Washington 114(2): 367–380.

———, M. Grasshoff, & J. Verseveldt (eds.). 1983. Illustrated trilingual glossary of morphological and anatomical terms applied to Octocorallia. E. J. Brill, Leiden, 75 pp.

Calder, D. R. 1993. Exploring Bermuda's underwater mountainside.—Rotunda, the Magazine of the Royal Ontario Museum 26(2):18–27.

Carpine, C., & M. Grasshoff. 1985. Gorgonaires, catalogue, Musée oéanographique de Monaco—Pannatulaires, catalogue, Musée océanographique de Monaco.—Bulletin de l'Institut océanographique, Monaco 73(1435):71 pp.

Deichmann, E. 1936. The Alcyonaria of the western part of the Atlantic Ocean.—Memoris of the Museum of Comparative Zoology at Harvard College 53:317 pp., 37 pls.

Duchassaing, P. 1870. Revue des Zoophytes et des Spongiaires des Antilles. 52 pp., 2 pls., Victor Masson et Fils, Paris.

———, & J. Michelotti. 1860. Mémoire sur les coralliaires des Antilles.—Mémoires des l'Accadémie des Sciences de Turin (2)19:279–365 [reprint paginated 1–88], 10 pls.

Grasshoff, M. (1981)1982a. Die Gorgonaria, Pennatularia und Antipatharia des Tiefwassers der Biskaya (Cnidaria, Anthozoa). I. Allgemeiner Teil.—Bulletin du Muséum national d'histoire Naturelle, Paris, Section A (4)3(3):731–766.

———. (1981)1982b. Die Gorgonaria, Pennatularia und Antipatharia des Tiefwassers der Biskaya (Cnidaria, Anthozoa). II. Taxonomischer Teil.—Bulletin du Muséum National d'histoire Naturelle, Paris, Section A (4)3(4):941–978.

———. 1985. Die Gorgonaria, Pennatularia und Antipatharia des Tiefwassers der Biskaya (Cnidaria, Anthozoa). III. Ergänzungen. *In* L. Laubier and C. Monniot, eds., Peuplements profonds du golfe de Gascogne. Brest, IFREMER, 17:299–310.

———. 1986. Die Gorgonaria der Expeditionen von "Travailleur" 1880–1882 und "Talisman" 1883 (Cnidaria, Anthozoa).—Bulletin du Muséum national d'Histoire Naturelle, Paris, Section A (4)8(1):9–38.

———. & H. Zibrowius. 1983. Kalkkrusten auf Achsen von Hornkorallen, rezent und fossil.—Senckenbergiana maritima 15(4/6):111–145.

Gray, J. E. 1858. Synopsis of the families and genera of axiferous Zoophytes or barked corals.—Proceedings of the Zoological Society of London 1857:278–294.

———. 1870. Catalogue of the lithophytes or stony corals in the collection of the British Museum. British Museum, London, 51 pp.

Kölliker, R. A. von. 1865. Icones histiologicae, oder Atlas der vergleichenden Gewebelehre. Zweite Abtheilung. Der feinere Bau der hoheren Thiere. Erstes Heft. Die Bindesubstanz der Ceolenteraten. Pp. 87–181, pls. 10–19, Verlag von Wilhelm Engelmann, Leipzig.

Kükenthal, W. 1915. System und Stammesgeschichte der Primnoidae.—Zoologischen Anzeiger 46(5):142–158.

———. 1919. Gorgonaria.—Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "*Valdivia*", 1898–1899 13(2):946 pp., pls. 30–89.

———. 1924. Coelenterata: Gorgonaria. Das Tierreich 47. Walter de Gruyter & Co., Berlin, 478 pp.

Pourtalès, L. F. 1868. Contributions to the fauna of the Gulf Stream at great depths (2nd series).—Bulletin of the Museum of Comparative Zoology 1:121–142.

Roule, L. 1896. Résultats scientifiques de la campagne du "Caudan" dans le Golfe de Gascogne—Aout–Septembre 1895. Coelentèrès.—Annales de l'Université de Lyon 26:299–323.

Stephens, J. 1909. Alcyonarian and madreporarian corals of the Irish coasts, with a description of a new species of *Stachyodes* by Professor S. J. Hickson, F. R. S.—Department of Agriculture and Technical Instruction for Ireland; Fisheries Branch. Scientific Investigations 1907, 5:1–28, 1 pl.

Stiasny, G. 1941. Studien über Alcyonaria und Gorgonaria. V. (Parerga und Paralipomena).—Zoologischen Anzeiger 135(3/4):75–88.

Studer, T. 1887. Versuch eines Systemes der *Alcyonaria.*—Archiv für Naturgeschichte 53(1):74 pp., 1 pl.

———. 1901. Alcyonaires provenant des campagnes de l'Hirondelle (1886–1888).—Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert Ier, Monaco 20:64 pp., 11 pls.

Thomson, J. A. 1927. Alcyonaires provenant des campagnes scientifiques du Prince Albert Ier de Monaco.—Résultats des Campagnes Scientifiques accomplies sur son yacht par Albert Ier, Monaco 73:77 pp., 6 pls.

Tixier-Durivault, A., & F. Lafargue. 1968. Quelques Octocoralliaires des côtes Françaises.—Bulletin du Muséum National d'Histoire Naturelle (2)40(3):621–629.

———, & M.-J. d'Hondt. 1974. Les Octocoralliaires des la campagne Biaçores.—Bulletin du Muséum National d'Histoire Naturelle, Zoologie (3)174(252):1361–1433.

Verrill, A. E. unpublished. The Alcyonaria of the "Blake" Expeditions. A. E. Verrill's unpublished plates.—140 pls.

Versluys, J. 1906. Die Gorgoniden der Siboga-Expedition. II. Die Primnoidae.—Siboga-Expeditie 13a:187 pp., 10 pls., 1 map.

Wright, E. P., & T. Studer. 1889. Report on the Alcyonaria collected by *H.M.S. Challenger* during the years 1873–76.—Report on the Scientific Results of the Voyage of *H.M.S. Challenger* during the years 1873–76, Zoology 31(64):314 pp., 43 pls.

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116(3):649–660. 2003.

A systematic review of the land snail *Euglandina singleyana* (Binney, 1892) (Mollusca: Gastropoda: Spiraxidae)

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Abstract.—A systematic review of *Euglandina singleyana* was undertaken to thoroughly examine shell morphology, allozyme, and mtDNA variation in specimens of *E. singleyana* endemic to central Texas. Allozyme similarity ranged from 95% in the most geographically proximal individuals of *E. singleyana* (Val Verde and Real counties) to 82% between the most distant individuals (Comal and Val Verde counties). DNA sequence similarity, based on a 397 bp partial 16S mtDNA sequence, ranged from 98% in eastern specimens (Comal and Kerr counties) to 95% in individuals from Kerr, Real, and Val Verde counties. Analysis of variation in shell morphology, allozyme similarity, and mtDNA sequences supports the existence of a single, highly variable, widespread species of *Euglandina* in central Texas. This study also examines the validity of *E. immemorata,* using morphometric and DNA sequence data and *E. exesa,* using morphometric data. The morphometric analysis showed that *E. immemorata* and *E. singleyana* differ significantly in shape. The current status of *E. immemorata* and *E. exesa* are also examined.

Euglandina singleyana (Binney, 1892) is found in a wide variety of habitats along the southern margin of the Edwards Plateau in Texas, from Terrell County in the west to Fayette County in the east, and south to Refugio County (Fig. 1; Singley 1893, Pilsbry 1946, Fullington & Pratt 1974, Hubricht 1985). In the eastern part of its range it is found under rocks and logs in wooded stream valleys in the limestone of the Edwards Plateau. In the clay and sandy areas of the Balcones Escarpment, it is restricted to wooded lowlands. The range of this species extends to the western Stockton Plateau where it is found under fallen *Yucca* and in rock crevices in desert shrub habitat dominated by *Lechuguilla* cactus (Fullington & Pratt 1974).

A great deal of the historical taxonomic confusion regarding this species appears to be related to its relatively wide geographical range of ~250 km, compared to the median range of land snail distribution of 50 km reported by Solem (1984) and high level of variation in shell morphology. Shells collected in the eastern part of the range can readily be distinguished from those collected in the western part of the range. One purpose of this study was to examine variation in shell morphology of specimens from throughout the range of the species in central Texas to determine if there are distinct differences in western versus eastern shell morphology or if there is continuous (clinal) change in shell shape and size across the range of the species. The purpose of this study was also to examine allozyme and DNA sequence variation in individuals from across the range of the species (Comal, Kerr, Real, and Val Verde counties) to determine if specimens conforming to the description of *E. singleyana* formed a monophyletic group. This study addresses the taxonomy of this species from a phy-

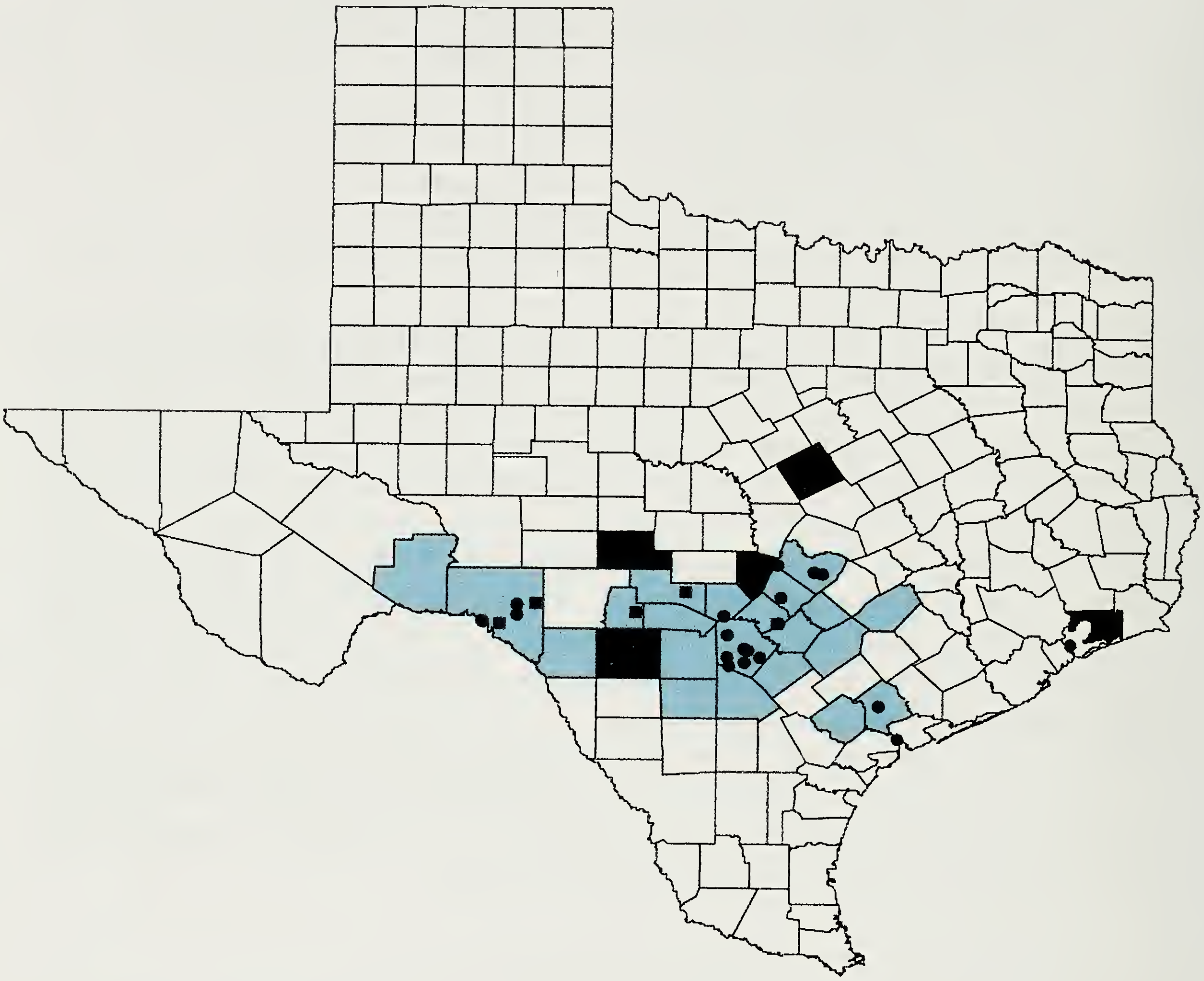

Fig. 1. The amended distribution of *Euglandina singleyana* in Texas. Counties in the historical literature are shown in gray. Counties added in this study (Blanco, Chambers, Coryell, Kimble, and Uvalde) are shown in black. Collection localities for allozyme and DNA studies are represented by a black square. Museum localities listed in the material examined are represented by a black circle. The distribution of this species is not continuous throughout the highlighted area, but instead occurs in isolated patches of appropriate habitat.

logenetic species concept approach using both monophyly (sequence analysis) and diagnosability (shell morphometrics) criteria (Minton & Lydeard 2003).

The carnivorous land snail genus *Euglandina* has a problematic taxonomic history. Von Martens (1901:47) noted that "many species have been described only from one or a few examples, and not figured. In this genus . . . it seems to be very difficult, or rather impossible, to draw a clear line of distinction between local variations and nearly allied species." In addition to these problems, Thompson (1987) also noted that many original descriptions are scattered among nineteenth century journals in several languages and often lack critical details of sculpture of the adult and embryonic shells.

Euglandina singleyana from central Texas appears typical of this group in having a history of confusion regarding its identity. Initially, Roemer (1849) identified specimens from New Braunfels as *Glandina truncata* (Gmelin, 1788). Binney & Bland (1869) later considered Texas specimens to be *Glandina corneola* Pfeiffer, 1857. Binney (1892) described and named this Texas snail *Glandina singleyana.* Pilsbry later (1907) noted that in the Binney (1885) monograph, shells from Texas were listed with the name *G. decussata* (Deshayes,

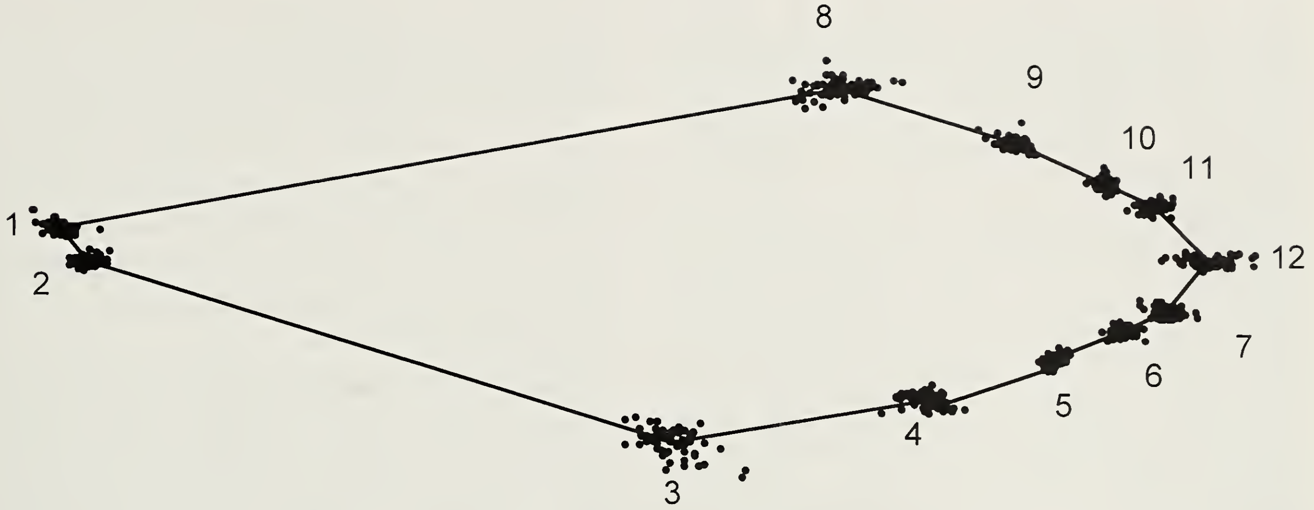

Fig. 2. Landmarks used in the geometric morphometric analysis. Numbers 1 and 12 were used as baselines in all analysis. Number 1 is the most distal point on the columella to Number 12 at the apex of the shell.

1850), the description and figure were of *G. corneola,* and the locality and anatomical descriptions were those of *G. singleyana.* Singley (1893) listed this species as *G. decussata* var. *singleyana.* Pilsbry (1907; p. 175) removed all Mexican and mainland members of *Glandina* to the genus *Euglandina* due to taxonomic confusion regarding the name and types of *Glandina* and subsequent workers (Pilsbry & Ferriss 1906, Pilsbry 1907, 1946, Fullington & Pratt 1974, Hubricht 1985) have retained this generic name.

Euglandina immemorata Pilsbry, 1907 is another species associated with some degree of taxonomic uncertainty. This species was described by Pilsbry (1907) on the basis of two shells from "Texas" (exact locality unknown). Fullington & Pratt (1974) stated that the holotype of *E. immemorata* is not especially distinct from *E. singleyana* but could not be precisely matched by any material they had seen. They concluded that *E. immemorata* is probably *E. singleyana* or, if distinct (based on the improved knowledge of the Texas fauna since 1946) is probably not a Texas species.

Euglandina exesa Cockerell, 1930 was described from a single shell found in a limestone deposit in a cinnabar mine at Terlingua, Brewster County, Texas. Fullington & Pratt (1974) state that the holotype does not differ from many western specimens of *E. singleyana.* They consider *E. exesa* to be simply a western range extension of *E. singleyana.*

A systematic review of *E. singleyana* was undertaken to thoroughly examine the observed morphological differences and add further evidence using genetic techniques. This study also tests the conclusions of Fullington & Pratt (1974) by examining the validity of *E. immemorata* using morphometric and DNA sequence data and *E. exesa* using morphometric data.

Materials and Methods

Morphometric analysis.—Programs used for morphometric analysis are part of the Integrated Morphometrics Package (www.canisius.edu/~sheets/morphsoft.html) made available by David Sheets, Miriam Zelditch, and Donald Swiderski. Specimens of *Euglandina singleyana* (64), *E. immemorata* (six—including both type specimens), and *E. exesa* (holotype) were examined (Appendix 1). Twelve landmarks on each shell were digitized from photographs using the program tpsDig version 1.31 (F. J. Rohlf. tpsDig32: Digitize coordinates of landmarks and capture outlines. http://life.bio.sunysb.edu/morph/index.html) (Fig. 2). The landmarks were chosen to be repeatable and homologous (Swiderski 1993) across all shells, and most landmarks represent shell sutures (Stone 1998). For each specimen, digitized landmark coordinates were transformed to procrustes distances using partial procrustes superimposition methods. This was carried out in CoordGen6 (H. D. Sheets, Dept. of Physics, Canisius College, 2001 Main St. Buffalo, New York 14208, sheets@gort.canisius.edu). A principal component analysis was performed using partial procrustes distances (PCAGen6e; H. D. Sheets). This program computes partial warp scores for each specimen, using a procrustes mean specimen based on all data for comparison. The principal components (eigenvectors of the covariance matrix) are then calculated based on the covariance matrix derived from the partial warp scores. Landmarks 1 and 12 were designated end points and all specimens were standardized according to this baseline. This transformation to partial warp scores accomplishes standardization so that the principal component analysis examines variation in shape, excluding variation due to scale, rotation, and translation (Swiderski 1993, Stone 1998).

A canonical variates analysis was performed using the program CVAGen6 (H. D. Sheets) to determine the set of axes that allows for the greatest possible ability to discriminate between two or more groups. This program computes partial warp scores with reference to a common mean specimen then performs a multivariate analysis of variance followed by a canonical variates analysis. It determines how many distinct axes there are in the data, ($p = 0.05$) and computes the canonical variates scores of all the specimens. It also uses Mahalanobis distances to assign specimens to one of the groups. The single specimen of *E. exesa* was coded as an unknown and assigned to a group based on the canonical variates axes formed in the prior analysis (CVAGen6; H. D. Sheets). Lastly, a comparison was performed to determine if there was a significant difference in shape between *E. singleyana* and *E. immemorata* (TwoGroup6c; H. D. Sheets).

Allozyme analysis.—Each collection locality of *Euglandina singleyana* was represented by one or two specimens. A total of seven specimens from five collection localities at ~50 km intervals throughout the geographic range of this species were examined (Appendix 1).

After collection, individuals were held without feeding for 7–10 days, then frozen in cryotubes in liquid nitrogen and stored in an ultracold freezer (−80°C) until analysis. Samples were homogenized in two volumes of distilled water using a glass rod and centrifuged to obtain an aqueous extract. Procedures for cellulose acetate electrophoresis and staining followed those of Hebert & Beaton (1993). Gels were purchased from Helena Laboratories Inc. (Beaumont, Texas), and the buffer used was tris-glycine pH 8.5. To examine variation within *E. singleyana,* scorable data for 19 loci (Table 1) were obtained and analyzed using Tools for Population Genetic Analysis 1.3 (M. P. Miller. Tools for Population Genetic Analysis (TFPGA 1.3): A windows program for the analysis of allozyme and molecular population genetic data. Computer software distributed by the author.). To determine genetic similarity, Nei's unbiased genetic identity was calculated (Nei 1978). An unweighted pair group method using arithmetic averages (UPGMA) cluster analysis was then performed using the genetic identity matrix.

DNA sequence analysis.—Twelve tissue samples were either preserved in 70% ethanol or frozen in liquid nitrogen and then stored in an ultracold freezer at −80°C. The outgroup taxa chosen were the closest relatives of *Euglandina* with sequences available on GenBank, relationships from Wade et al. (2001). Total genomic DNA was extracted from several milligrams of foot tissue by digestion with lysis buffer and Proteinase K and then purified by phenol: chloroform extraction according to standard procedures (see Palumbi, S., A. Martin, S.

Romano, W. O. McMillan, L. Stice, & G. Grabowski. 1991. The Simple Fool's Guide to PCR. Privately distributed, Honolulu, Hawaii, 40 pp.).

Mitochondrial DNA sequences were obtained for an amplified segment of the 16S rDNA gene using 16sar and 16sbr primers (see Palumbi above). Approximately 10 ng of genomic DNA provided templates for double-stranded reactions via the polymerase chain reaction (PCR). PCR reactions were done in a 50 μL solution containing each dNTP at 0.22 μM, each primer at 0.1 μM, 1.5 mM $MgCl_2$, 1 unit Taq DNA polymerase, and 1X PCR reaction buffer. Reactions were amplified for 30 cycles of 92°C for 45 sec, 50°C for 45 sec, and 68°C for 2 min. Samples were purified and double-stranded DNA provided the template for cycle-sequencing using BigDye (ABI) chemistry followed by analysis on an ABI3100 automated sequencer.

Contigs were assembled in Sequencher™ 4.0.5 (Gene Codes Corporation, Ann Arbor, Michigan and aligned by eye using BioEdit (Hall 1999) with reference to secondary structure models to refine the alignment and identify regions corresponding to loops and stems (Lydeard et al. 2000). Sequences were deposited with Genbank (Accession Numbers: AF405235–AF405241, AY149279, AY167887–AY167889). Aligned sequences were analyzed using maximum parsimony with PAUP*4.0b10 (Swofford 2002) using a heuristic search (10 addition replicates). The following options were used: uninformative characters were ignored, only minimal trees were kept, gaps were treated as missing, and zero length branches were collapsed. A bootstrap analysis with 1000 iterations was conducted (Felsenstein 1985). Bremer support values (Bremer 1994) were calculated using the Decay function of MacClade 4.03 (Maddison & Maddison 2000).

Results and Discussion

Morphometric analysis.—In the examination of shell variation within *Euglandina singleyana* the first principal component (PC1) accounted for 67.42% of the variation present in the measurements and PC2 accounted for 9.66% of the variation present. A scatterplot, with specimens grouped by county, comparing the first two principal component axes, does not show any distinct groups within *E. singleyana* (Fig. 3). Shell variation described by principal component 1 appears to be continuous and the results of this analysis do not allow *E. singleyana* to be separated into groups based on shell characteristics.

The canonical variates analysis (Fig. 4) to determine if *E. immemorata* could be distinguished from *E. singleyana* was significant, (df = 20, p = 3.70685 × 10^{-5}) with 100% correct reclassification of both species. A two-group comparison showed that the shapes of the two species are significantly different (Hotelling's $T^2 f = 6.52$, $df = 24, 45, p = 3.8316 \times 10^{-8}$). This result indicates that *E. immemorata* is morphologically distinct from *E. singleyana*. This re-

Table 1.—Presumptive enzymatic loci resolved. Tris-glycine (pH 8.5) was used as the buffer system for all of the enzymes listed. All stain and buffer recipes are from Hebert & Beaton (1993).

Enzyme system and abbreviation	Enzyme commission number
Adenylate Kinase (ADK)	2.7.4.3
Alcohol Dehydrogenase (ADH)	1.1.99.8
Alcohol Oxidase (AOX)	1.1.3.13
Aspartate Aminotransferase (AAT)	2.6.1.1
Glucokinase (GK)	2.7.1.2
Glucose-6-phosphate Dehydrogenase (G6PDH)	1.1.1.49
Hexokinase (HK)	2.7.1.1
L-Iditol Dehydrogenase (IDDH)	1.1.1.14
Isocitrate Dehydrogenase (IDH)	1.1.1.42
L-lactate Dehydrogenase (LDH)	1.1.1.27
Malate Dehydrogenase (MDH-1 & 2)	1.1.1.37
Malate Dehydrogenase (NADP+) (MDHP-1 & 2)	1.1.1.40
Nucleoside Phosphorylase (NSP)	2.3.2.1
Phosphoglucomutase (PGM)	5.4.2.2
Phosphogluconate Dehydrogenase (PGDH)	1.1.1.44
Superoxide Dismutase (SOD)	1.15.1.1
Triosephosphate Isomerase (TPI)	5.3.1.1

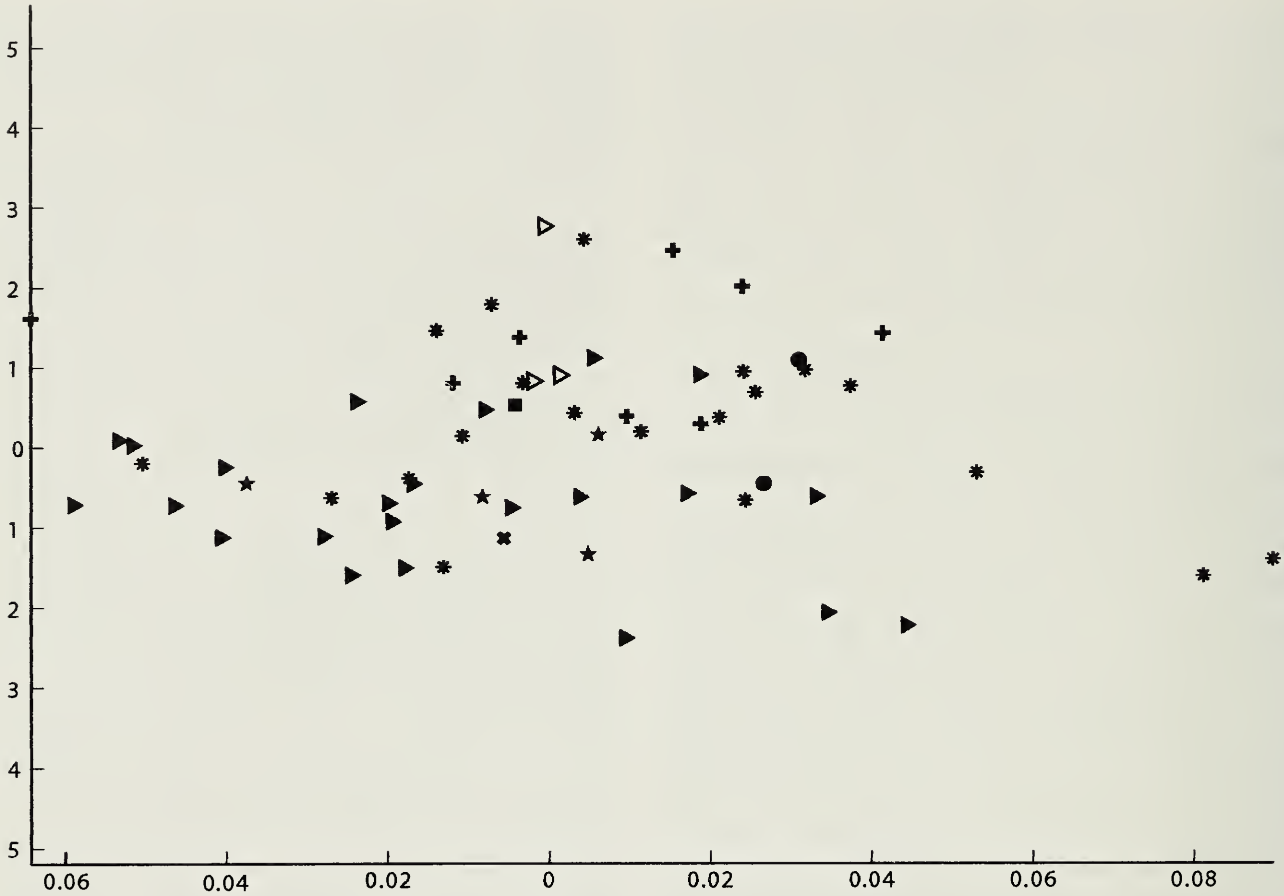

Fig. 3. Scatterplot displaying principal component scores of *Euglandina singleyana.* X-axis is principal component one, Y-axis is principal component two. Texas counties are represented by the following symbols: Bexar (asterisk) type-locality, Chambers (circle), Comal (plus sign), Coryell & Travis (star), Hays (square), Kimble, Uvalde, & Real (hollow triangle), Val Verde (filled triangle), Victoria (X).

sult, along with the discovery of specimens of *E. immemorata* in Nuevo Leon, Mexico (Correo-Sandoval 1993), supports the removal of *E. immemorata* from Texas faunal listings.

The unknown assignment test to determine the placement of *E. exesa* placed the single specimen in a cluster formed by *E. singleyana* (Fig. 4); however, this result was not significant ($p \geq 0.001$). This species is represented by only one specimen. Therefore, this test is not replicable and has little statistical power. It is interesting that the CVA placed the specimen of *E. exesa* within *E. singleyana,* supporting the statements of Fullington & Pratt (1974) about this species. However, without more evidence, nothing conclusive can be stated about the validity of this species.

Allozyme analysis.—The results of this study reveal a moderate to high degree of genetic similarity in all specimens of *Euglandina singleyana* examined across its range. Seven of 19 loci (MDH-2, MDHP-2, IDH, LDH, SOD, G6PDH, PGM) were monomorphic for all specimens. The Val Verde County specimens exhibited polymorphisms at nine enzymatic loci (MDH-1, MDHP-1, PGD, AOX, AAT-1, ADK, IDDH, ADH, HK), the Real County specimens exhibited polymorphism at six (MDH-1, MDHP-1, AOX, HK, NSP, ADH). In the specimens examined, there were no fixed allelic differences among populations of *E. singleyana* across its geographic range.

Allozyme variation appeared to follow a general geographic pattern with specimens having the smallest genetic distance from their most proximal geographic neighbors (Fig. 5). Genetic divergence calculated using Nei's unbiased genetic identity resulted

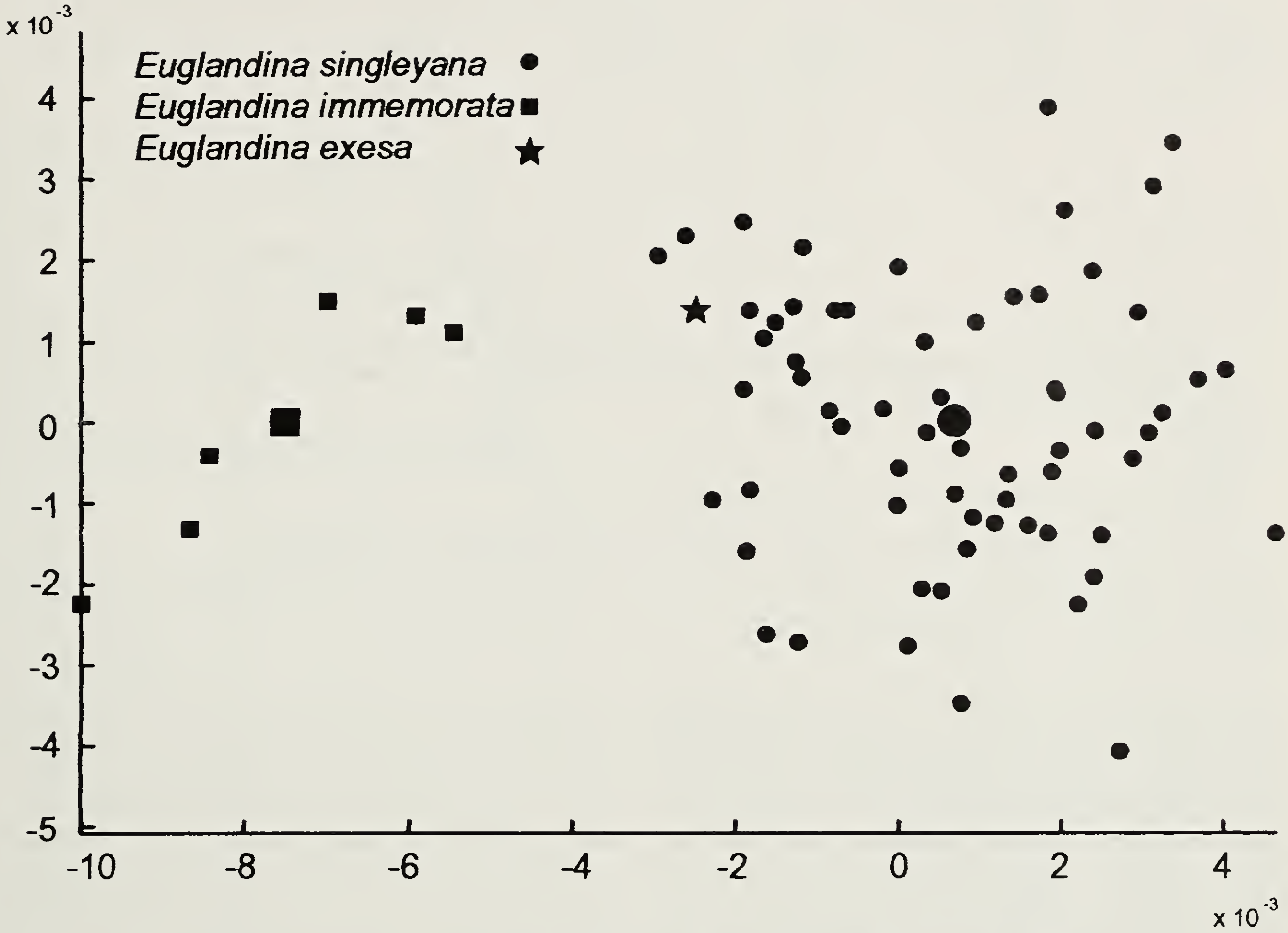

Fig. 4. Graph of the canonical variates axes displaying the separation between the means of *Euglandina singleyana* and *E. immemorata.* Plotted as an unknown is *E. exesa.* Oversized symbols indicate the means. X-axis is CVA 1, Y-axis is CVA 2.

in the most western specimens from Val Verde County and the Real County specimens displaying a genetic similarity of 94.5%. The Val Verde+Real cluster was genetically similar to the more centrally located Kerr County specimen at a level of 89.7%. This cluster is 85.2% similar to the most eastern specimen from Comal County.

Perez & Strenth (2002) found that specimens of *Euglandina texasiana* (Pfeiffer, 1857) from collection localities 150 km distant, in south Texas and northern Tamaulipas, had a similarity of 94.5%. In comparison, this study observed 94.5% similarity between specimens of *E. singleyana* located 157 km apart, and 85.2% similarity between the most geographically distant specimens (246 km) from Comal and Val Verde Counties. *Euglandina singleyana* was found to display enzyme polymorphism at 12 of 19 loci examined. This level of allozyme variability is more similar to the results of studies on *Helix aspersa* (Selander & Kauffman 1975) and differs from results found in *Liguus* by Hillis et al. (1991) and *Rumina decollata* by Selander & Kaufman (1975), which were notably less variable.

The levels of genetic distance among the widely separated populations of *Euglandina singleyana* are within the range found in other organisms for genetic divergence between subspecies (Quicke 1993). However, there are no fixed differences among the populations and genetic distance is low between geographically proximal populations. This analysis indicates that the specimens of *E. singleyana* examined represent a single species.

DNA sequence analysis.—The region of 16S mtDNA that was sequenced resulted in

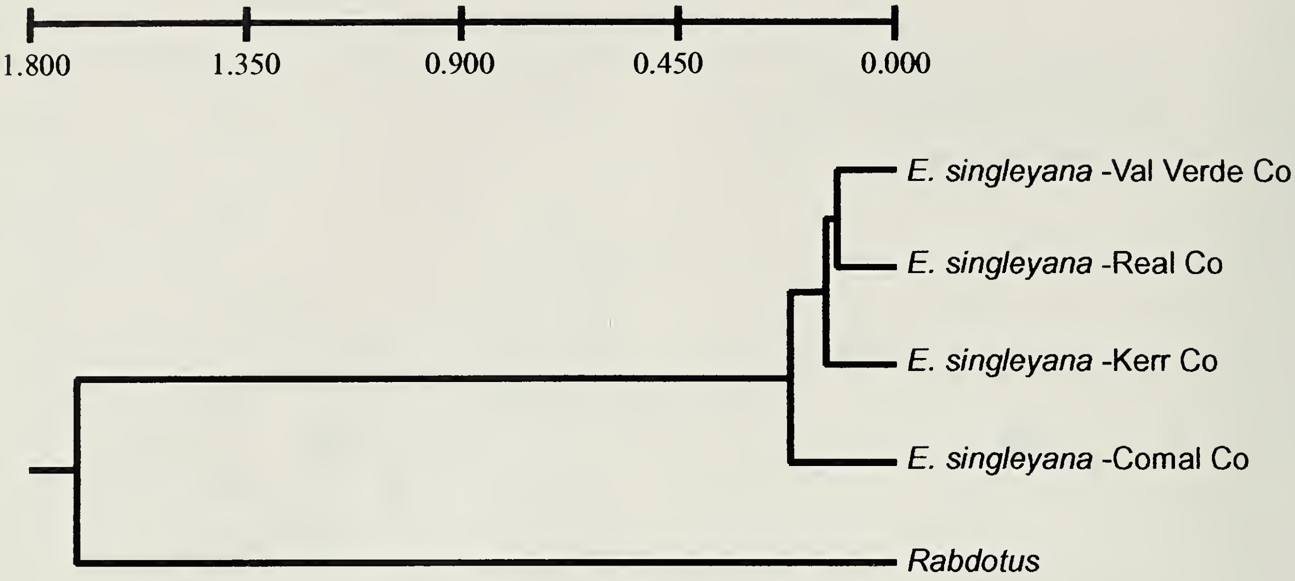

Fig. 5. A dendrogram of allozyme similarity in *Euglandina singleyana* produced by UPGMA on a matrix produced using Nei's unbiased genetic identity.

an aligned data matrix of 397 base pairs of which 191 were phylogenetically informative. Phylogenetic analysis of the data using maximum-parsimony analysis resulted in three equally parsimonious trees of 480 steps (CI = 0.8646, g1 = −2.024336). These three trees differed only in the placement of the Comal County (eastern) specimen relative to the Kerr County specimen. One topology places the Kerr County specimen (central) sister to the Real+Devil's River clade (Central & Western). An alternate topology places the Comal County specimen in this position, and the final topology describes Comal and Kerr County specimens as each others' closest relative. Bootstrap analysis (1000 pseudoreplicates) of the aligned data matrix using maximum-parsimony produced the tree shown in Fig. 6. *Euglandina singleyana* forms a monophyletic group. The sister taxon to *E. singleyana* is the specimen of *Euglandina* from Northern Coahuila. Also outside this grouping is *E. corneola* from Tamaulipas, Mexico. Pairwise sequence identity was calculated for each clade. Within the Val Verde County cluster (Devil's River and Comstock) there is 98–100% sequence similarity. The two Real County specimens had identical 16S sequences (=100% similarity). Sequence similarity between Kerr County and Comal County was 97%. All possible combinations of pairwise comparisons were performed with a minimum similarity of 95% among specimens from Kerr and Real County. The two specimens of *E. immemorata* formed a group apparently not closely related to *E. singleyana.*

Both allozyme and sequence analyses show an interesting geographic pattern with populations most closely related to their geographically proximal neighbors. This pattern of strong geographic structuring is often seen in land snail species (Thomaz et al. 1996, Schilthuizen et al. 1999). Thomaz et al. (1996) examined geographic variation within *Cepea nemoralis* and *Helix aspersa* and found very high levels of sequence divergence (12%) within these species of land snails. The authors conclude that the most likely explanation for the observed levels of divergence is the population structure of land snails with low dispersal and large populations divided into infrequently interacting demes.

Avise et al. (1987) presents several tests of this hypothesis, one of which is: phylogenetic differentiation between long separated demes should be reflected in nuclear as well as mitochondrial assays. The congruence of the allozyme and mitochondrial data in the present study appear to fulfill

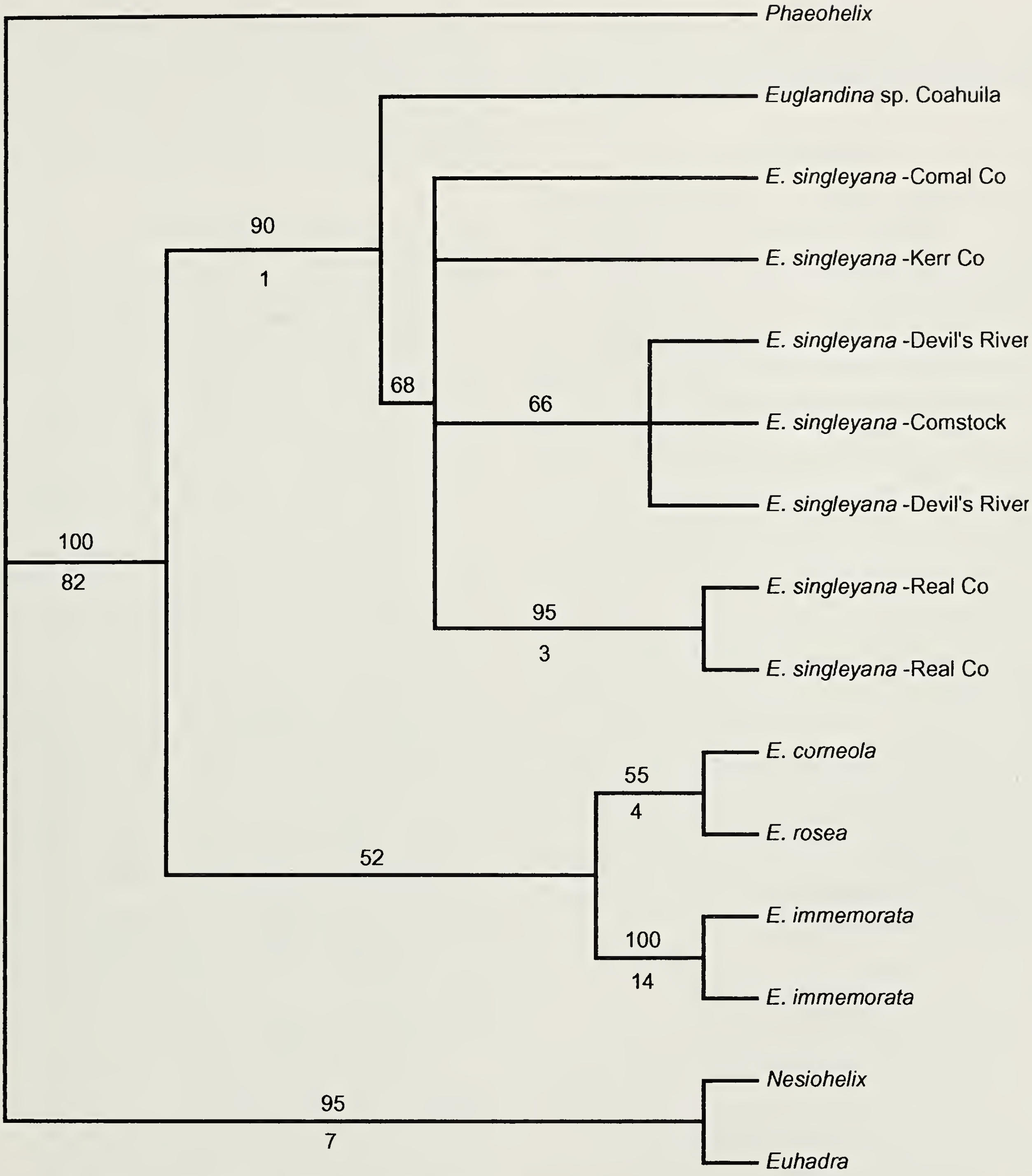

Fig. 6. Strict consensus of three most parsimonious trees of partial 16S mtDNA sequences of specimens of *Euglandina singleyana* from Comal, Kerr, Real, and Val Verde counties. Numbers above the branches are bootstrap support percentages (1000 pseudoreplicates). Numbers below the branches are Bremer's support values.

this requirement, lending credence to the idea that the specimens of *E. singleyana* examined in this study represent a single species. The present study does not have enough samples to conclusively examine geographic partitioning within this species; however, there does appear to be some geographic structure in the data.

Although sample sizes were low, they appear to be adequate to address the questions posed in this research. *Euglandina singleyana* is considered to be an uncommon species (Singley 1893; Neck 1984, 1988), and the area where they are found is rapidly being disturbed ecologically due to a growing human population. As a result of their very specialized feeding habits, rarity, habitat preferences, and human activities, the live specimens examined during this study represent a significant collection of living specimens of *Euglandina singleyana.*

Conclusions

All of the analyses, including morphometric, allozyme, and mtDNA sequences, support the premise that *Euglandina singleyana* is a single, widespread, highly variable species. Both allozyme and DNA sequence results indicate that there are some detectable genetic geographic patterns within *E. singleyana,* as well as the observable morphological gradient across the range of this species. The geographically most distant specimens are the most genetically dissimilar and geographically proximal specimens are more similar.

The results of the morphometric and sequence analyses indicate that *E. immemorata* is distinct from *E. singleyana.* This result, combined with the recent discovery of specimens of *E. immemorata* from Nuevo Leon, Mexico leads to the conclusion that *E. immemorata* should be removed from Texas faunal listings. The taxonomic placement of *Euglandina exesa* could not be definitively determined.

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Literature Cited

Avise, J. C. et al. 1987. Intraspecific phylogeography: The mitochondrial DNA bridge between population genetics and systematics.—Annual Review of Ecology and Systematics 18:489–522.

Binney, W. G., 1885. A manual of american land shells. Government Printing Office, Washington D.C., 351 pp.

———, 1892. Fourth Supplement to Terrestrial Molluscs.—Bulletin of the Museum of Comparative Zoology 22:163.

———, & T. Bland. 1869. Land and fresh water shells of North America. Part 1. Pulmonata Geophila.—Smithsonian Miscellaneous Collections, 194:13–21.

Bremer, K. 1994. Branch support and tree stability.—Cladistics 10:295–304.

Cheatum, E. P., R. Fullington, & L. Pratt. 1972. Molluscan records from west Texas.—Sterkiana 46: 6–10.

Chiba, S. 1999. Accelerated evolution of land snails *Mandarina* in the oceanic Bonin Islands: evidence from mitochondrial DNA sequences.—Evolution 53:460–471.

Cockerell, T. D. A. 1930. An apparently extinct *Euglandina* from Texas.—Proceedings of the Colorado Museum of Natural History 9:52–53.

Correo-Sandoval, A. 1993. Caracoles terrestres (Mollusca: Gastropoda) de Santiago, Nuevo León, México.—Revista de Biologia Tropical 41:683–687.

Deshayes, G. P. 1850. *in* Ferussac. 1820–1852. Histoire naturelle générale et particulière des Mollusques terrestres et fluviatiles. II, p. 182.

Felsenstein, J. F. 1985. Confidence limits on phylogenies: an approach using the bootstrap.—Evolution 39:783–791.

Fullington, R. W., & W. L. Pratt. 1974. The aquatic and land mollusca of Texas.—Bulletin of the Dallas Museum of Natural History 1(3). 48 pp.

Gmelin. 1788–1790.—Systema Naturae 13. p. 3434, number 49.

Hall, T. A. 1999. Bioedit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT.—Nucleic Acids Symposium Series 41:95–98.

Hebert, P., & M. J. Beaton. 1993. Methodologies for allozyme analysis using cellulose acetate electrophoresis. Helena Laboratories. Beaumont, Texas, 32 pp.

Hillis, D. M., M. T. Dixon, & A. L. Jones. 1991. Minimal genetic variation in a morphologically diverse species (Florida tree snail, *Liguus fasciatus*).—Journal of Heredity 82:282–286.

Hubricht, L. 1985. The distribution of the native land molluscs of the eastern United States.—Fieldiana Zoology 24, 191 pp.

Lydeard, C., W. E. Holznagel, M. N. Schnare, & R. R. Gutell. 2000. Phylogenetic analysis of molluscan mitochondrial LSU rDNA sequences and secondary structure.—Molecular Phylogenetics and Evolution 15:83–102.

Maddison, W. P., & D. R. Maddison. 2000. MacClade 4.03: analysis of phylogeny and character evolution. Sinauer Associates, Sunderland, Massachusetts, U.S.A.

Martens, E. von. 1890–1901. Biologia Centrali-Americana. Pp 46–79 *in* F. D. Godman, ed., R. H. Porter, and Dulau and Co., Soho Square W, London.

McGee, P. L. 1971. Distribution and ecology of the terrestrial mollusks of the Texas coastal counties.—Molluscana, pp. 25–29, 37–39, 49–52, 61–64, 73–76, 85–88, 13–16, 25–28, 39–42, 53–57.

Minton, R. L., & C. Lydeard. 2003. Phylogeny, taxonomy, genetics and global heritage ranks of an imperiled, freshwater snail genus *Lithasia* (Pleuroceridae).—Molecular Ecology (12) (in press).

Neck, R. W. 1984. Restricted and declining nonmarine mollusks of Texas.—Texas Parks and Wildlife Department Technical Series No. 34, 17 pp.

———. 1988. Urban refugia which support dense concentrations of *Euglandina singleyana*.—Texas Conchologist 24:78–82.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals.—Genetics 890:583–590.

Perez, K. E., & N. E. Strenth. 2002. Enzymatic variation in the land snail *Euglandina texasiana* (Gastropoda: Pulmonata) from South Texas and Northeastern Mexico.—Texas Journal of Science 54:37–44.

Pfeiffer, von L. 1857. Novitates conchologicae. 8. p. 82, pl. xxii, fig. 11, 12.

Pilsbry, H. A. 1907. Oleacinidae, Ferussacidae, vol. XIX *in* G. W. Tryon's Manual of Conchology. Academy of Natural Sciences of Philadelphia, 366 pp. + 52 plates.

———. 1946. Land mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia. Monograph 3, vol. 2(1):188–199.

———, & J. H. Ferriss. 1906. Mollusca of the southwestern states, II.—Proceedings of the Academy of Natural Sciences of Philadelphia 58:123–175.

Quicke, D. L. J. 1993. Principles and techniques of contemporary taxonomy. Blackie Academic and Professional, Glasgow, 311 pp.

Roemer, F. 1849. Mit einem naturwissenschaftlichen Anhange *in* A. Marcus, ed., Molluscs, 456 pp.

Schilthuizen, M., J. J. Vermuelen, G. W. H. Davidson, & E. Gittenberger. 1999. Population structure in a snail species from isolated Malaysian limestone hills, inferred from ribosomal DNA sequences.—Malacologia 41:283–296.

Selander, R. K., & D. W. Kaufman. 1975. Genetic structure of populations of the brown snail (Helix aspersa). I. Microgeographic variation.—Evolution 29:385–401.

Singley, J. A. 1893. Texas molluscs. Geological Survey of Texas. Fourth Annual Report, part 2. 375 pp.

Solem, A. 1984. A world model of land snail diversity and abundance. Pp. 6–22 *in* A. Solem & A. C. van Bruggen, eds., World-wide snails: biogeographical studies of non-marine mollusca. Brill, Leiden, 289 pp.

Stone, J. R. 1998. Landmark-based thin-plate spline relative warp analysis of gastropod shells.—Systematic Biology 47:254–263.

Strecker, J. K. 1935. Land and fresh-water snails of Texas.—Transactions of the Texas Academy of Science 17:4–50.

Swiderski, D. L. 1993. Morphological evolution of the scapula in tree squirrels, chipmunks, and grand squirrels (Sciuridae): an analysis using thin-plate splines.—Evolution 47:1854–1873.

Swofford, D. L. 2002. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4.0b10. Sinauer Associates, Sunderland, Massachusetts.

Thomaz, D., A. Guiller, & B. Clarke. 1996. Extreme divergence of mitochondrial DNA within species of pulmonate land snails.—Proceedings of the Royal Society of London, Serial B 263:363–368.

Thompson, F. G. 1987. Giant carnivorous land snails from Mexico and Central America.—Bulletin of the Florida State Museum: Biological Sciences 2, 52 pp.

Wade, C. M., P. B. Mordan, & B. Clarke. 2001. A phylogeny of the land snails (Gastropoda: Pulmonata).—Proceedings of the Royal Society of London, Serial B. 268:413–422.

Appendix 1

Material Examined and Distribution

Morphometric Analysis

Euglandina singleyana (64): The number of specimens of each lot that were used follows the museum catalog number in parenthesis (all undamaged shells with 5 or more whorls were used). Field Museum of Natural History: 29 specimens: FMNH 22347 (1), 30850 (2), 36309 (5), 50011 (4), 58295 (3), 62416 (6), 74849 (1), 78560 (2), 98199 (2), 109097 (1), and 175899 (1). The Academy of Natural Sciences of Philadelphia: 22 specimens: ANSP 186729 (1), 186731 (1), 346372 (3), 84622 (2), 104753 (1), 4312 (1), 84637 (1), 158379 (1), 134180 (4), 76849 (3), 150798 (1), 76837 (1) topotype, 186733 (1), and 87425 (1). Angelo State Natural History Collection: 13 specimens, individually numbered: (ASNHC 0008–0014, 042, 044–048).

Euglandina immemorata (6): FMNH 11777 (1), 4359 (1) locality unknown, types; Florida Museum of Natural History 189621 (1), Nuevo Leon, Mexico, Santiago, 1 km. N of Laguna de Sanchez. University of Alabama Gastropod Collection, 3 specimens, individually numbered: 632–634, Nuevo Leon, Mexico 25°23′00.9″N; 100°14′28.6″W, 1 km N of Laguna de Sanchez.

Allozyme Analysis

Euglandina singleyana (7): Specimens used in this analysis are deposited in the Strecker Museum of Natural History, (SMNH) Baylor University (Accession Number 2001-A-1-1; Catalog Numbers SM32439-SM32446). (1) Landa Park, New Braunfels, Comal County, Texas; (1) Kerrville, Kerr County, Texas; (2) 9 miles N of Leakey, Real County, Texas; (2) Devil's River State Natural Area (DRSNA), Val Verde County, Texas; (1) Comstock, Val Verde County, Texas. *Rabdotus alternatus* from Val Verde County was selected as an outgroup.

DNA Sequence Analysis

The same specimens listed in the above section on allozyme analysis provided the tissue samples which were used in the sequence analysis. Additionally included were a specimen of an unidentified *Euglandina* from La Cuesta in Northern Coahuila; *Euglandina corneola* from 4 miles SW of Mante, Tamaulipas, Mexico; 2 specimens of *E. immemorata* from Nuevo Leon, Mexico 25°23′00.9″N; 100°14′28.6″W, 1 km N of Laguna de Sanchez; and one specimen of *E. rosea* from Lake County, Florida 28°30′53″N; 81°44′15″W.

Euhadra amaliae (AF098712), *Phaeohelix phaeogramma* (AF098714), and *Nesiohelix omphalina* (AF098713) sequences from Chiba (1999) were used as outgroups.

Distribution

Strecker (1935) listed *Euglandina singleyana* as occurring in Bexar, Caldwell, Comal, Goliad, Hays, Travis, Victoria, Atascosa, Frio, Gonzales, Guadalupe, and Wilson counties. McGee (1971) added Bandera, Fayette, Kendall, Kerr, Kinney, Val Verde, Medina, and Real counties. Cheatum et al. (1972) added Terrell County to the distribution. Collections by the authors and examinations of museum specimens from the Academy of Natural Sciences in Philadelphia and the Field Museum of Natural History during this study add Uvalde, Kimble, Chambers, Coryell, and Blanco counties to the known distribution (Fig. 1).

County records.—FMNH 78560, Horse Creek, Coryell Co., Texas; FMNH 98199, Galveston, Chambers Co., Texas; FMNH 210, 103/1, River Drift, Pedernales Falls State Park, Blanco Co., Texas; ANSP 186731, Garner State Park, Uvalde Co., Texas; ANSP 186727, Roadside Park, Nueces River W of Uvalde, Uvalde Co., Texas; ANSP 186733, Llano River, Highway 29, 12 miles S of Junction, Kimble Co., Texas.

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Redescription of adults and description of copepodid development of *Dermatomyzon nigripes* (Brady & Robertson, 1876) and of *Asterocheres lilljeborgi* Boeck, 1859 (Copepoda: Siphonostomatoida: Asterocheridae)

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Abstract.—Adult and immature copepodids of *Dermatomyzon nigripes* (Brady & Robertson, 1876) and *Asterocheres lilljeborgi* Boeck, 1859 were collected by SCUBA from the White Sea. All copepodids of *D. nigripes* were found on the bryozoan *Flustra foliacea* (Linnaeus, 1758); adults of *D. nigripes* also were washed out from the sponge *Halichondria panicea* (Pallas, 1766), the ophiuroid *Ophiopholis aculeata* (Linnaeus, 1767), and were collected among hydrozoans and other invertebrates from dead shells swept by tidal currents. Copepodids of *A. lilljeborgi* were washed from the starfish *Henricia sanguinolenta* (O. F. Müller, 1776). Comparative analysis of development of *D. nigripes* and *A. lilljeborgi* with the related *Scottomyzon gibberum* (Scott & Scott, 1894) shows that both genders of *A. lilljeborgi* and *S. gibberum* suppress the formation of fourth abdominal somite. Females of *A. lilljeborgi* and *D. nigripes* develop a simple segmental complex when the arthrodial membrane separating the genital somite from the second abdominal somite fails to form; this arthrodial membrane develops on females of *S. gibberum* so that there is no genital complex. The antennule of *A. lilljeborgi* with a single, proximal complex of three segments appears most similar to the ancestral siphonostomatoid. The antennule of *D. nigripes* has a proximal complex of two segments and a distal complex of three segments; the antennule of *S. gibberum* has a proximal complex of three segments and a distal complex of four segments. Setation of the maxilliped of *D. nigripes* and *A. lilljeborgi* are identical and appear similar to the ancestral siphonostomatoid; the maxilliped of *S. gibberum* differs in that it fails to add a seta to its syncoxa and loses a seta on the penultimate endopodal segment. *Asterocheres lilljeborgi* and *S. gibberum* share derived states of setation on the exopod of swimming legs 1–4, leg 5 and leg 6; *D. nigripes* and *S. gibberum* share derived states of setation on the endopod of swimming legs 3 and 4.

Copepods belonging to the family Asterocheridae Giesbrecht 1899 have been collected as free-living from the benthopelagic zone, or from benthic samples taken in association with cnidarians, echinoderms, sponges, ascidians and bryozoans from all oceans of the world. Forty of 45 genera of asterocherids have been described from shallow marine waters, and five from deep waters. Four of the five deep water genera are found in galls of corals (Stock 1981, 1984); the monotypic genus *Cheramomyzon* Humes, 1989 is found in deep water seeps off Florida. In addition, one species of the shallow water genus *Collocherides* Canu, 1893 has been collected from a deep water hydrothermal vent in the northeast Pacific Ocean (Humes 1999). The family Asterocheridae and the deep water hydrothermal vent family Dirivultidae Humes & Dojiri, 1980 share character states often considered ancestral for the order Siphonostomatoida in phylogenetic analyses of copepod orders (Ho 1990, Huys & Boxshall 1991, Martínez Arbizu 2003). Detailed descriptions of development of asterocherid species are essential in analyzing the ancestral states, transformations, and homologies of characters of that order and of the subclass Copepoda. Ivanenko et al. (2001) provide the only description of development of a siphonostomatoid, *Scottomyzon gibberum* (Scott & Scott, 1894), associated with an invertebrate, the starfish *Asterias rubens* Linnaeus, 1758. *Scottomyzon gibberum* previously was included in Asterocheridae, but was placed in Scottomyzontidae by Ivanenko et al. (2001). In the present paper, adults are redescribed and all juvenile copepodid stages are described of *Dermatomyzon nigripes* (Brady & Robertson, 1876) and *Asterocheres lilljeborgi* Boeck, 1859, both collected from the White Sea. *Dermatomyzon nigripes* is the only species of the genus. *Asterocheres lilljeborgi* is the oldest of 60 nominal species in its genus, and taxonomic studies of the genus have been published continuously since its discovery.

Methods

All measurements and dissections were made for copepodids from the Karelian coast of the Gulf of Kandalaksha, White Sea, near the Marine Station of Moscow State University, 66°31′N, 33°07′W. Benthic invertebrates were collected individually in plastic bags during SCUBA dives from 5–25 m. About five volumes of fresh water were added to one volume of the seawater in the plastic bag with invertebrates for 30 min. The bag was agitated and the water passed through a 20 micron mesh net. Copepodids conforming to stages I–VI were recovered from these net samples and fixed with 70% ethanol; no nauplii were collected. Copepodids were cleared in lactic acid following the method of Humes & Gooding (1964), and stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% freshwater (Ferrari 1995). Drawings were made with a camera lucida.

The first to sixth copepodid stages are CI–CVI. Thoracic somites are abbreviated Th; abdominal somites are Abd. CR is the caudal ramus. Somites are numbered according to their relative developmental age following Hulsemann (1991); thoracic somites and abdominal somites, except the most posterior anal somite, increase in age and decrease in numeral designation anteriorly. The anal somite bearing the caudal rami is designated as the first abdominal somite because developmentally it is the oldest abdominal somite. The first thoracic somite bears the maxilliped; the genital openings are found on the seventh thoracic somite.

The number of segments of the antennule often are difficult to determine because the arthrodial membrane separating segments may be very thin and difficult to observe; armament of an antennular segment is given as "setae + aesthetascs". Although patterning of copepod swimming legs during development are only incompletely known, the model of proximal patterning (Ferrari & Benforado 1998) is followed here. Ramal segments of swimming legs 1–4 (thoracopods 2–5) are referred to by their presentation during development (Ferrari 1995). The terms "seta" and "spine" are used for articulating cuticular elements connected by an arthrodial membrane to an appendage segment; setae appear to be less rigid than spines. In order to maintain continuity among descriptive publications, tables of setae and spines on swimming legs 1–4 in the descriptive section follow the formula introduced by Lang (1934). In the formula, Roman numerals indicate spines and Arabic numerals are setae. Numerals to the left of a comma or dash indicate lateral elements; numerals between two commas are terminal elements, and numerals to the right of a comma or dash are medial elements. A semicolon separates ramal segments and an asterisk indicates that the segment is absent. It should be noted, however, that this kind of formula is not derived from the way a swimming leg is patterned during development, in which the distal arthrodial membrane of a segment is formed one copepodid stage later than the formation of the initial seta of the segment (Ferrari & Benforado 1998). Thus, setal and segmental homologies cannot be determined correctly from the formula. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite. Only authors who have contributed descriptions and/or illustrations are cited in the synonymy section.

Dermatomyzon nigripes (Brady & Robertson, 1876)
Figs. 1–8

Dermatomyzon nigripes Brady and Robertson, 1876.—Giesbrecht, 1899:77–78, pl. 1, fig. 4, pl. 5, figs. 1–14.—Sars, 1914: 95–97, pls. 59, 60.—Lang, 1949:5, fig. 8.—Eiselt, 1965:155–158, fig. 3A–J.—Boxshall, 1990:537–539, figs. 9–11.—Gotto, 1993:166, figs. 40P–Q, 41A–D.

Dermatomyzon giesbrechti Brady, 1910: 574–577, textfigure 60, pl. 58, fig. 11.

Dermatomyzon nigripes giesbrechti Brady, 1910.—Eiselt, 1965:155.

Dermatomyzon elegans Claus, 1889:351, pl. 6.

Dermatomyzon herdmani Brady, 1910:575, fig. 61.

Cyclopicera nigripes Brady & Robertson, 1876:197.—Brady, 1880:54–56, pl. 89, figs. 1–11.—Thompson, 1893:36, pl. 25, fig. 7.

Ascomyzon thorelli Sars, 1880:474–75.

CVI female (Fig. 1A, B).—Body length range 1.20–1.36 mm (based on 3 specimens); average length of prosome 0.84 mm; maximum width of prosome 0.62 mm; length of urosome 0.46 mm; length of genital complex 0.15 mm; width of genital complex 0.17; ratio of length to width of prosome 1.4; ratio of length of prosome to length of urosome 1.8.

Prosome (Fig. 1A, B): 4 articulating sections; 1st a complex of 5 cephalic somites plus Th1, 2; Th3–5 articulating.

Urosome (Fig. 1C, D): 5 articulating sections; Th6, genital complex of Th7 fused to Abd2 [an unsclerotized area separates anterior neck from remaining part of Th7], Abd3, 4, 1 articulating. On genital complex, paired copulatory pores ventral-lateral to oviducal openings; paired oviducal openings dorsal.

Egg sacs spherical with up to 8 eggs (Fig. 1F).

Rostrum (Fig. 1B): Pointed in lateral view.

Oral cone (Fig. 1E): Beak-like.

Antennule (Fig. 1G, H): 19 articulating segments with 1, 2, 4, 2, 2, 2, 2, 6, 1, 2, 2, 2, 2, 2, 2, 2, 2+1, 1, 11.

Antenna (Fig. 1I): Coxa and basis without setae; basis with denticle. Exopod 1-segmented with 1 terminal seta and 1 proximal seta. Endopod 2-segmented; 1st segment with denticles; 2nd segment with denticles and 5 setae, largest thick and with curved tip.

Mandible (Fig. 1J): Gnathobase 2× length of palp, tapering and slightly curved distally with denticles; 1-segmented palp with denticles and 2 terminal setae.

Maxillule (Fig. 1K): Inner lobe bearing several series of denticles and armed with 5 setae; outer lobe articulating proximally, with 1 short and 2 long setae terminally and 1 long subterminal seta.

Maxilla (Fig. 2C): Apparently 2-segmented subchela; 1st segment with proximal asthetasc; 2nd segment curved and pointed distally with indistinct arthrodial membranes at distal 3rd and distal 6th of

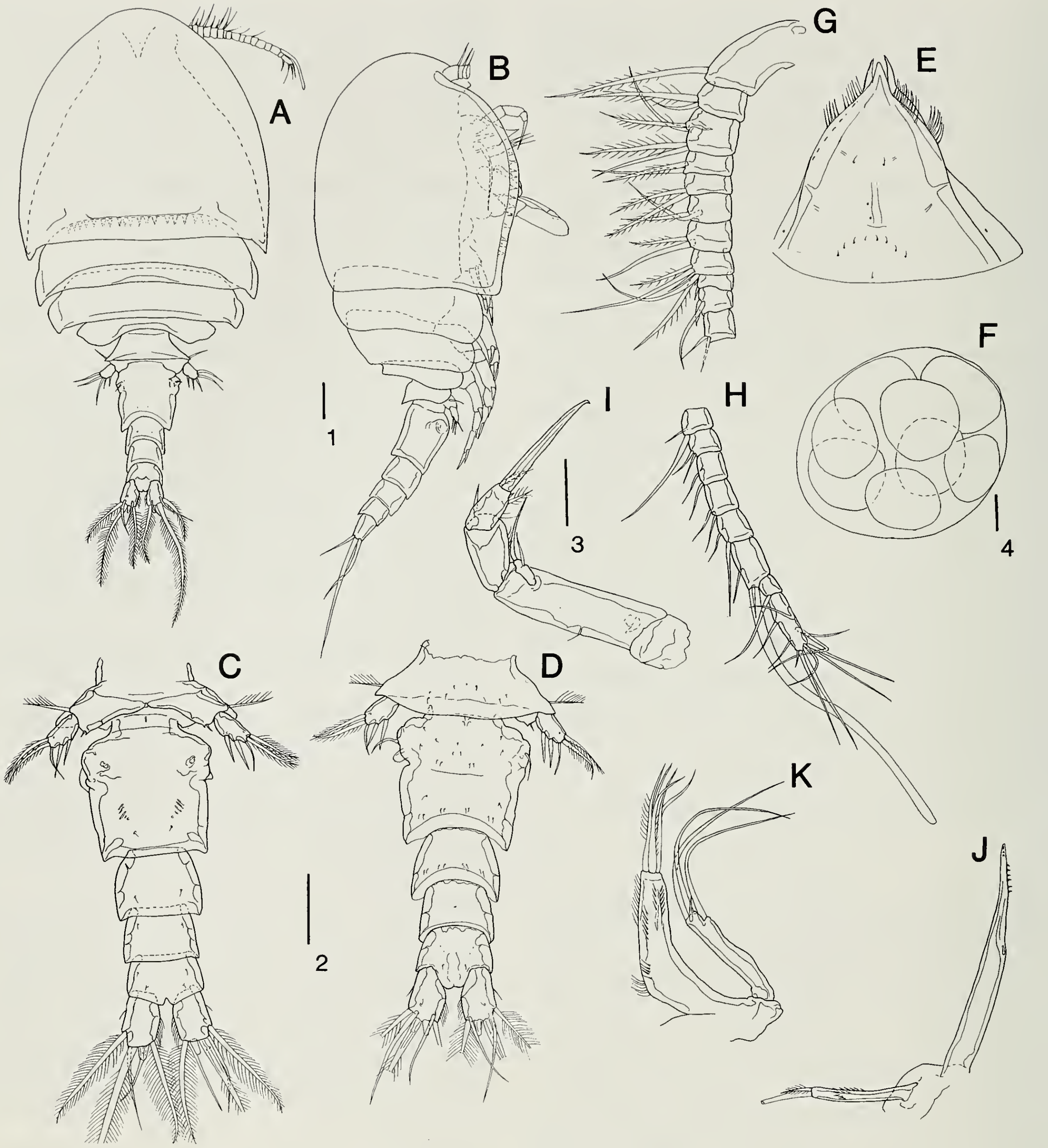

Fig. 1. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CVI Female: A, habitus, dorsal; B, habitus, lateral; C, urosome, ventral; D, urosome, dorsal; E, labrum, anterior; F, eggs; G, antennule, segments 1–11; H, antennule, segments 12–19; I, antenna; J, mandible; K, maxillule. Scale line 1 is 0.1 mm for A, B; line 2 is 0.1 mm for C, D; line 3 is 0.1 mm for E, G–K; line 4 is 0.1 mm for F.

its length, with small, inner seta and several sets of denticles.

Maxilliped (Fig. 2A, B): Short, syncoxa with 1 inner seta, long basis with 1 inner seta on medial margin; endopod of proximal, short, apparently subdivided section with 1 medially and 2 distally polarized setae, and distal segment with 2 terminal setae, largest thick and claw-like.

Swimming legs 1–4 (Fig. 2D–G): Biramal, with 3-segmented rami; all with intercoxal sclerite and 2-segmented protopods. Formula for spines and setae (Table 1). Distal exopodal seta adjacent to terminal spine of swimming legs 3–4 very small.

Leg 5 (Fig. 2I): Basis not articulating with somite and bearing medial denticle and lateral seta; exopod elongate with 1 thin

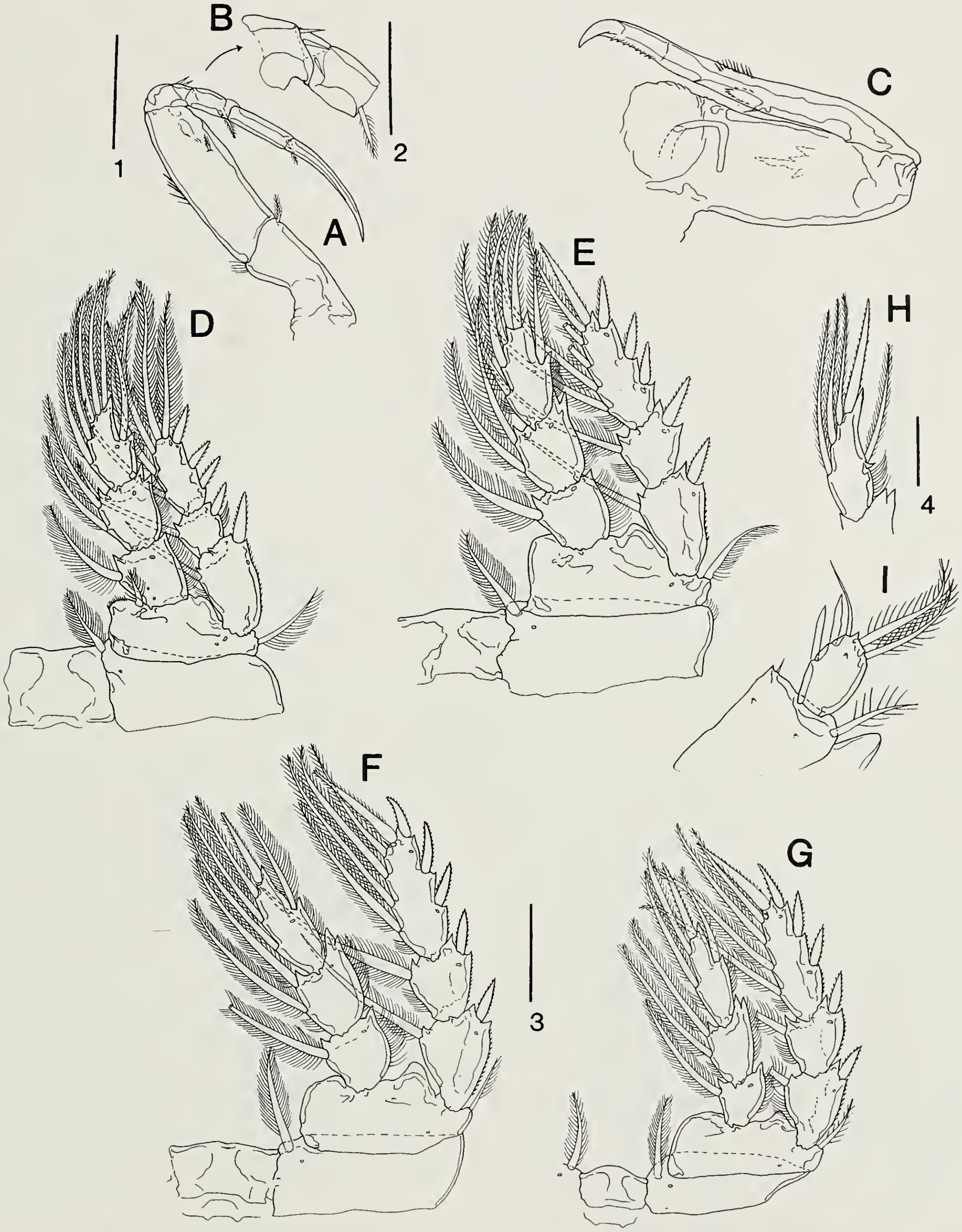

Fig. 2. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CVI Female: A, maxilliped; B, proximal part of endopod of maxilliped, posterior; C, maxilla; D, swimming leg 1; E, swimming leg 2; F, swimming leg 3; G, swimming leg 4; I, leg 5. *Dermatomyzon nigripes* CVI male: H, swimming leg 3, distal segment of endopod. Scale line 1 is 0.1 mm for A; line 2 is 0.05 mm for B; line 3 is 0.1 mm for C–G; line 4 is 0.05 mm for H, I.

Table 1.—Spines and setae on swimming legs 1–4 of *Dermatomyzon nigripes* CVI female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; I-1; III, 1, 4	0–1; 0–2; 1, 2, 3
Leg 2	0–1	1–0	I-1; I-1; III, I, 5	0–1; 0–2; 1, 2, 3
Leg 3	0–1	1–0	I-1; I-1; III, I, 5	0–1; 0–2; 1, I, 3
Leg 4	0–1	1–0	I-1; I-1; III, I, 5	0–1; 0–2; 1, I, 2

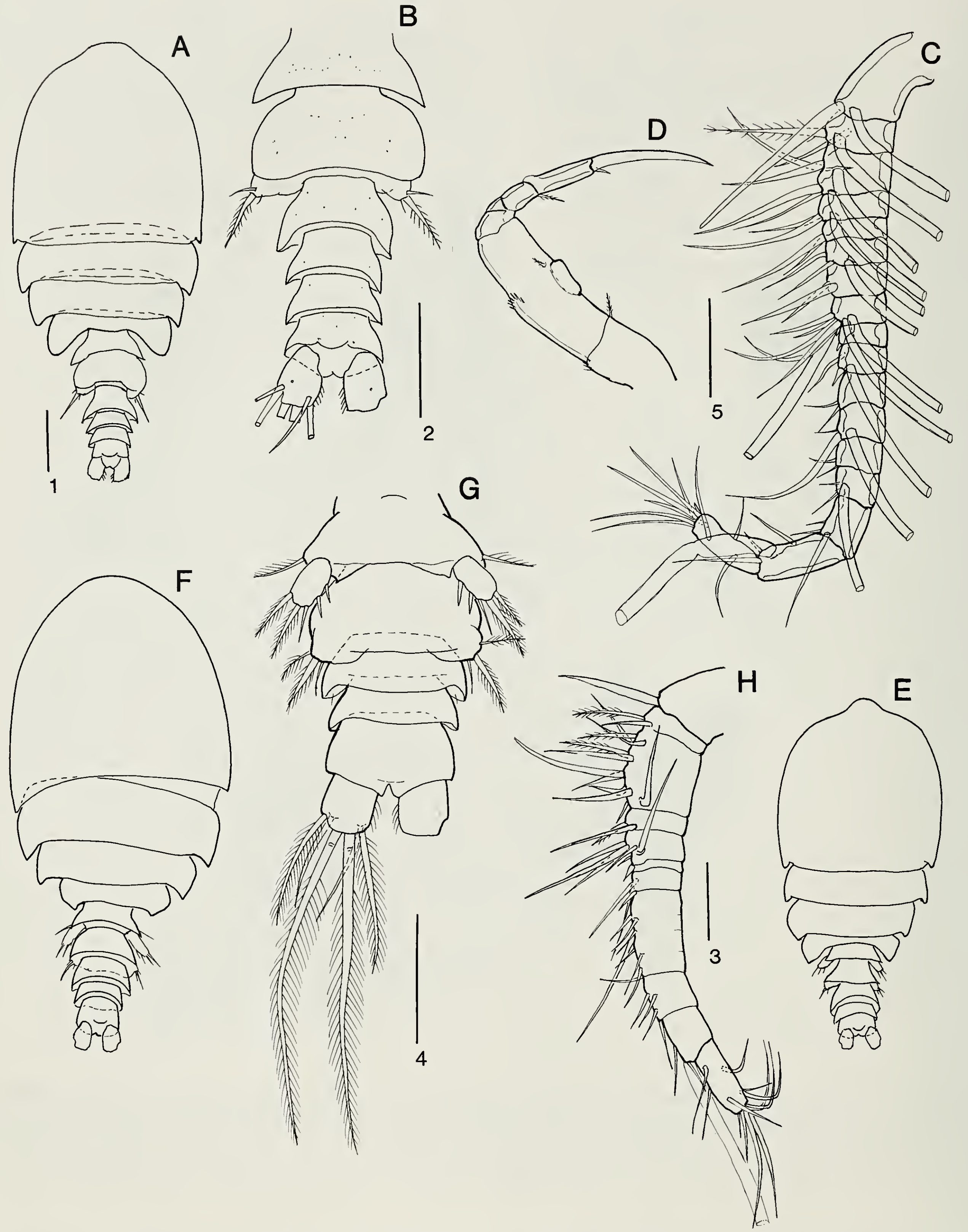

Fig. 3. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CVI Male: A, habitus, dorsal; B, urosome, dorsal; C, antennule; D, maxilliped. *Dermatomyzon nigripes* CV Male: E, habitus, dorsal. *Dermatomyzon nigripes* CV Female: F, habitus, dorsal; G, urosome, ventral; H, antennule. Scale line 1 is 0.1 mm for A, E, F; line 2 is 0.1 mm for B; line 3 is 0.1 mm for H; line 4 is 0.1 mm for D, G; line 5 is 0.1 mm for C.

and 2 thick unarmed setae laterally and 2 longer setae with setules medially.

Leg 6 (Fig. 1D): 1 long, thin seta and 2 very small setae near oviducal opening.

CR (Fig. 1C, D): Subquadrate with denticles and 1 lateral, dorsal seta, 1 medial dorsal seta, and 4 terminal setae.

CVI male (Fig. 3A).—Differs from CVI female as follows: Body length range 0.90–1.08 mm (based on 3 specimens); average length of prosome 0.59 mm; maximum width of prosome 0.42 mm; length of urosome 0.33 mm; ratio of length to width of prosome 1.4; ratio of length of prosome to length of urosome 1.8.

Urosome (Fig. 3B): 6 somites; Th7 articulating with Abd2; copulatory pore ventrolateral.

Antennule (Fig. 3C): 17 articulating segments with: 1+1, 2+1, 4+2, 2+1, 2, 2+1, 2, 6+3, 1, 2+1, 2, 2+1, 2, 2+1, 3, 3+1, 10. Geniculation between articulating segments 16 and 17; articulating segments 14–17 arc-like with articulating segment 15 flexed ventrally toward segment 14 and articulating segment 16 flexed ventrally toward segment 15.

Maxilliped (Fig. 3D): Basis with raised pad-like section proximally and medially.

Swimming leg 3 (Fig. 2H): Tip of lateral seta of distal endopodal segment not reaching to apex of terminal spine; segmental attenuation proximal to lateral seta points medially, not distally.

Leg 6 (Fig. 3B): 3 distolateral setae.

CV female (Fig. 3F).—Differs from CVI female as follows: Body length range 0.98–1.00 mm (based on 2 specimens); average length of prosome 0.67 mm; maximum width of prosome 0.47 mm; length of urosome 0.32 mm; ratio of length to width of prosome 1.4; ratio of length of prosome to length of urosome 2.1.

Urosome (Fig. 3G): 5 articulating sections; Th6, 7, Abd1–3 articulating. Th7 without copulatory pores or oviducal openings.

Antennule (Fig. 3H): 11 articulating segments with 1, 2, 11, 2, 6, 1, 3, 8, 4, 2+1, 12.

Leg 6 (Fig. 3G): 3 distolateral setae.

CV male (Fig. 3E).—Differs from CV female as follows: Body length range 0.73–0.74 mm (based on 2 specimens); average length of prosome 0.49 mm; maximum width of prosome 0.33 mm; length of urosome 0.25 mm; ratio of length to width of prosome 1.5; ratio of length of prosome to length of urosome 2.0.

Antennule: 11 articulating segments with 1, 2, 10, 2, 6, 1, 3, 8, 4, 2+1, 12.

CIV (Fig. 4A).—Differs from CV female as follows: Body length range 0.65–0.72 mm (based on 2 specimens); average length of prosome 0.48 mm; maximum width of prosome 0.32 mm; length of urosome 0.21 mm; ratio of length to width of prosome 1.5; ratio of length of prosome to length of urosome 2.3.

Urosome (Fig. 4B): 4 articulating sections; Th6, 7, Abd2, 1 articulating.

Antennule (Fig. 4C): 9 articulating segments with 1, 6, 1, 5, 2, 8, 4, 2+1, 12.

Antenna (Fig. 4D), maxillule (Fig. 4E) and maxilliped (Fig. 4F, G): As illustrated.

Swimming legs 1–4 (Figs. 4H, I; 5A, B): Small, distal seta adjacent to terminal spine of the exopod of swimming legs 3–4. Formula for spines and setae (Table 2).

Leg 5 (Fig. 4B): Basis not articulating with somite and bearing lateral seta; exopod elongate with 1 thin, unarmed seta medially, 1 thick, unarmed seta laterally and 1 terminal seta with setules.

Leg 6 (Fig. 4B): 2 distal setae.

CIII.—Differs from CIV female as follows: Body length 0.51 mm (based on 1 specimen); length of prosome 0.36 mm; maximum width of prosome 0.26 mm; length of urosome 0.15 mm; ratio of length to width of prosome 1.4; ratio of length of prosome to length of urosome 2.4.

Urosome (Fig. 5C, D): Th6, 7, Abd1 articulating.

Antennule (Fig. 5G): 8 articulating segments with 2, 3, 4, 1, 4, 2, 2+1, 11.

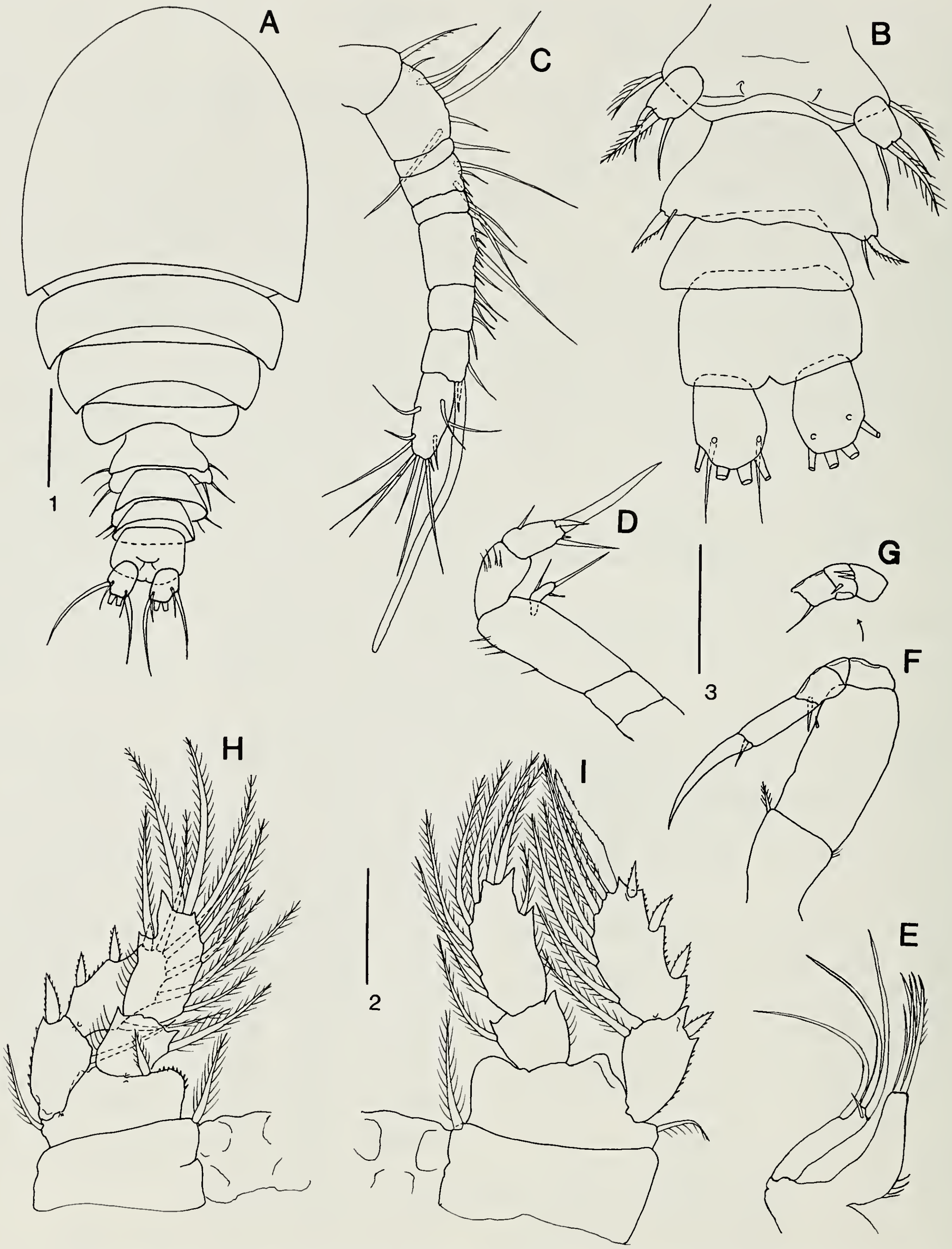

Fig. 4. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CIV Female: A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, maxillule; F, maxilliped; G, maxilliped, proximal part of endopod, posterior; H, swimming leg 1; I, swimming leg 2. Scale line 1 is 0.1 mm for A; line 2 is 0.05 mm for B, C, H, I; line 3 is 0.05 mm for D–G.

Antenna (Fig. 6B) and mandible (Fig. 6A): As illustrated.

Maxillule (Fig. 6C): Outer lobe with 3 setae; inner lobe with 4 setae.

Maxilla (Fig. 6D): 3-segmented with indistinct arthrodial membrane distally.

Maxilliped (Fig. 6E): Proximally, endopod indistinctly segmented with 1 seta.

Swimming legs 1–4 (Fig. 6F–I): Swimming legs 1–3 with 2-segmented rami, swimming leg 4 with 1-segmented rami. Distal exopodal seta adjacent to terminal

Table 2.—Spines and setae on swimming legs 1–4 of *Dermatomyzon nigripes* CIV female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; *; III, 5	0–1; *; 1, 2, 5
Leg 2	0–1	1–0	I-1; *; III, 1, 5	0–1; *; 1, 2, 5
Leg 3	0–1	1–0	I-1; *; III, I, 5	0–1; *; 1, I, 4
Leg 4	0–1	1–0	I-0; *; III, I, 5	0–1; *; 1, I, 3

spine of swimming legs 3, 4 tiny. Formula for setae and spines (Table 3).

Leg 5 (Fig. 5E): A unilobe ventrolateral bud with 1 distal spine and 1 distal seta.

CR (Fig. 5F): As illustrated.

CII.—Differs from CIII as follows: Body length 0.4 mm (based on 1 specimen); length of prosome 0.29 mm; maximum width of prosome 0.19 mm; length of urosome 0.13 mm; ratio of length to width of prosome 1.5; ratio of length of prosome to length of urosome 2.2.

Prosome (Fig. 7A, B): 3 articulating sections; 1st complex of 5 cephalic somites plus Th1, 2; Th3, 4 articulating.

Urosome (Fig. 7A, B): Th5, 6, Abd1 articulating.

Antennule (Fig. 7D): 6 articulating segments with 2, 3, 3, 1, 1+1, 11.

Antenna (Fig. 7E), mandible (Fig. 7H) and maxilla (Fig. 7F): As illustrated.

Maxillule (Fig. 7I): Inner lobe with 3 setae.

Maxilliped (Fig. 7G): Syncoxa without seta, basis without seta; proximal section of endopod with 1 distally polarized seta and 1 medial seta; distal segment with 2 terminal setae, 1 claw-like.

Swimming legs 1–3 (Fig. 7K–M): Swimming legs 1–2 with 2-segmented rami, swimming leg 3 with 1-segmented rami. Tiny distal seta adjacent to terminal spine of the exopod of swimming leg 3. Formula for spines and setae (Table 4).

Swimming leg 4 (Fig. 7C): A ventrolateral, bilobe bud; dorsal lobe with 1 distal spine and 1 distal seta; ventral lobe unarmed.

CR (Fig. 7J): As illustrated.

CI.—Differs from CII as follows based on 1 specimen: length 0.36 mm; maximum width 0.16 mm; length of prosome 0.22 mm, urosome 0.14 mm; ratio of length to width 2.25:1; ratio of length of prosome to that of urosome 1.65:1.

Prosome (Fig. 8A, B): 2 articulating sections; 1st, complex of 5 cephalic somites plus Th1, 2; Th3 articulating.

Urosome (Fig. 8A, B): Th4, 5, Abd1 articulating.

Antennule (Fig. 8E): 4 articulating segments with 2, 2, 1, 11+1.

Antenna (Fig. 8F), mandible (Fig. 8G), maxillule (Fig. 8H) and maxilla (Fig. 8I): As illustrated.

Maxilliped (Fig. 8L): Syncoxa and basis unarmed. Endopod of 2 distinct segments; proximal segment with 1 medial seta and distal segment with 2 setae.

Swimming legs 1–2 (Fig. 8J, K): 1-segmented rami. Formula for spines and setae (Table 5).

Swimming leg 3 (Fig. 8C): Ventrolateral, bilobe bud; dorsal lobe with 1 distal spine and 1 distal seta; ventral lobe unarmed.

CR (Fig. 8D): Inner terminal seta longest; remaining terminal setae decreasing in length from inner to outer.

Remarks.—The monotypic genera *Dermatomyzon* Claus, 1889, *Australomyzon* Nicholls, 1944, and *Cheramomyzon* Humes, 1989 share appendage segmentation and segmental armature with species of *Rhynchomyzon* Giesbrecht, 1895. Females of *Dermatomyzon* with a 19-segmented antennule differ from females of *Australomyzon* with a 21-segmented antennule. Females of *Dermatomyzon* differ from females of the poorly-diagnosed *Rhynchomyzon* with antennules of between 14 and 16 segments, by the well-developed rostrum or by the posterolateral extensions of thoracomeres 3 and 4. The mandibular palp of *Cheramomyzon* is 2-segmented but 1-segmented in *Dermatomyzon*. The fifth leg of *Australomyzon* is 1-segmented but 2-segmented in *Dermatomyzon*. *Dermatomyzon*

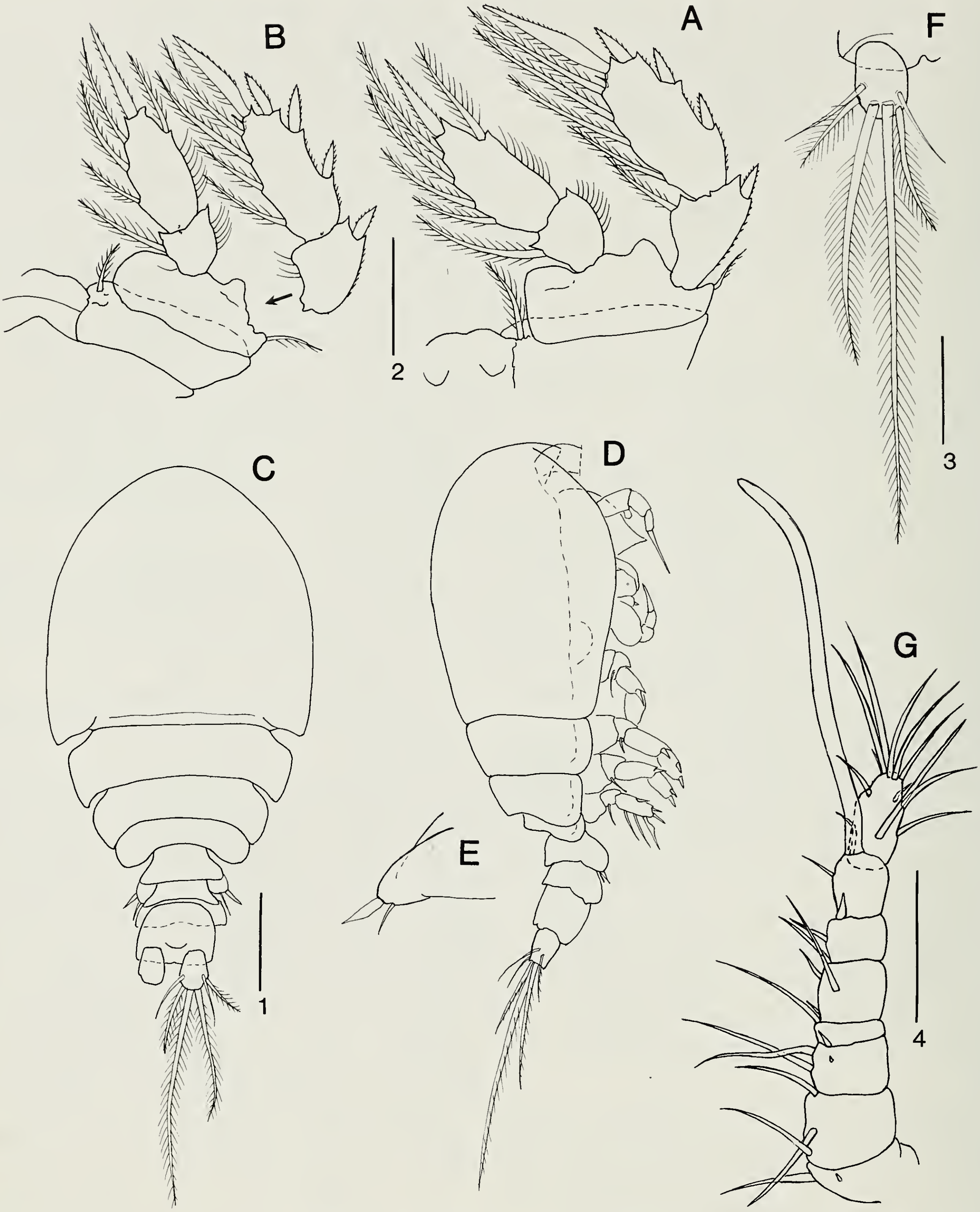

Fig. 5. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CIV Female: A, swimming leg 3; B, swimming leg 4. *Dermatomyzon nigripes* CIII: C, habitus, dorsal; D, habitus, lateral; E, leg 5; F, caudal ramus, dorsal; G, antennule. Scale line 1 is 0.1 mm for C, D; line 2 is 0.05 mm for A, B; line 3 is 0.05 mm for E–F; line 4 is 0.05 mm for G.

nigripes initially was described from the North Sea coast of England. Subsequently it has been reported from areas adjacent to the North Sea (Hansen 1923, Stephensen 1929, Jespersen 1940, Lang 1949), the Mediterranean Sea (Giesbrecht 1899), the Arctic Ocean (Shih et al. 1971), the Indian Ocean (Sewell 1949, Ummerkutty 1966), the Pacific Ocean (Boxshall 1990), and the Southern Ocean (Brady 1910). In the White Sea, copepodids of *D. nigripes* were found on the bryozoan *Flustra foliacea* (Linnaeus,

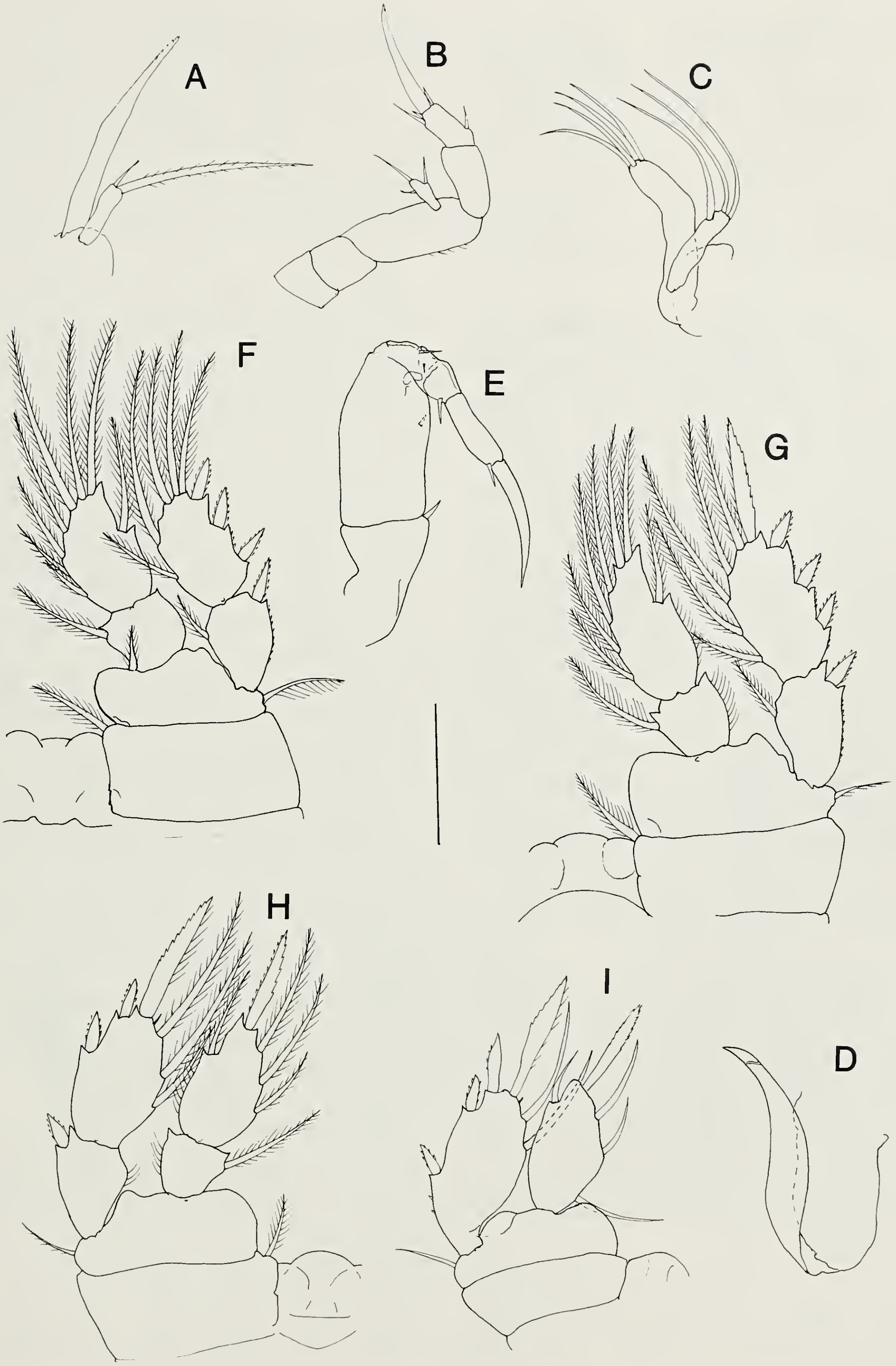

Fig. 6. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CIII: A, mandible; B, antenna; C, maxillule; D, maxilla; E, maxilliped; F, swimming leg 1; G, swimming leg 2; H, swimming leg 3; I, swimming leg 4. Scale line is 0.05 mm.

Table 3.—Spines and setae on swimming legs 1–4 of *Dermatomyzon nigripes* CIII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; *; III, 4	0–1; *; 1, 2, 5
Leg 2	0–1	1–0	I-1; *; III, I, 5	0–1; *; 1, 2, 4
Leg 3	0–1	1–0	I-0; *; II, I, 4	0–1; *; 1, I, 3
Leg 4	0–0	1–0	*; *; III, I, 3	*; *; 1, I, 3

Table 4.—Spines and setae on swimming legs 1–3 of *Dermatomyzon nigripes* CII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-0; *; III, 5	0–1; *; 1, 2, 4
Leg 2	0–1	1–0	I-0; *; II, I, 4	0–1; *; 1, 2, 3
Leg 3	0–0	1–0	*; *; III, I, 3	*; *; 1, I, 3

1758). A small number of adults of *D. nigripes* were washed from the sponge *Halichondria panicea* (Pallas, 1766) and the echinoderm *Ophiopholis aculeata* (Linnaeus, 1767). Adults also were collected around hydrozoans and other invertebrates from bottom covered by dead shells scoured by strong tidal currents. These findings suggest that adults of *D. nigripes* may be an unspecialized symbiont associated with different invertebrates of the White Sea sublittoral. However, immature copepodids of *D. nigripes,* along with other copepods, were associated only with *Flustra foliacea* (see Ivanenko & Smurov 1997) suggesting that the bryozoan may be the preferred host of the immature copepodids.

Asterocheres lilljeborgi Boeck, 1859
Figs. 9–18

Asterocheres lilljeborgi Boeck, 1859:176, pl. 2, figs. 1–11.—Brady, 1880:64–65.—Canu, 1892:264, pl. 27, figs. 1–6.—Giesbrecht, 1899:70, 73, pl. 3, figs. 21–26.—Wilson, 1944:547, pl. 30, figs. 161–162.—Roettger et al. 1972:259, figs. 1–9.—Gotto, 1993:153, fig. 36 B–J.

Ascomyzon asterocheres Sars, 1914:85–87, pls. 51–52.

CVI female.—Body length range 1.41–1.47 mm (based on 3 specimens); average length of prosome 0.99 mm; maximum width of prosome 1.09 mm; length of urosome 0.44 mm; length of genital complex 0.16 mm; width of genital complex 0.21; ratio of length to width of prosome 0.9; ratio of length of prosome to length of urosome 2.3.

Prosome (Fig. 9A): Flattened dorsoventrally with tergites pointed posteriorly; 4 articulating sections; 1st complex of 5 cephalic somites plus Th1, 2 with spinules; Th3–5 articulating.

Urosome (Fig. 9B): 4 articulating sections; Th6, genital complex of Th7 fused to Abd2, Abd3, and Abd1. Th6 and genital complex with spinules; paired copulatory pores ventrolateral; paired oviducal openings dorsolateral.

Rostral area flattened; rostrum absent.

Oral siphon (Fig. 10D): Tip reaching beyond base of maxilla.

Labrum: With spinules on tip.

Antennule (Fig. 9E, F): 21 articulating segments with 2, 2, 2, 2, 2, 2, 2, 2, 6, 2, 2, 2, 2, 2, 2, 2, 2, 2+1, 2, 2, 8.

Antenna (Fig. 10A): Coxa and basis without setae. Exopod apparently 1-segmented with 2 terminal setae and proximal medial seta (Fig. 10B). Endopod 3-segmented; 1st segment with denticles, 2nd with 1 seta, 3rd with denticles and 4 setae, including large terminal claw.

Mandible (Fig. 10C): Gnathobase slightly longer than palp, tapering distally with denticles; 2-segmented palp, both segments with denticles, distal segment with 2 terminal setae.

Maxillule (Fig. 10E): Inner lobe with several sets of denticles, 4 large setae and 1 small seta; outer articulating lobe with denticles and 4 terminal setae.

Maxilla (Fig. 10F): An apparently 2-segmented subchela; 1st segment unarmed; 2nd segment distally pointed, curved, with set of denticles but without setae.

Maxilliped (Fig. 10G, H): Short syncoxa

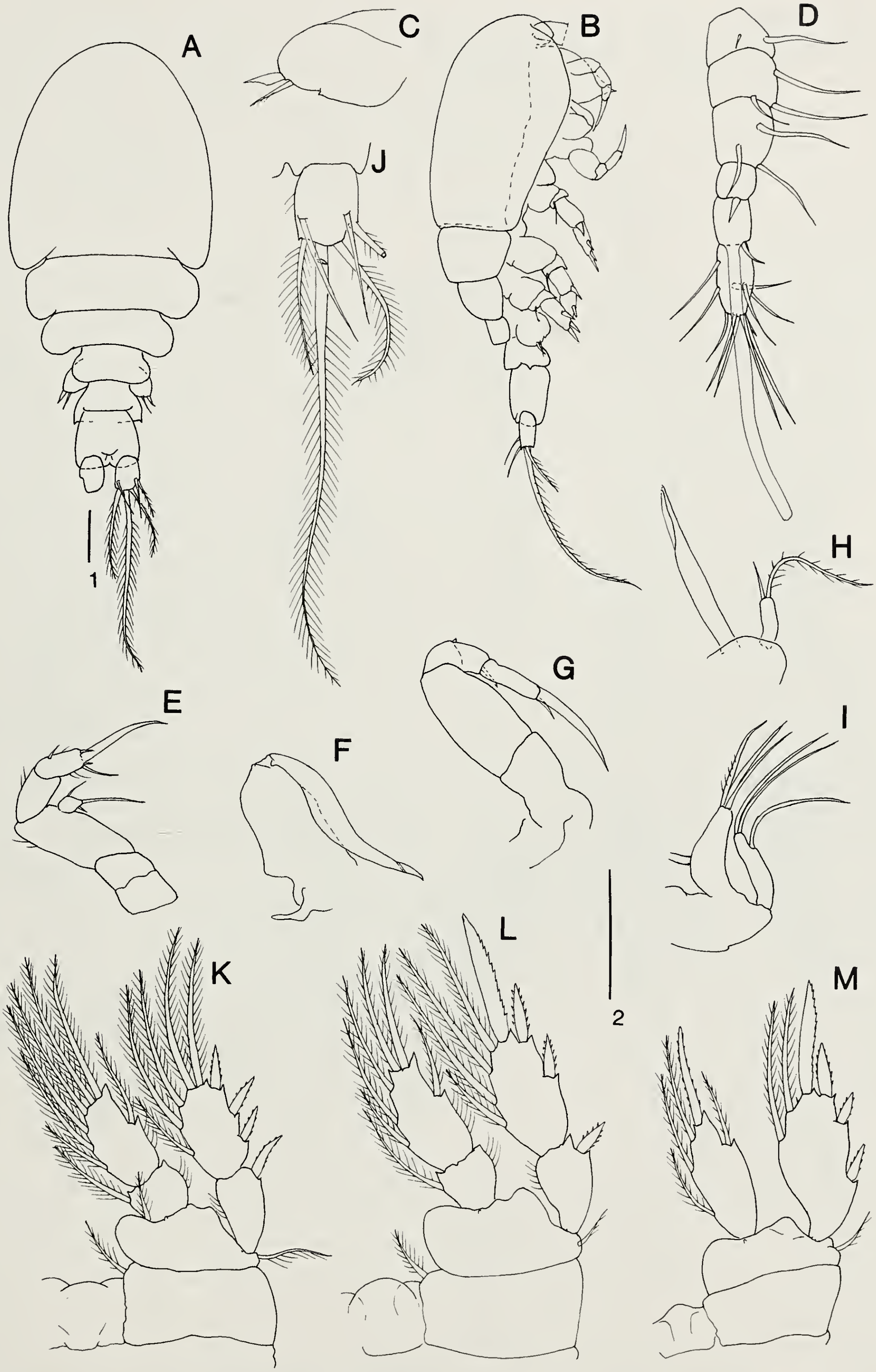

Fig. 7. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CII: A, habitus, dorsal; B, habitus, lateral; C, swimming leg 3; D, antennule; E, antenna; F, maxilla; G, maxilliped; H, mandible; I, maxillule; J, caudal ramus; K, swimming leg 1; L, swimming leg 2; M, swimming leg 3. Scale line 1 is 0.05 mm for A, B; line 2 is 0.05 mm for C–M.

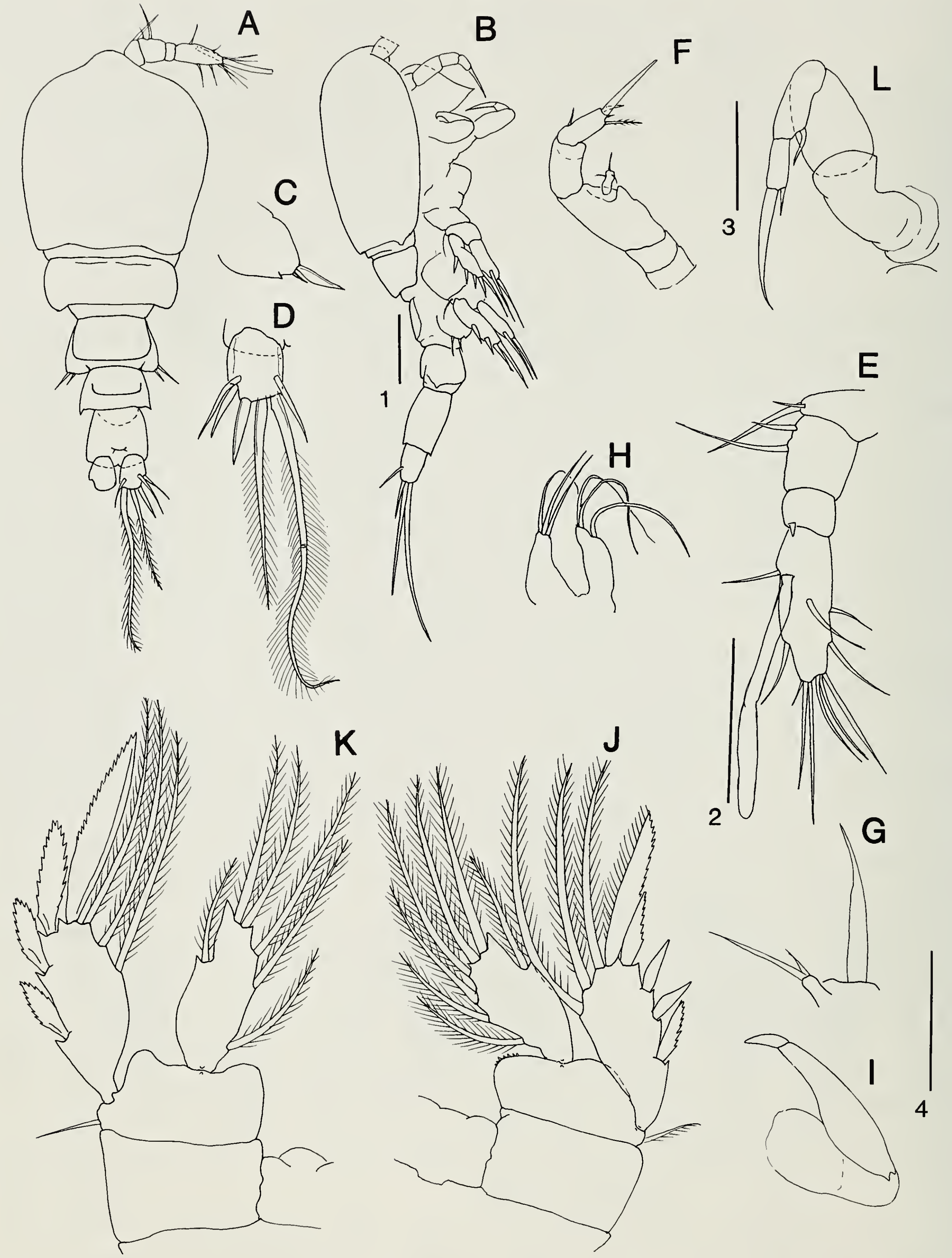

Fig. 8. *Dermatomyzon nigripes* (Brady & Robertson, 1876), CI: A, habitus, dorsal; B, habitus, lateral; C, swimming leg 3; D, caudal ramus; E, antennule; F, antenna; G, mandible; H, maxillule; I, maxilla; J, swimming leg 1; K, swimming leg 2; L, maxilliped. Scale line 1 is 0.05 mm for A, B; line 2 is 0.05 mm for C–E, J, K; line 3 is 0.05 mm for F, H, L; line 4 is 0.05 mm for G, I.

Table 5.—Spines and setae on swimming legs 1–2 of *Dermatomyzon nigripes* CI.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–0	1–0	*; *; IV, I, 3	*; *; 1, 2, 4
Leg 2	0–0	1–0	*; *; III, I, 3	*; *; 1, 2, 3

with 1 inner seta, long basis with 1 tiny, inner seta on medial margin; endopod of proximal, short, apparently subdivided section with 4 setae, 2 proximal, 1 middle, 1 distal; long distal segment with denticles and 2 terminal setae, largest thick and curved.

Swimming legs 1–4 (Fig. 11A–E): Biramal, with 3-segmented rami. Formula for spines and setae (Table 6). Lateral seta of the distal endopodal segment of swimming leg 3 not reaching tip of lateral apical seta; lateral apical seta of the distal endopodal segment of swimming leg 4 half the length of apical spine.

Leg 5 (Fig. 11F): Basis not articulating with somite, with lateral seta; articulating segment elongate with 2 unarmed terminal setae and 1 medial seta, plus medial and lateral denticles.

Leg 6 (Fig. 9C): 1 long seta and 1 short seta near oviducal openings.

CR (Fig. 9D): Subquadrate with 2 dorsal setae and 4 terminal setae.

CVI male.—Differs from CVI female as follows: Body length range 1.01–1.06 mm (based on 3 specimens); average length of prosome 0.70 mm; maximum width of prosome 0.70 mm; length of urosome 0.36 mm; ratio of length to width of prosome 1.0; ratio of length of prosome to length of urosome 1.9.

Urosome (Fig. 12A): Th6, 7, Abd2, 3, 1 articulating. Th7 with copulatory pore ventrolaterally.

Antennule (Fig. 12B–D): 18 articulating segments with: 2, 2, 2, 2, 2, 2, 2, 2, 6, 2, 2, 2, 2, 2, 2, 4, 3+1, 12. Geniculation between 15th and 16th articulating segments; segment 10 unsclerotized dorsally.

Maxilla (Fig. 12G): Apparently 3-segmented subchela; 1st segment with proximal denticles; 2nd with 1 small seta; 3rd distally pointed and curved.

Maxilliped (Fig. 12H): Basis with raised bump proximally and medially.

Swimming legs 1–4 (Fig. 11G–J): Swimming leg 1 with denticles on distal segment of endopod. Distal attenuation of middle segment of endopod of swimming leg 2 relatively longer than corresponding structure on other swimming legs; denticles on distal segment of endopod. Lateral seta on distal endopodal segment of swimming leg 3 almost reaching to tip of apical seta. Lateral apical seta on distal endopodal segment of swimming leg 4 reaching ¾ length of apical spine.

Leg 5 (Fig. 12F): As illustrated.

Leg 6 (Fig. 12E): Several sets of denticles and 2 setae, distal thickest.

CV female (Fig. 13A).—Differs from CVI female as follows: Body length range 0.84–1.05 mm (based on 7 specimens); average length of prosome 0.64 mm; maximum width of prosome 0.62 mm; length of urosome 0.30 mm; ratio of length to width of prosome 1.0; ratio of length of prosome to length of urosome 2.1.

Urosome (Fig. 13A): Th6, 7, Abd2, 3,1 articulating; no copulatory pore or oviducal openings on Th7.

Antennule (Fig. 13C): 18 articulating segments with 2, 2, 2, 2, 2, 2, 2, 2, 8, 2, 2, 4, 2, 2, 2, 2, 2+1, 14.

Leg 6 (Fig. 13A): Uniramal bud with 1 lateral seta and medial denticles.

CV male (Fig. 13B).—Differs from CV female as follows: Body length range 0.85–0.89 mm (based on 2 specimens); average length of prosome 0.59 mm; maximum width of prosome 0.54 mm; length of urosome 0.29 mm; ratio of length to width of prosome 1.1; ratio of length of prosome to length of urosome 2.5.

Leg 6: Unilobe bud with 1 lateral seta and 1 terminal seta.

CIV.—Differs from CV female as follows: Body length range 0.65–0.80 mm (based on 7 specimens); average length of

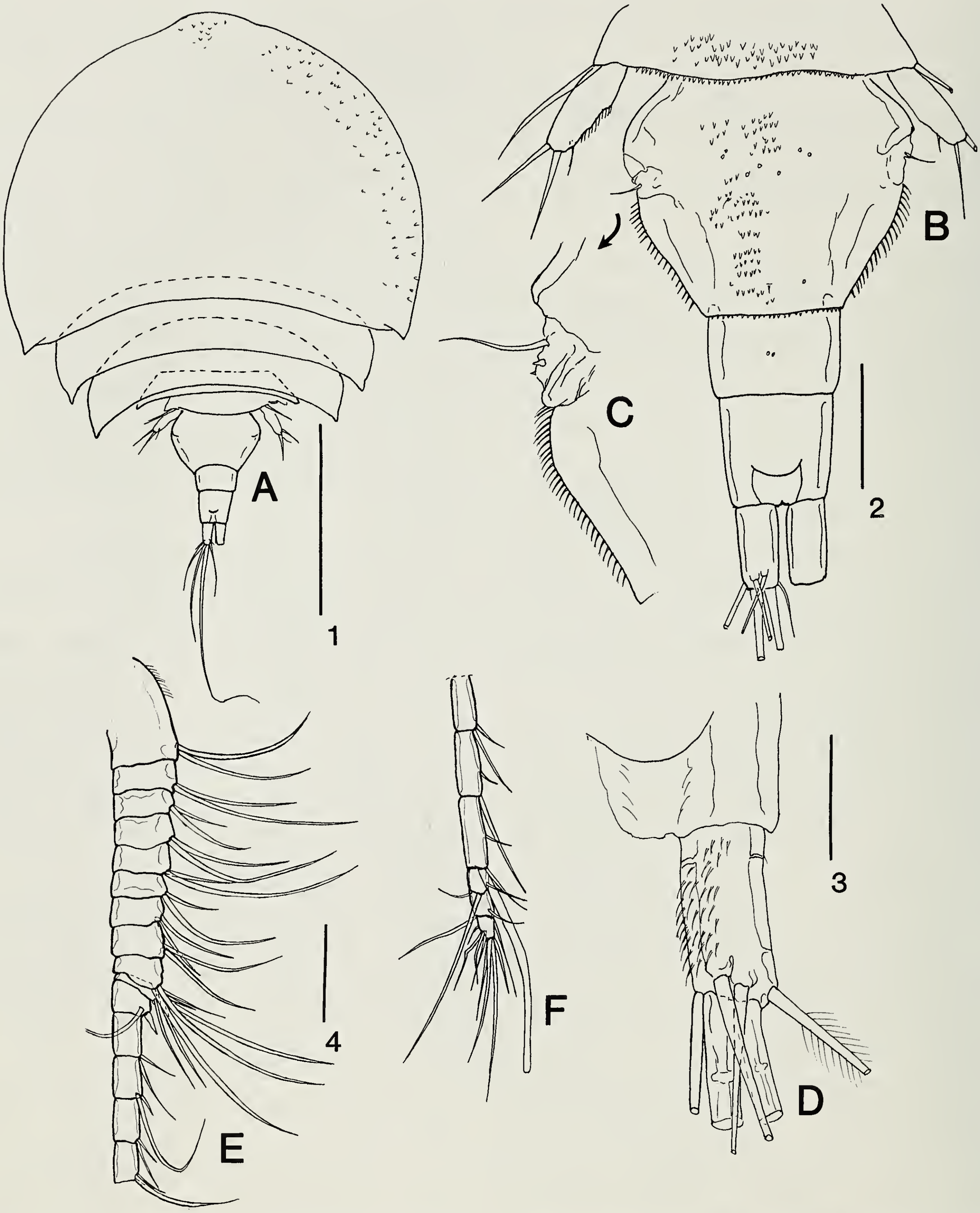

Fig. 9. *Asterocheres lilljeborgi* Boeck, 1859, CVI: A, Female, habitus, dorsal; B, urosome, dorsal; C, leg 6; D, caudal ramus, dorsal; E, antennule, segments 1–15; F, antennule, segments 16–21. Scale line 1 is 0.1 mm for A; line 2 is 0.1 mm for B; line 3 is 0.1 mm for C, D; line 4 is 0.1 mm for E, F.

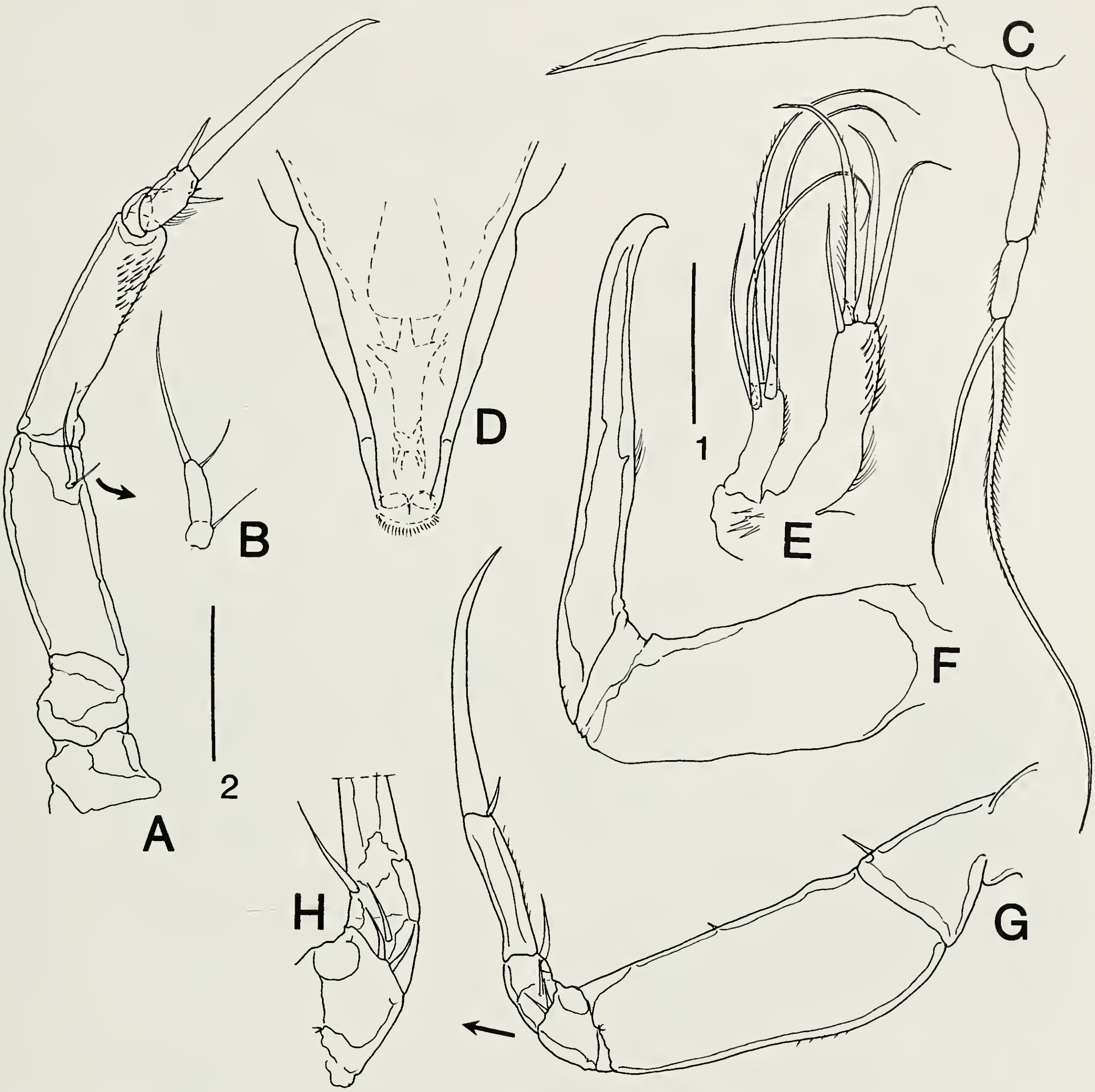

Fig. 10. *Asterocheres lilljeborgi* Boeck, 1859, CVI Female: A, antenna; B, exopod of antenna; C, mandible; D, oral siphon; E, maxillule; F, maxilla; G, maxilliped; H, proximal part of endopod of maxilliped, posterior. Scale line 1 is 0.1 mm for A, C–G; line 2 is 0.05 mm for B, H.

prosome 0.48 mm; maximum width of prosome 0.40 mm; length of urosome 0.22 mm; ratio of length to width of prosome 1.2; ratio of length of prosome to length of urosome 2.2 (Fig. 13E).

Urosome (Fig. 13G): Th6, 7, Abd2, 1 articulating.

Antennule (Fig. 13F): 17 articulating segments with 2, 1, 1, 1, 1, 1, 1, 1, 4, 1, 2, 4, 4, 2, 2, 2+1, 14.

Maxilla as illustrated (Fig. 14A).

Swimming legs 1–4 (Figs. 14B–F): 2-segmented rami. Formula for spines and setae (Table 7).

Leg 5 (Fig. 13G): Basis not articulating with somite, with lateral seta; free segment with 1 small seta laterally and 2 thick, unarmed setae distally.

Leg 6 (Fig. 13G): Unilobe bud with 1 seta.

CIII.—Differs from CIV as follows: Body length range 0.50–0.54 mm (based on 3 specimens); average length of prosome 0.37 mm; maximum width of prosome 0.30

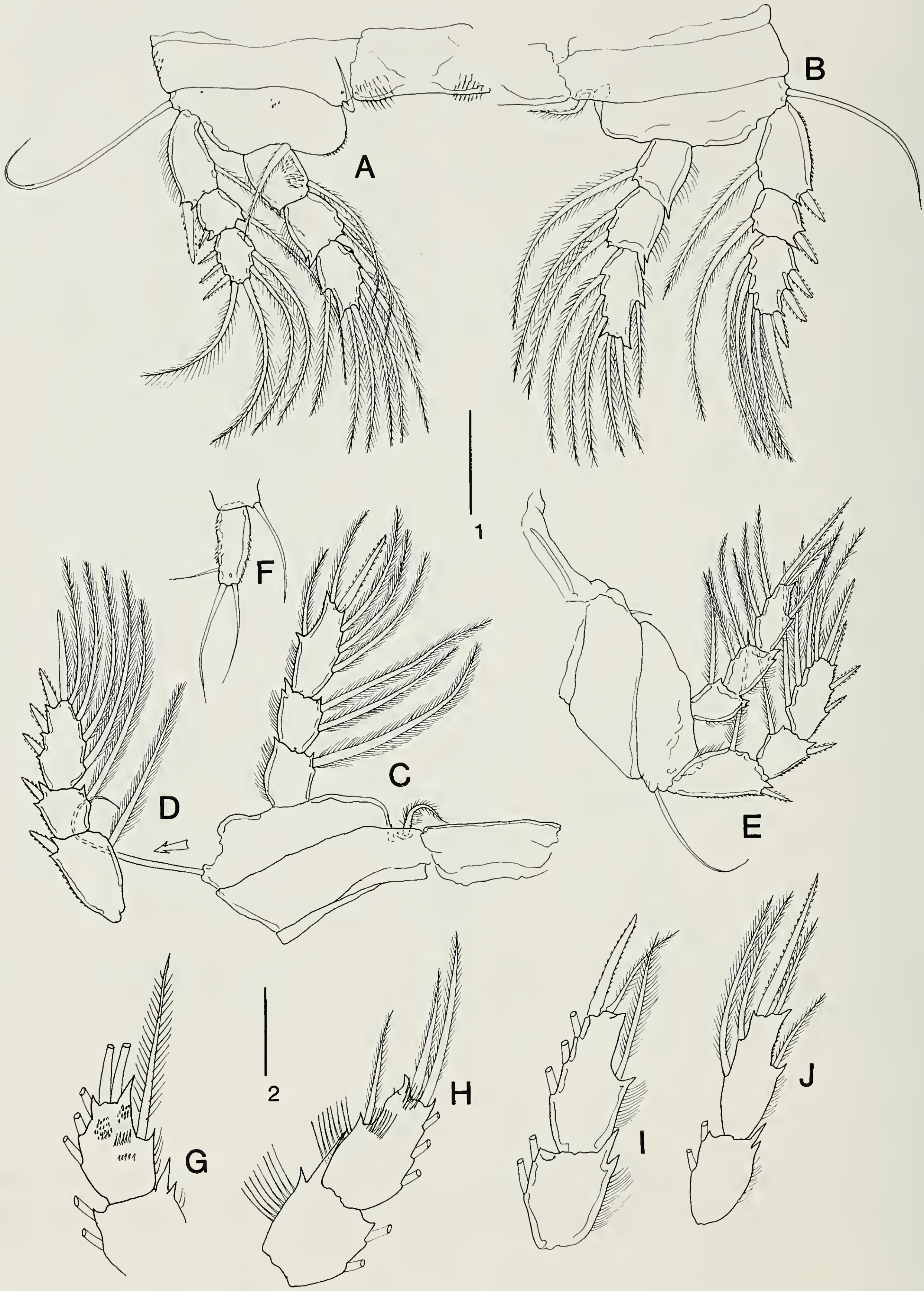

Fig. 11. *Asterocheres lilljeborgi* Boeck, 1859, CVI Female: A, swimming leg 1; B, swimming leg 2; C, intercoxal sclerite, protopod, and endopod of swimming leg 3; D, exopod, swimming leg 3; E, swimming leg 4; F, leg 5. *Asterocheres lilljeborgi,* CVI Male, distal segments of endopod of G, swimming leg 1; H, swimming leg 2; I, swimming leg 3; J, swimming leg 4. Scale line 1 is 0.1 mm for A–F; line 2 is 0.1 mm for G–J.

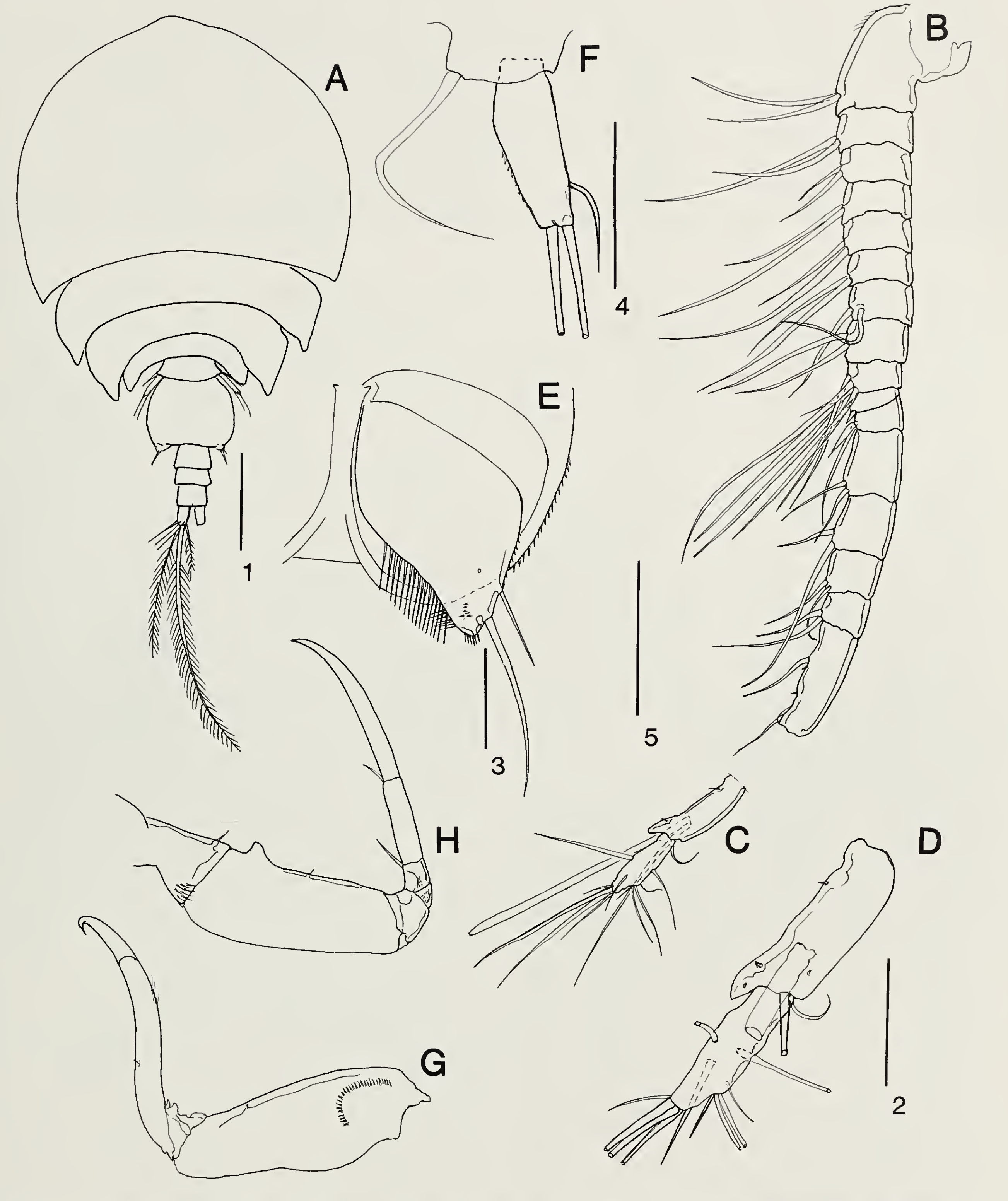

Fig. 12. *Asterocheres lilljeborgi* Boeck, 1859, CVI Male: A, habitus, dorsal; B, antennule, segments 1–16; C, antennule, segments 17–18 anterior; D, antennule, segments 17–18 anterior; E, leg 6; F, leg 5; G, maxilla; H, maxilliped. Scale line 1 is 0.1 mm for A; line 2 is 0.05 mm for D; line 3 is 0.05 mm for E; line 4 is 0.05 mm for B, C, F; line 5 is 0.1 mm for G, H.

mm; length of urosome 0.14 mm; ratio of length to width of prosome 1.2; ratio of length of prosome to length of urosome 2.6.

Urosome (Fig. 15A): Th6, 7, Abd1 articulating.

Antennule (Fig. 15C): 12 articulating segments with 2, 1, 1, 1, 3, 1, 1, 2, 2, 2, 3+1, 14.

Antenna (Fig. 15D), mandible (Fig. 15E) and maxilla (Fig. 15G): As illustrated.

Table 6.—Spines and setae on swimming legs 1–4 of *Asterocheres lilljeborgi* adult female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; I-1; III, I, 3	0–1; 0–2; 1, 2, 3
Leg 2	0–1	1–0	I-1; I-1; III, I, 4	0–1; 0–2; 1, 2, 3
Leg 3	0–1	1–0	I-1; I-1; III, I, 4	0–1; 0–2; 1, 1+I, 3
Leg 4	0–1	1–0	I-1; I-1; III, I, 4	0–1; 0–2; 1, 1+I, 2

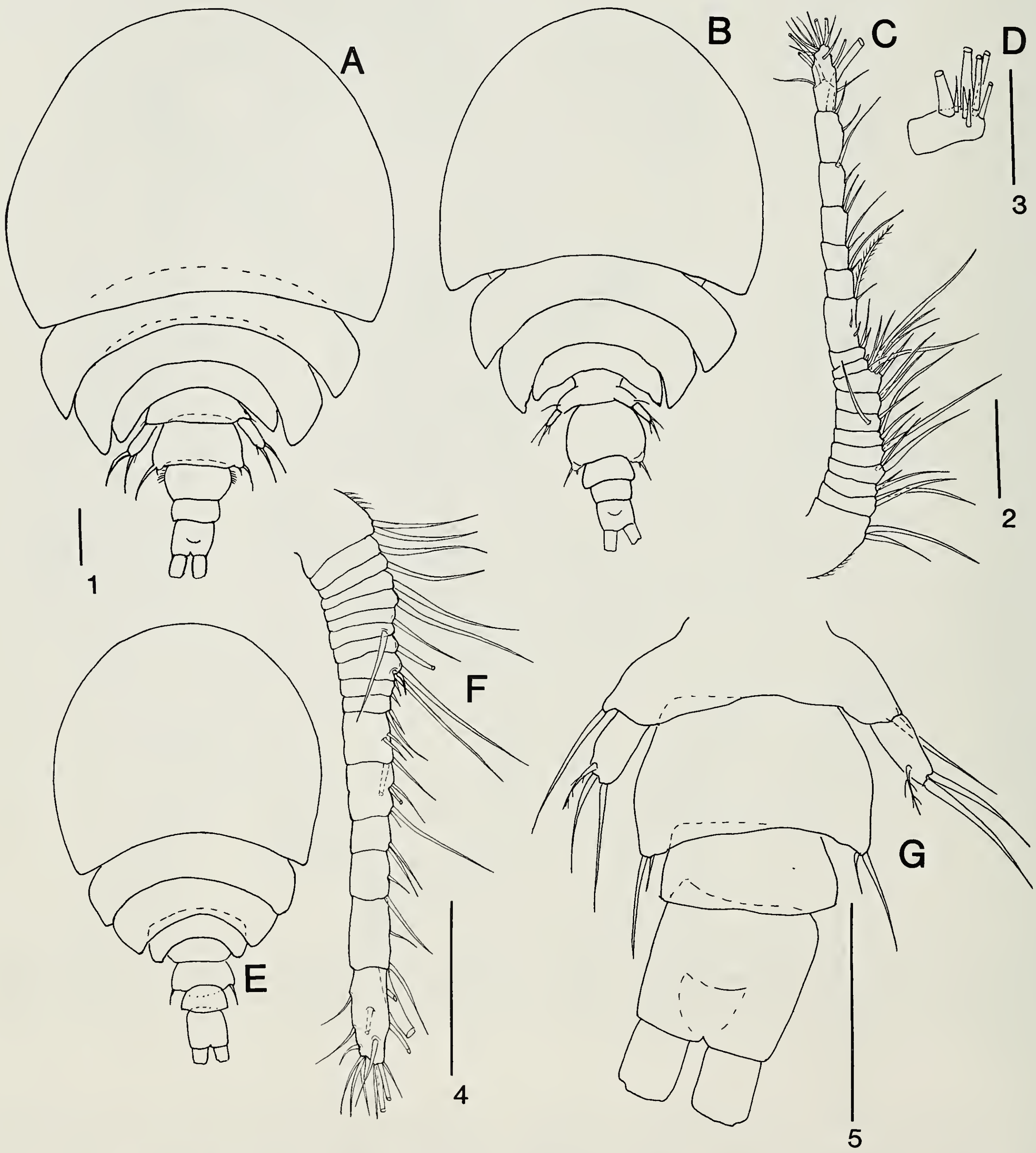

Fig. 13. *Asterocheres lilljeborgi* Boeck, 1859, CV Female: A, habitus, dorsal. *Asterocheres lilljeborgi* CV Male: B, male, habitus, dorsal; C, antennule; D, antennule, segment 9. *Asterocheres lilljeborgi,* CIV: E, habitus, dorsal; F, antennule; G, urosome, ventral. Scale line 1 is 0.1 mm for A, B, E; line 2 is 0.1 mm for C; line 3 is 0.1 mm for D; line 4 is 0.1 mm for F; line 5 is 0.1 mm for G.

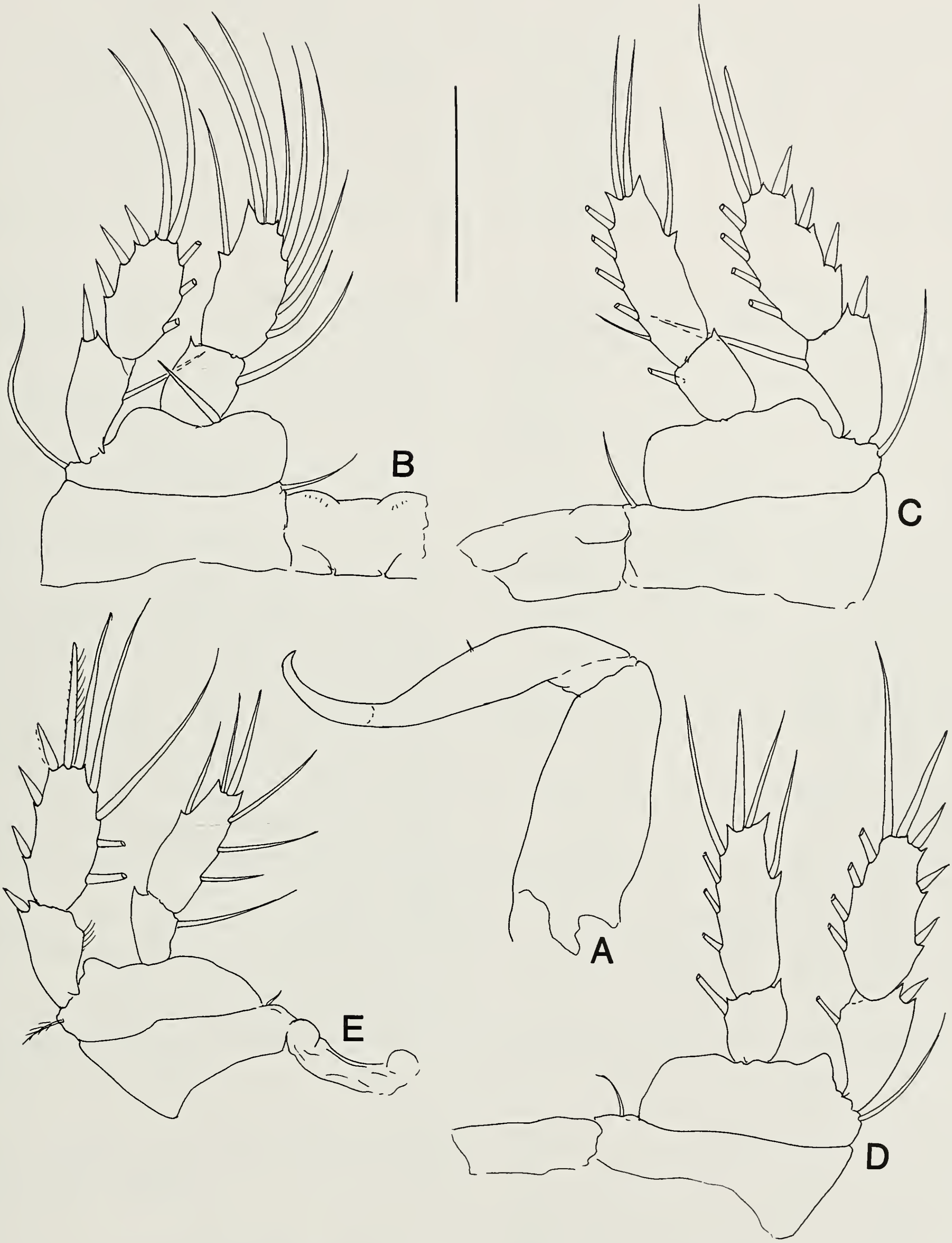

Fig. 14. *Asterocheres lilljeborgi* Boeck, 1859, CIV: A, maxilla; B, swimming leg 1; C, swimming leg 2; D, swimming leg 3; E, swimming leg 4. Scale line is 0.1 mm.

Maxillule (Fig. 15F): Outer lobe with 3 setae.

Maxilliped (Fig. 16A): Proximal section of endopod 3-segmented each with 1 distally polarized seta; distal segment with 2 terminal setae.

Swimming legs 1–4 (Fig. 16B–E): Biramal; swimming legs 1–3 with 2-segmented

Table 7.—Spines and setae on swimming legs 1–4 of *Asterocheres lilljeborgi* CIV female.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; *; III, 1, 4	0–1; *; 1, 2, 5
Leg 2	0–1	1–0	I-1; *; III, 1, 5	0–1; *; 1, 2, 5
Leg 3	0–1	1–0	I-1; *; III, I, 5	0–1; *; 1, 1+I, 4
Leg 4	0–1	1–0	I-0; *; III, I, 5	0–1; *; 1, 1+I, 3

rami, swimming leg 4 with 1-segmented rami. Formula for spines and setae (Table 8).

Leg 5 (Fig. 15B): Unilobe bud with 1 distal spine and 1 distal seta.

CII.—Differs from CIII as follows based on 5 specimens: length range 0.41–0.44 mm; average maximum width 0.2–0.22 mm; greatest dorsoventral thickness 0.13–0.14 mm; length of prosome 0.26–0.29 mm, urosome 0.14–0.15 mm; ratio of length to width 2.02:1; ratio of length of prosome to that of urosome 1.95:1.

Prosome (Fig. 17A): 3 articulating sections; 1st a complex of 5 cephalic somites plus Th1, 2; Th3, 4 articulating; Th4 narrow.

Urosome (Fig. 17A): Th5, Th6, Abd1 articulating.

Antennule (Fig. 17C): 9 articulating segments with 2, 1, 2, 1, 1, 1, 1, 1+1, 14.

Antenna (Fig. 17D), mandible (Fig. 17E) and maxilla (Fig. 17F): As illustrated.

Maxillule (Fig. 17H): Inner lobe with 3 setae.

Maxilliped (Fig. 17G): Syncoxa without seta, basis without seta. Endopod 3-segmented; proximal and middle segment each with 1 seta, distal segment with 2 terminal setae.

Swimming legs 1–3 (Fig. 17I–M): Swimming legs 1–2 with 2-segmented rami, swimming leg 3 with 1-segmented rami. Formula for spines and setae (Table 9).

Swimming leg 4 (Fig. 17B): A bilobed bud; dorsal lobe with 1 distal spine and 1 distal setae; ventral lobe unarmed.

CI.—Differs from CII as follows: Body length range 0.38 mm (based on 1 specimen); length of prosome 0.26 mm; maximum width of prosome 0.16 mm; length of urosome 0.12 mm; ratio of length to width of prosome 1.6; ratio of length of prosome to length of urosome 2.2.

Prosome (Fig. 18A): 2 articulating sections; 1st complex of 5 cephalic somites plus Th1, 2; Th3 articulating.

Urosome (Fig. 18B): Th4, 5, Abd1 articulating.

Antennule (Fig. 18C): 4 articulating segments with 2, 2, 1, 14+1.

Antenna (Fig. 18D), mandible (Fig. 18E), maxillule (Fig. 18F) and maxilla (Fig. 18G): As illustrated.

Maxilliped (Fig. 18H): Syncoxa and basis unarmed; endopod 2-segmented; proximal segment with 1 medial seta and distal segment with 1 thick and 1 thin seta.

Swimming legs 1–2 (Fig. 18I, J): 1-segmented rami. Formula for spines and setae (Table 10).

Swimming leg 3 (Fig. 18B): Bilobed bud; dorsal lobe with 1 distal spine and 1 distal seta; ventral lobe unarmed.

CR (Fig. 18B): As illustrated.

Remarks.—*Asterocheres lilljeborgi,* the type species of the family, can be distinguished from its congeners by exceptionally wide tergites of the dorsoventrally flattened prosome. It has been collected in the Davis Strait, off coasts of the British Isles, Sweden, Norway and France, associated with the starfish *Henricia sanguinolenta* (O. F. Müller, 1776) and other echinoderms (Humes 1986, Gotto 1993). Wilson (1944) found *A. lilljeborgi* associated with *Henricia leviuscula* (Stimpson, 1857) in the Aleutian Islands near Alaska. Marchenkov (1997) reported that *A. lilljeborgi* at the White Sea is associated with *H. sanguinolenta.* Roettger et al. (1972) studied ecology

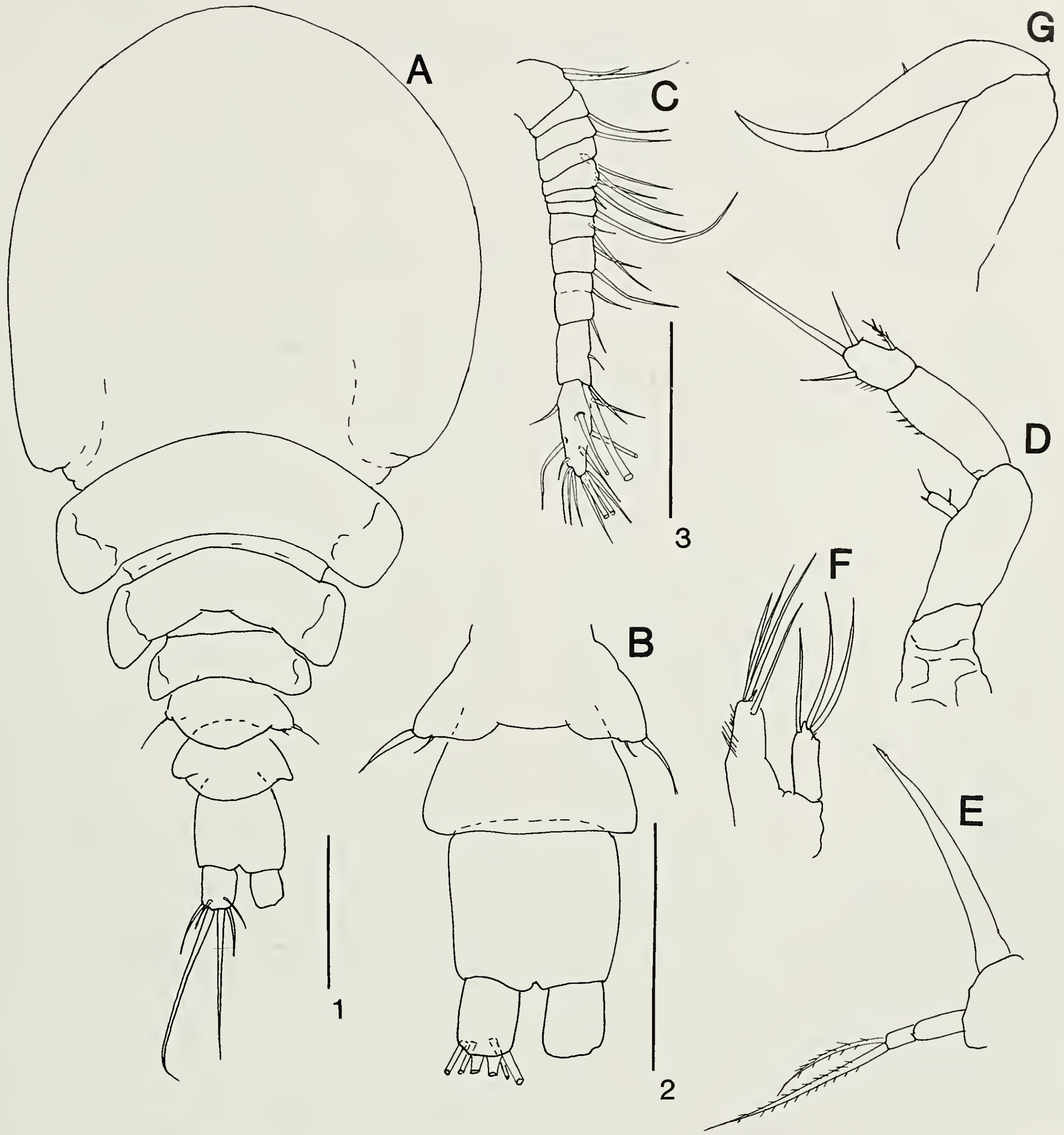

Fig. 15. *Asterocheres lilljeborgi* Boeck, 1859, CIII: A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla. Scale line 1 is 0.1 mm for A; line 2 is 0.1 mm for B, D–F; line 3 is 0.1 mm for C.

of *A. lilljeborgi* from *H. sanguinolenta* collected near Sweden.

Discussion

One somite is added to the body of both genders of *Dermatomyzon nigripes* and *Asterocheres lilljeborgi* during the molts to copepodids II–IV, a pattern similar to the related siphonostomatoid *Scottomyzon gibberum* (see Ivanenko et al. 2001). During the molt to copepodid V, both genders of *D. nigripes* add a fourth abdominal somite, but females and males of *A. lilljeborgi* appear to suppress the formation of the fourth somite as do both genders of *S. gibberum*. During the terminal adult molt to CVI, females of *A. lilljeborgi* and *D. nigripes* develop a simple genital complex when an arthrodial membrane separating the genital somite from the second abdominal somite fails to form. This arthrodial membrane does form in females of *S. gibberum* and in males of all three species. The body of the ancestral copepod is assumed to have added

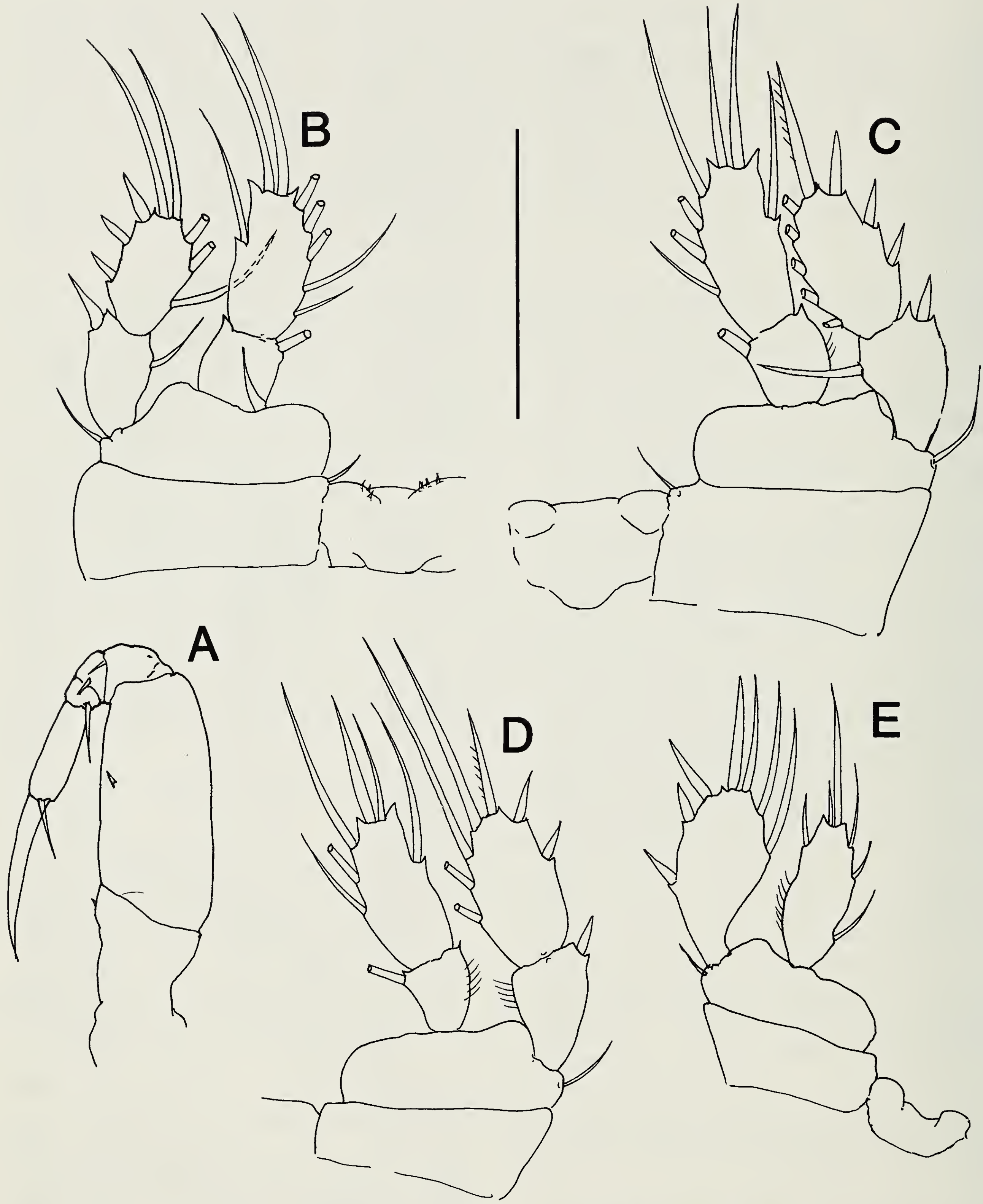

Fig. 16. *Asterocheres lilljeborgi* Boeck, 1859, CIII: A, maxilliped; B, swimming leg 1; C, swimming leg 2; D, swimming leg 3; E, swimming leg 4. Scale line 1 is 0.1 mm.

a somite during the molt of each copepodid stage (Hulsemann 1991), and the arthrodial membrane separating the genital somite from the second abdominal somite remained during the molt to copepodid VI of females, as it does for a few podoplean neocopepods (Martinez Arbizu 2003). The body of the ancestral siphonostomatoid is assumed to have added a somite during the molt of each copepodid stage but the arthrodial membrane separating the female genital somite from the second abdominal

Table 8.—Spines and setae on swimming legs 1–4 of *Asterocheres lilljeborgi* CIII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-1; *; III, 1, 4	0–1; *; 1, 2, 5
Leg 2	0–1	1–0	I-1; *; III, I, 5	0–1; *; 1, 2, 4
Leg 3	0–1	1–0	I-0; *; II, I, 4	0–1; *; 1, 1+I, 3
Leg 4	0–0	1–0	*; *; III, I, 3	*; *; 1, 1+I, 3

somite failed to form during the molt to copepodid VI. The body of *D. nigripes* appears to be identical to the ancestral siphonostomatoid. The body of *A. lilljeborgi* is derived because the fourth abdominal somite fails to form during the molt to copepodid V of both genders. The body of *S. gibberum* also is derived because a fourth abdominal somite fails to form and because an arthrodial membrane separates the genital somite from the second abdominal somite of females, a character state reversal.

The maxilliped of *D. nigripes* and *A. lilljeborgi,* like *S. gibberum,* begins development at copepodid I with an unarmed syncoxa, an unarmed basis, and a 2-segmented endopod with one seta on the proximal segment and two setae on the distal segment. Both *D. nigripes* and *A. lilljeborgi* add one seta each to the syncoxa and basis at copepodid III. One seta also is added to a distinctly segmented endopod at copepodid II and at copepodid III; a third seta juxtaposed to the proximal seta of the endopod is added at copepodid IV. Patterning of the endopod of the maxilliped of *D. nigripes* and *A. lilljeborgi* during development is assumed to follow the general model for copepods (Ferrari 1995, Ferrari & Dahms 1998, Ferrari & Ivanenko 2001), as it is applicable to siphonostomatoids (Ivanenko et al. 2001). Based on the stage at which each seta is added and its location, the endopod of adult *D. nigripes* and *A. lilljeborgi* is interpreted as 4-segmented. The maxilliped of *S. gibberum* fails to add a seta to its syncoxa during development and the seta on the second, or penultimate, endopodal segment is lost at CIV; both of these states are interpreted as derived.

Swimming leg 1 of copepodid I of *D. nigripes* and *A. lilljeborgi* bears eight exopodal setae and seven endopodal setae, the most common number of elements for these rami at this stage of copepod development (Ferrari 2000). Development from copepodid I is similar for both species with one exception. The proximal medial seta on the third exopodal segment (or the ventral seta on the presumptive fourth segment) of *D. nigripes* fails to form on *A. lilljeborgi* during the molt to CV so that there are three inner setae, not four, on the adult of *A. lilljeborgi.*

Swimming leg 2 of copepodid I of *D. nigripes* and *A. lilljeborgi* bears seven exopodal setae and six endopodal setae, the most common number of elements for these rami at this stage of copepod development (Ferrari 2000). Development from copepodid I is similar for both species with one exception. The proximal medial seta on the third exopodal segment, or ventral seta on the presumptive fourth segment, of *D. nigripes* fails to form on *A. lilljeborgi* during the molt to CV so that there are four medial setae, not five, on the adult of *A. lilljeborgi.*

Swimming leg 3 of copepodid I of both species is a bud with two setal elements on the dorsal lobe, the presumptive exopod, and none on the ventral lobe, the presumptive endopod. The common situation for copepods is three setae on the presumptive exopod and two setae the presumptive endopod (Ferrari 2000). At copepodid II, the transformed limb of *D. nigripes* and *A. lilljeborgi* bears seven exopodal setae and six endopodal setae, the most common number of elements for these rami at this stage of copepod development (Ferrari 2000). De-

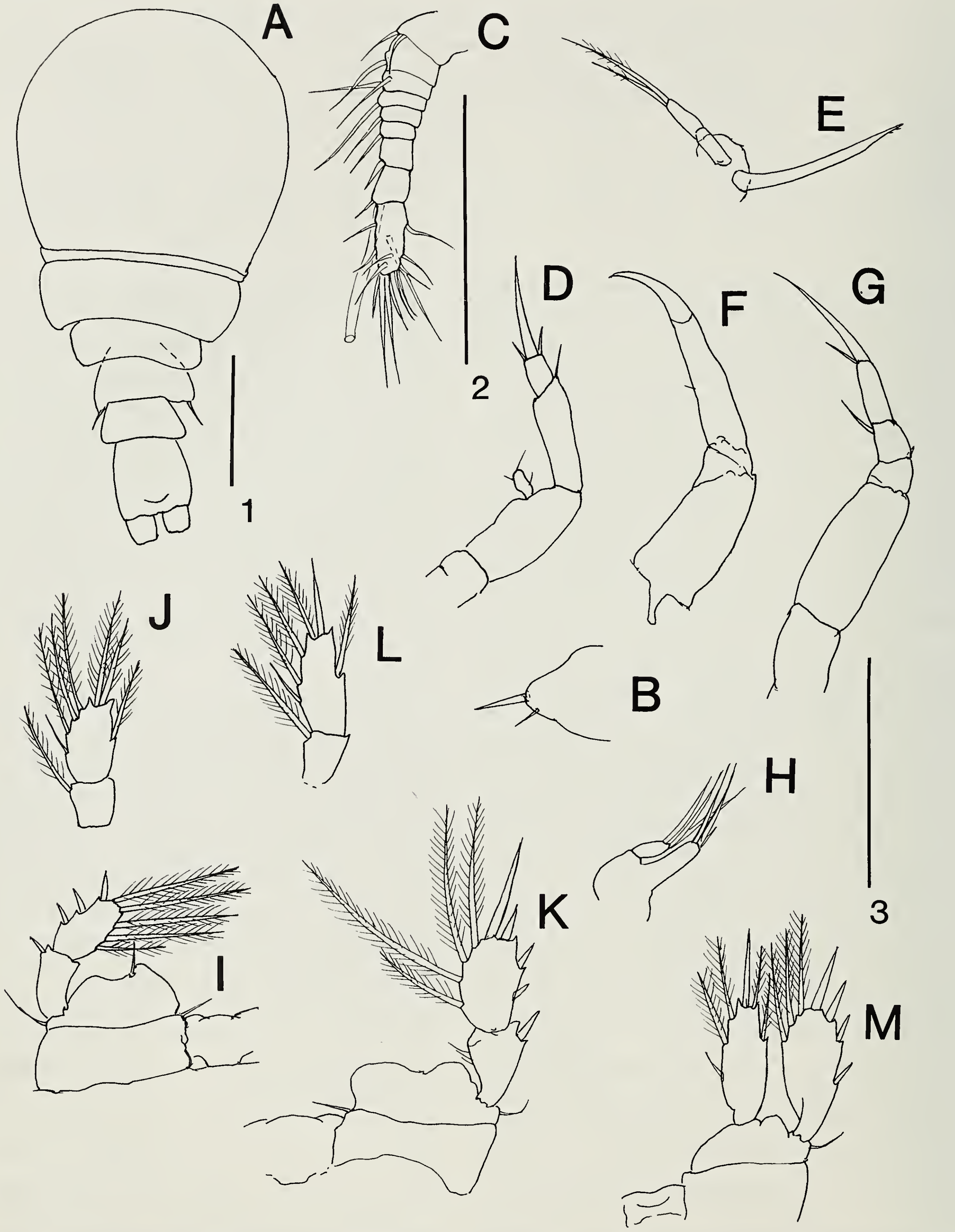

Fig. 17. *Asterocheres lilljeborgi* Boeck, 1859, CII: A, habitus, dorsal; B, swimming leg 4; C, antennule; D, antenna; E, mandible; F, maxilla; G, maxilliped; H, maxillule; I, swimming leg 1, protopod, exopod and intercoxal sclerite; J, endopod of swimming leg 1; K, swimming leg 2, protopod, exopod and intercoxal sclerite; L, endopod of swimming leg 2; M, swimming leg 3. Scale line 1 is 0.1 mm for A; line 2 is 0.1 mm for C; line 3 is 0.1 mm for B, D–M.

Table 9.—Spines and setae on swimming legs 1–3 of *Asterocheres lilljeborgi* CII.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–1	1–1	I-0; *; III, 1, 4	0–1; *; 1, 2, 4
Leg 2	0–1	1–0	I-0; *; III, I, 4	0–1; *; 1, 1+I, 3
Leg 3	0–0	1–0	*; *; III, I, 3	*; *; 1, 1+I, 3

velopment from copepodid II is similar for both species with two exceptions. *D. nigripes* fails to add a second terminal element to the endopod during the molt to copepodid III, while *A. lilljeborgi* adds this second terminal element. The proximal medial seta on the third exopodal segment, or ventral seta on the presumptive fourth segment, of *D. nigripes* fails to form on *A. lilljeborgi* during the molt to CV so that there are four medial setae, not five, on the adult of *A. lilljeborgi.*

Swimming leg 4 of copepodid II of both species is a bud with two setal elements on the dorsal lobe, the presumptive exopod, and none on the ventral lobe, the presumptive endopod. The common situation for copepods is three setae on the presumptive exopod and two setae the presumptive endopod (Ferrari 2000). At copepodid III, the transformed limb of *D. nigripes* and *A. lilljeborgi* bears seven exopodal setae and six endopodal setae, the most common number of elements for these rami at this stage of copepod development (Ferrari 2000). Development from copepodid III is similar for both species with two exceptions. *D. nigripes* fails to add a second terminal element on the endopod during the molt to copepodid III, while *A. lilljeborgi* adds this second terminal element. The proximal medial seta on the third exopodal segment, or ventral seta on the presumptive fourth segment, of *D. nigripes* fails to form on *A. lilljeborgi* during the molt to CV so that there are four medial setae, not five, on the adult of *A. lilljeborgi.*

Leg 5 of copepodid III of both species is a bud with two setal elements on the dorsal lobe, the presumptive exopod; there is no ventral lobe. At copepodid IV, the transformed limb of both species bears three exopodal setae. At copepodid V of *D. nigripes* a medial and lateral seta are added to the exopod; no setae are added to *A. lilljeborgi.* Leg 6 of copepodid IV of *D. nigripes* is a bud with two setae on the dorsal lobe which is assumed to be the presumptive exopod; a third seta is added during the molt to copepodid V. Leg 6 of copepodid IV of *A. lilljeborgi* is a bud with one seta on the dorsal lobe; a second seta is added to the male during the molt to copepodid V, and to the female during the molt to copepodid VI.

Following the simplifying assumption of oligomerization (Dogiel 1954, Monchenko & Von Vaupel Klein 1999) to infer derived states of swimming legs which develop from serially repeated elements, adults of *S. gibberum* share with those of *D. nigripes* absence of a second terminal element on the third endopodal segment of swimming legs 3–4. Adults of *S. gibberum* share with those of *A. lilljeborgi* absence of the proximal medial seta on the third exopodal segment of swimming legs 1–4, three setae on the exopod of leg 5 and two setae the presumptive exopod of leg 6. Derived states of adult *S. gibberum* include absence of the medial basal seta on leg 1, absence of the medial coxal seta of leg 4, and absence of the proximal lateral seta on the third exopodal segment, or dorsal seta of the presumptive fourth segment, of swimming legs 1–4.

The proximal segment of the antennule of the adult female and male of *A. lilljeborgi* bears two setae. The proximal segment of the antennule of the adult female of *D. nigripes* and *S. gibberum* bears only one seta. One of two setae present on the proximal segment of *D. nigripes* early in

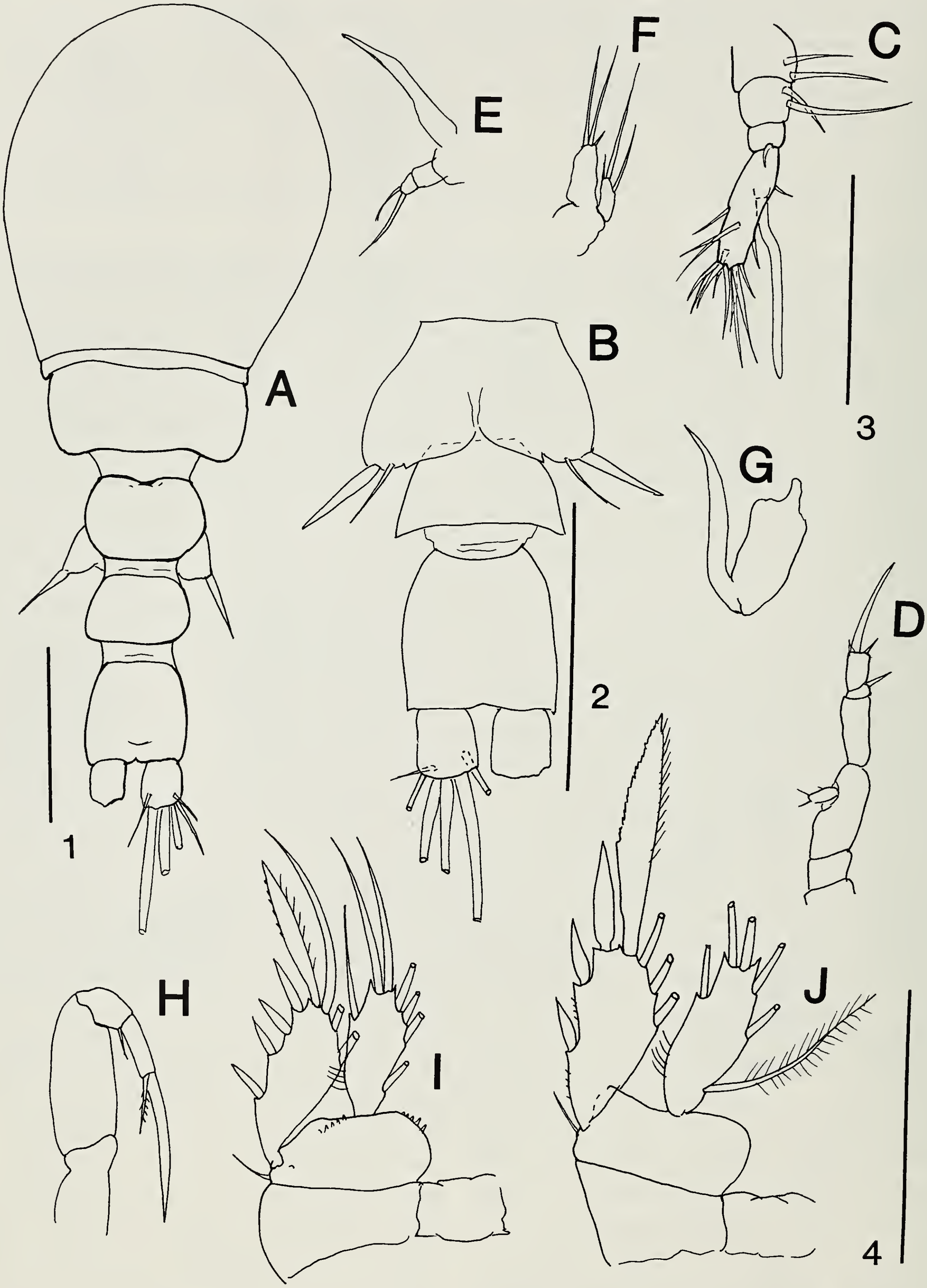

Fig. 18. *Asterocheres lilljeborgi* Boeck, 1859, CI: A, habitus, dorsal; B, urosome, ventral; C, antennule; D, antenna; E, mandible; F, maxillule; G, maxilla; H, maxilliped; J, swimming leg 1; I, swimming leg 2. Scale line 1 is 0.1 mm for A; line 2 is 0.1 mm for B; line 3 is 0.1 mm for C; line 4 is 0.1 mm for D–I.

Table 10.—Spines and setae on swimming legs 1–2 of *Asterocheres lilljeborgi* CI.

	Coxa	Basis	Exopod 2nd; 3rd; 1st	Endopod 2nd; 3rd; 1st
Leg 1	0–0	1–0	*; *; IV, I, 3	*; *; 1, 2, 4
Leg 2	0–0	1–0	*; *; III, I, 3	*; *; 1, 2, 3

development fails to form during the molt to copepodid IV; in contrast the proximal segment of *S. gibberum* bears only one seta throughout the copepodid phase of development.

The ninth articulating segment of the adult female of *D. nigripes* bears only one seta as does the sixth articulating segment of the adult female of *S. gibberum*; these segments are not homologous. The ninth articulating segment of the antennule of the adult female of *A. lilljeborgi* is considered a complex of three segments with six setae, two from each segment. The third articulating segment of the antennule of the adult female of *D. nigripes* is considered a complex of two segments with four setae, two from each segment. The eighth articulating segment of *D. nigripes* is considered a complex of three segments also with six setae, and which corresponds to the complex of *A. lilljeborgi.* The antennule of the adult female of *S. gibberum* also has two complexes, a proximal complex of three segments of six setae and a distal complex of four segments with eight setae. These two complexes correspond to the two of *D. nigripes* but with the following articulating segment of *D. nigripes* fused to the corresponding complex of *S. gibberum.*

The antennule of *A. lilljeborgi* appears to have the fewest derived states: only one segmental complex composed of three proximal segments. The antennule of *D. nigripes* has the following derived states: one seta on the proximal segment; a proximal segmental complex of two segments; and a distal complex of three segments. The antennule of *S. gibberum* has the following derived states: one seta on the proximal segment; a proximal complex of three segments; and a distal complex of four segments.

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Literature Cited

Boeck, A. 1859. Tvende nye parasitiske Krebsdyr, *Artotrogus orbicularis* og *Asterocheres Liljeborgii.*—Forhandlinger i Videnskabers Selskabet i Kristiania 1859:171–182.

Boxshall, G. A. 1990. Siphonostome copepods associated with sponges from Hong Kong.—Pp. 523–547 *in* B. Morton, ed., The marine flora and fauna of Hong Kong and Southern China, vol. 2. Taxonomy and ecology. Hong Kong University Press, Hong Kong, 449–942.

Brady, G. S. 1880. A monograph of the free and semi-parasitic Copepoda of the British Islands. The Ray Society, London, 3:1–83.

———. 1910. Die marinen Copepoden der deutschen Sudpolar-Expedition 1901–1903. 1. Uber die Copepoden der Stamme Harpacticoida, Cyclopoida, Notodelphyoida und Caligoida.—Deutsche Sudpolar Expedition 1901–1903, 11 (Zoology 3) (5):499–593.

Brady, G. S., & D. Robertson. 1876. Report on dredgings off the coast of Durham and North-Yorkshire in 1874.—Report to the British Association for the Advancement of Science 45:185–199.

Canu, E. 1892. Les Copepodes du Boulonnais. Morphologie, embryologie, taxonomie.—Travaux de l'Institut Zoologique de Lille, Travaux de la Station de Zoologie Maritime de Wimereux 6: 1–292, pls. 1–30.

———. 1893. Un Copepode ascomyzontide sur une algue pelagique.—Notes de biologie marine, fauniques ou ethologiques. I. Annales de la Station Aquicole de Boulogne-sur-Mer 1:100–107, pls. 6–7.

Claus, C. 1889. Ueber neue oder wenig bekannte halbparasitische Copepoden insbesondere der Lichomolgiden- und Ascomyzontiden-Gruppe.—Arbeiten des Zoologischen Institut der Universitat Wien 8:327–370.

Dogiel, V. A. 1954. Oligomerization of the homologous organs as one of the main paths in an animal evolution.—Leningrad University Press, Leningrad [now St. Petersburg], 368 pp.

Eiselt, J. 1965. Revision und Neubeschreibung weiterer siphonostomer Cyclopoiden (Copepoda, Crust.) aus der Antarktis.—Sitzungsberichten der Osterreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, Abteilung I. 174:51–169.

Ferrari, F. D. 1995. Six copepodid stages of *Ridgewayia klausruetzleri,* a new species of calanoid copepod (Ridgewayiidae) from the barrier reef in Belize, with comments on appendage development.—Proceedings of the Biological Society of Washington 108:180–200.

———. 2000. Patterns of setal numbers conserved during early development of swimming legs of copepods (Crustacea).—Hydrobiologia 417:81–90.

———, & A. Benforado. 1998. Relationships between arthrodial membrane formation and addition of setae to swimming legs 1–4 of *Dioithona oculata, Ridgewayia klausruetzleri, Pleuromamma xiphias,* and *Temora longicornis* (Crustacea: Copepoda).—Crustaceana 71:545–564.

———, & H.-E. Dahms. 1998. Segmental homologies of the maxilliped of some copepods as inferred by comparing setal numbers during copepodid development.—Journal of Crustacean Biology 18:298–307.

———, & V. N. Ivanenko. 2001. Interpreting segment homologies of the maxilliped of cyclopoid copepods by comparing stage-specific changes during development.—Organisms, Diversity and Evolution 1:113–131.

Giesbrecht, W. 1895. The subfamilies, genera, and species of the copepod family Ascomyzontidae, Thorell: diagnosis, synonymy and distribution.—Annals and Magazine of Natural History (6)16:173–186.

———. 1899. Die Asterocheriden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte.—Fauna und Flora des Golfes von Neapel und der Angrenzenden Meeres-Abschnitte, Herausgegeben von der Zoologischen Station zu Neapel 25, 217 pp., pls. 1–11.

Gotto, R. V. 1993. Commensal and parasitic copepods associated with marine invertebrates (and whales): keys and notes for identification of the species.—Synopses of the British Fauna, New Series 46:1–264.

Hansen, H. J. 1923. Crustacea Copepoda. II. Copepoda Parasita and Hemiparasita.—Danish Ingolf-Expedition 3, 92 pp.

Ho, J-s. 1990. A phylogenetic analysis of copepod orders.—Journal of Crustacean Biology 10:528–536. Hulsemann, K. 1991. Tracing homologies in appendages during ontogenetic development of calanoid copepods.—Bulletin of the Plankton Society of Japan, Special Volume, 105–114.

Hulsemann, K. 1991. Tracing homologies in appendages during ontogenetic development of calanoid copepods.—Bulletin of the Plankton Society of Japan, Special Volume, 105–114.

Humes, A. G. 1986. Synopsis of copepods associated with asteroid echinoderms, including new species from the Moluccas.—Journal of Natural History 20:981–1020.

———. 1989. Copepoda from deep-sea hydrothermal vents at the East Pacific Rise.—Bulletin Muséum national d'Histoire naturelle, Paris, 4e série 11, section A. no. 4:829–849.

———. 1999. *Collocherides brychius,* a new species (Copepoda: Siphonostomatoida) from a deep-water hydrothermal site in the northeastern Pacific.—Proceedings of the Biological Society of Washington 112:181–188.

———, & R. U. Gooding. 1964. A method for studying the external anatomy of copepods.—Crustaceana 6:238–240.

Huys, R., & G. A. Boxshall. 1991. Copepod Evolution.—The Ray Society vol. 159, 468 pp.

Ivanenko, V. N., F. D. Ferrari, & A. V. Smurov. 2001. Nauplii and copepodids of *Scottomyzon gibberum* (Copepoda: Siphonostomatoida: Scottomyzontidae, new family), a symbiont of *Asterias rubens* (Asteroidea).—Proceedings of the Biological Society of Washington 114:237–261.

———, & A. V. Smurov. 1997. *Asterocheres flustrae* n. sp. (Copepoda; Siphonostomatoida; Asterocheridae), associated with *Flustra foliacea* L. (Bryozoa) from the White Sea.—Systematic Parasitology 38:111–130.

Jespersen, P. 1940. Non-parasitic Copepoda.—The Zoology of Iceland 3 (33), 116 pp.

Lang, K. 1934. Marine Harpacticiden von der Campbell-Insel und einigen anderen Suedlichen Inseln.—Kunglia Fysiografiska Saellskapets I Lund Handlingar n.f. 45:1–56.

———. 1949. On some Swedish marine semi-parasitic and parasitic copepods.—Arkiv for Zoologi (A) 42(22):1–10.

Linnaeus, C. 1758. Systema Naturae, per regna tria naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Ed. decima, reformata. I, Regnum animale: 1–823. Laurentius Salvius, Holmiae.

———. 1767. Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species cum characteribus, differentiis, synonymis, locis. Ed. duodecima, reformata, 1(2):533–1327. Laurentius Salvius, Holmiae.

Marchenkov, A. V. 1997. Fauna of symbiotic and parasitic crustaceans (Copepoda, Isopoda, Cirripedia, Amphipoda) from the benthic invertebrates of the White Sea and Arctic seas.—Parasitologiya 31:24–44.

Martínez Arbizu, P. 2003. The paraphyly of Cyclopinidae Sars, 1913, and the phylogenetic position of poecilostome families within Cyclopoida Sars, 1913 (Copepoda: Crustacea) development.—Organisms, Diversity and Evolution 3 (in press).

Monchenko, V. I., & J. C. von Vaupel Klein. 1999. Oligomerization in Copepoda Cyclopoida as a kind of orthogenetic evolution in the animal kingdom.—Crustaceana 72:241–264.

Mueller, O. F. 1776. Zoologiae Danicae Prodromus, seu Animalium Daniae et Norvegiae indigenarum characteres, nomina et synonyma imprimis popularium. M. Hallager, Havniae, 274 pp.

Nicholls, A. G. 1944. Littoral Copepoda from South Australia. II. Calanoida, Cyclopoida, Notodelphyoida, Monstrilloida and Caligoida.—Records of the Australian Museum 8:1–62.

Pallas, P. S. 1766. Elenchus Zoophytorum, Sistens Generum Adumbrationes Generaliores et Specierum Cognitarum Succinctas Descriptiones, cum Selectis Auctorum Synonymis. Hagae-Comitum, 451 pp.

Roettger, R., H. Astheimer, M. Spindler, & J. Steinborn. 1972. Okologie von *Asterocheres lilljeborgi,* eines auf *Henricia sanguinolenta* parasitisch lebenden Copepoden.—Marine Biology (Berlin) 13:259–266.

Sars, G. O. 1880. Crustacea et Pycnogonida nova in itinere 2do et 3tio expeditionis norvegicae anno 1877 & 78 collecta.—Archiv for Matematik og Naturvidenskab, Christiana 4:427–476 + 60 pls.

———. 1914. Copepoda Cyclopoida. Parts VII & VIII. Cyclopidae (concluded), Ascomyzontidae.—An Account of the Crustacea of Norway, with short descriptions and figures of all the species. Bergen Museum, Bergen 6:81–104, pls. 49–64.

Scott, T. & A. Scott. 1894. On some new and rare Crustacea from Scotland.—Annals and Magazine of Natural History (series 6) 13:137–149.

Sewell, R. B. S. 1949. The littoral and semi-parasitic Cyclopoida, the Monstrilloida and Notodelphyoida.—Scientific Reports of the John Murray Expedition 9:17–199.

Shih, C. T., J. G. Figueira, & E. H. Grainger. 1971. A synopsis of Canadian marine zooplankton.—Bulletin of the Fisheries Research Board of Canada 176:1–264.

Stephensen, K. 1929. Marine parasitic, semiparasitic and non-pelagic Crustacea Copepoda.—The Zoology of the Faroes 2, part 1, section 30:1–18.

Stimpson, W. M. 1857. On the Crustacea and Echinodermata of the Pacific Shores of North America, and is pp. 444–532.—Boston Journal of Natural History 6:444–532.

Stock, J. 1981. Associations of *Hydrocorallia stylasterina* with gall-inhabiting Copepoda Siphonostomatoidea from the south-west Pacific. Part II. On six species belonging to four new genera of the copepod family Asterocheridae.—Bijdragen Tot De Dierkunde 51:287–312.

———. 1984. On the presence of gall-inducing Copepoda on stylasterine corals. Studies on Copepoda II.—Crustaceana supplement 7:377–380.

Thompson, I. C. 1893. Revised report on the Copepoda of Liverpool Bay.—Transactions of the Liverpool Biological Society 7:175–230.

Ummerkutty, A. N. P. 1966. Studies on Indian copepods. 13. Brief notes on the asterocherid copepods obtained from the south east coast of India with description of *Indomyzon qasimi* n. gen., n. sp. and a discussion of the family Asterocheridae.—Crustaceana 11:17–32.

Wilson, C. B. 1944. Parasitic copepods in the United States National Museum.—Proceedings of the United States National Museum 94:529–582.

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A new *Pseudocetopsis* species (Siluriformes: Cetopsidae) from Suriname and French Guiana

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Abstract.—Pseudocetopsis orientale, a new catfish species of small body size of the cetopsid subfamily Cetopsinae is described from several Atlantic-slope rivers of Suriname and French Guiana. The combination of the presence of a dorsal fin with an ossified spinelet, the possession of pectoral- and dorsal-fin spines, the length of the pelvic and pectoral fins, the relative depth of the body, and the alignment of the dorsal and ventral profiles of the portion of the body posterior of the dorsal-fin base serve to distinguish the new species from all other cetopsines.

Résumé.—Pseudocetopsis orientale, une nouvelle espèce de poisson chat Cetopsinae de la famille des Cetopsidae, est décrit de plusieurs rivières du Suriname et de Guyane française. La combinaison de plusieurs caractères incluant la présence d'une nageoire dorsale avec un crochet ossifié, la présence d'épines dorsales et pectorales, la longueur des nageoires pelviennes et pectorales, la hauteur relative du corps et l'alignement des profils dorsaux et ventraux à l'arrière de la nageoire dorsale permet de distinguer cette espèce de toutes les autres Cetopsinae.

Recent studies have demonstrated that the species-level diversity among catfishes of the South American subfamily Cetopsinae as defined by de Pinna & Vari (1995) is significantly higher than the 12 species recognized by Burgess (1989), with five additional species described by Ferraris & Brown (1991), Lundberg & Rapp Py-Daniel (1994), Ferraris (1996), and Oliveira et al. (2001). Ongoing studies indicate that these 17 species, nonetheless, represent a significant underestimate of the actual species-level diversity within the subfamily, and we herein describe a new species from Suriname and French Guiana discovered independently during a revisionary study of the subfamily (RPV, CJF) and faunal studies of the ichthyofauna of French Guiana (PK).

Materials and Methods

All measurements were taken as straight line distances between points with head length (HL) measured from the tip of the snout to the end of the fleshy gill cover. Interorbital width was taken as the shortest distance between the orbits, but is, however, difficult to measure unambiguously because of the fleshy tissues around the orbits. The soft bodies of most cetopsins make it difficult to accurately measure most standard morphometric features. As a consequence we do not provide these values for the species. Size of examined specimens is reported as standard length (SL) rounded to the nearest whole millimeter. Median fin ray counts include all elements apparent in radiographs. The number of vertebrae was

Fig. 1. *Pseudocetopsis orientale,* holotype, MHNG 2621.040, 27 mm SL, Suriname, Brokopondo District, Mindrineti Kreek, close to mouth of Maykaboeka Kreek, on the Gros Rosevel Mining concession (5°07′08.8″N, 55°16′59.4″W).

taken from radiographs and includes the four elements of the Weberian apparatus and one element for the ural complex. Vertebrae were separated into preanal, precaudal, and caudal elements with total vertebrae the sum of precaudal and caudal vertebrae. The presence of the sexually dimorphic features present in males of other cetopsin species was considered indicative of the sex for those specimens that could not be dissected but with these attributes.

The range of values for meristic and morphometric features in the species is presented first, followed by the values for the holotype in square brackets. Numbers of specimens is indicated by "ex." Institutional abbreviations are: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences, Philadelphia; FMNH, Field Museum of Natural History, Chicago; MNHG, Muséum d'Histoire Naturelle, Geneva; MNHN, Muséum National d'Histoire Naturelle, Paris; MZUSP, Museu de Zoologia da Universidade de São Paulo; NZCS, National Zoological Collection of Suriname, Paramaribo; and USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Pseudocetopsis orientale, new species
Fig. 1

Hemicetopsis sp., Boujard et al., 1990:347 [French Guiana, Fleuve Arataye]. Ponton & Copp, 1997:241 [French Guiana, Fleuve Sinnamary].

Pseudocetopsis cf. *minutus* Le Bail et al., 2000:146, unnumbered figure [French Guiana, Fleuve Maroni, Fleuve Iracoubo, Fleuve Comté, Fleuve Oyapock].

Holotype.—MHNG 2621-040, 27 mm SL, Suriname, Brokopondo District, Mindrineti Kreek, close to mouth of Maykaboeka Kreek, Saramacca River basin, on Gros Rosevel Mining concession (5°07′08.8″N, 55°16′59.4″W), R. Commergnat, J. Mol, and C. Weber.

Paratypes.—All Suriname, Brokopondo District, Saramacca River basin: MHNG 2626.013, 9 ex., 18–27 mm SL (collected with holotype); USNM 369732, 2 ex., 21–24 mm SL (collected with holotype); MNHN 2002.1625, 1 ex., 26 mm SL (collected with holotype); NZCS F7048, 1 specimen, 23 mm SL (collected with holotype). MHNG 2621.044, 2 ex., 22–22 mm SL and MHNG 2621.039, 4 ex., 21–26 mm SL, close to mouth of Maykaboeka Kreek, on Gros Rosebel Mining concession (collected close to type locality), R. Commergnat, J. Mol, and C. Weber. MZUSP 65404, 1 ex., 27 mm SL, Maykaboeka Kreek, Gros Rosebel Area, near Golden Star Concession (5°04′45″N, 55°16′09″W), C.A. Figueiredo, F. Breden, and H. Brook, Jan 2000.

Non-type specimens examined.—31 specimens, 18–49 mm SL.

FRENCH GUIANA. MNHN 2002-1103, 3 ex., 38–39 mm SL, no specific locality. MNHN 1994-0092, 1 ex., 30 mm SL, Fleuve Arataye, Saut Parare (4°03′N, 52°42′W). MNHN 2002-1099, 2 ex., 38–39 mm SL; Crique Boulanger of Fleuve Comté (4°36′N, 52°19′W). MNHN 2002-1100, 1 ex., 22 mm SL; MNHN 2002-1098, 2 ex., 43–49 mm SL, Crique Balatée of Fleuve Maroni (5°29′N, 54°03′W). MNHN 2002-1101, 8 ex., 24–44 mm SL, Degrad Florian of Fleuve Iracoubo (5°29′N, 53°33′W). MNHN 2002-1102, 11 ex., 40–49 mm SL, Fleuve Oyapock.

SURINAME. All Nickerie District. FMNH 96268, 1 ex., 25 mm SL, Kaiserberg River (approximately 3°03′N, 56°35′W). AMNH 54828, 1 ex., 22 mm SL, stream near Avanavero, approximately 3 miles (=4.8 km) downstream of DeVis Falls (~4°48′N, 57°26′W). AMNH 55001, 1 ex., 32 mm SL, small stream on road from Lucie River Camp to Paramaribo, 25 km N of Sisa Creek (~3°34′N, 57°37′W). USNM 226146, 2 ex., 22–23 mm SL, woodland stream, 0.5 km from Camp Mataway (4°48′N, 57°43′W). USNM 226147, 7 ex., 18–24 mm SL (2 ex. cleared and stained), stream near Camp Anjoemara (4°50′N, 57°26′W). USNM 226148, 1 ex., 30 mm SL, stream at km 212 of road from Amotopo to Camp Geology, at Machine Park—Camp 212 (3°50′N, 57°34′W).

Diagnosis.—The combination of the presence of a dorsal fin with an ossified spinelet and the presence of pectoral and dorsal spines distinguishes *Pseudocetopsis orientale* from all other members of the Cetopsinae with the exception of *P. minuta* (Eigenmann, 1912) from the Essequibo River basin of Guyana. *Pseudocetopsis orientale* differs from *P. minuta* in the length of the pelvic fin (tip of fin reaches posteriorly to anterior margin of vent versus to anal-fin origin, respectively), in the length of the pectoral fin (tip of fin falls distinctly short of vertical through pelvic-fin insertion versus reaches that line), the relative depth of the body (0.21–0.23 of SL versus 0.17–0.19, respectively), and in the alignment of the dorsal and ventral profiles of the portion of the body posterior of the dorsal fin (converging slightly posteriorly versus parallel, respectively).

Description.—Body moderately robust, somewhat compressed laterally anteriorly and becoming progressively distinctly compressed posteriorly. Body depth at dorsal-fin origin approximately 0.21–0.23 of SL, and approximately equal to distance from anterior of eye to rear of head. Lateral line on body unbranched, midlateral, incomplete, and extending from vertical through pectoral-fin base posteriorly to point within region delimited anteriorly by vertical through middle of anal-fin base and posteriorly by vertical located proximate to anterior terminus of caudal peduncle. Dorsal profile of body nearly straight to slightly convex from nape to dorsal-fin origin and straight from that point to caudal-fin base. Ventral profile of body slightly convex along abdomen, approximately straight along anal-fin base and converging towards dorsal profile of body posteriorly. Caudal-peduncle depth greater than caudal-peduncle length.

Head in profile acutely triangular overall with bluntly pointed snout. Dorsal profile of head slightly convex from tip of snout to vertical through posterior margin of orbit and broadly convex from that point to nape. Ventral profile of head slightly convex. Margin of snout in dorsal view broadly rounded. Postorbital margins of head slightly convex on each side from dorsal view. Enlarged jaw musculature very evident on dorsal and lateral surfaces of postorbital portion of head.

Opercular membrane attached to isthmus only anterior of vertical through pectoral-fin insertion. Opercular opening moderately elongate; opening extending anteroventral of pectoral-fin insertion by distance approximately equal to one-third of head length and extending dorsal of pectoral-fin insertion by distance equal to width of eye.

Eye situated on lateral surface of head; located entirely dorsal to horizontal through pectoral-fin insertion; eye visible in dorsal view, but not in ventral view, of head. Middle of orbit at approximately 0.30 of HL. Eye diameter approximately one-third of snout length. Interorbital width approximately equal to distance from tip of snout to point within region between middle of eye and posterior margin of orbit. Anterior narial opening circular, surrounded by short, anteriorly directed, tubular rim of skin. Opening of anterior nares located slightly dorsal of horizontal that extends through maxillary-barbel origin and at, or slightly ventral of, horizontal through tip of snout. Distance between anterior nares approximately equal to distance from tip of snout to middle of orbit. Posterior narial opening located on dorsal surface of head, situated dorsal to anterior one-third of orbit. Narial opening nearly round and with flap of skin that nearly encircles opening, but with small gap posteriorly; flap highest anterolaterally.

Mouth subterminal, very wide; its width approximately 0.60 of HL. Margin of lower jaw gently rounded, its posterior limit reaching to vertical through middle of orbit. Premaxillary tooth patch in form of gently arched band continuous across midline; anterior margin convex, and posterior margin concave and parallel to anterior margin. Teeth on premaxilla small, conical, sharply pointed, and arranged in three regular rows of uniform-sized teeth across entire premaxilla. Vomerine teeth in single arched row, with distinct gap in series at midline. Vomerine teeth conical, all of approximately uniform size, and with largest teeth in series approximately same size as largest teeth on premaxilla. Dentary teeth comparable in shape to, but slightly larger than, premaxillary teeth. Dentary with three irregular tooth rows medially that taper to one row laterally.

Maxillary barbel slender, its length approximately equal to length of orbit plus postorbital portion of head, and slightly greater than three-quarters of HL; barbel origin located ventral to anterior margin of orbit. Medial mental barbel slightly shorter than lateral mental barbel, with latter shorter than maxillary barbel. Medial mental-barbel origin located along vertical through rictus. Lateral mental-barbel origin situated slightly posterior of vertical through medial mental-barbel origin. Tips of adpressed mental barbels extend to, or barely beyond, opercular margin.

Dorsal-fin rays 6 [6]. Dorsal fin moderate, its base approximately 0.38–0.40 of HL. Longest branched dorsal-fin ray, not including distal filament present in mature males, equal in length to approximately two-thirds of HL. Dorsal-fin spinelet present, first dorsal-fin ray spinous for basal one-half of length and flexible more distally, with distal filament present in mature males. Distal margin of dorsal fin slightly convex, with first branched ray longest. Dorsal-fin origin located at approximately 0.29–0.33 of SL and along vertical that extends through middle of adpressed pectoral fin. Tip of adpressed dorsal fin, not including distal filament present in mature males, reaching to vertical through anterior margin of vent. Last dorsal-fin ray with slight basal posterior membranous attachment to body.

Caudal-fin rays i,7,8,i [i,7,8,i]. Caudal fin deeply forked, lobes symmetrical; tips of lobes rounded. Length of longest caudal-fin ray approximately two times length of middle rays.

Anal-fin rays 23 to 27 [26], rarely 27. Anal-fin base moderately long. Anal-fin origin located distinctly posterior of middle of SL and anterior of middle of total length. Anal-fin margin nearly straight in most examined specimens, but convex in presumed mature male as evidenced by presence of filamentous dorsal- and pectoral-fin rays. Last anal-fin ray with slight membranous attachment to body.

Pelvic-fin rays i,5 [i,5]. Pelvic fin small; distal margin slightly convex with middle rays longest. Pelvic-fin insertion located anterior to middle of SL and along vertical through posterior limit of dorsal-fin base. Tip of adpressed pelvic fin extending past middle of SL and reaching anterior margin of vent. Last pelvic-fin ray with membranous attachment to body along basal one-half of its length.

Pectoral-fin rays 7 or 8 [7], rarely 8. Pectoral fin moderately long, its length slightly more than 0.60 of HL. Pectoral-fin margin distinctly convex, with middle ray longest. First pectoral-fin ray spinous with smooth margins, spine short with length slightly more than one-half that of first branched ray; ray prolonged as filament in presumed mature male specimens.

Preanal vertebrae 12 to 15 [15]; precaudal vertebrae 10 to 13 [11]; caudal vertebrae 27 to 29 [28]; total vertebrae 39 to 42 [39], with 39 and 40 vertebrae most common, and 42 vertebrae in only 1 of 54 radiographed specimens (total includes radiographed non-type specimens). Ribs 8 to 11 [10].

Coloration in alcohol.—Overall ground coloration of head and body pale and overlain with rounded, large, brown chromatophores. Dark pigmentation on head and body tends to be more concentrated dorsally. Expanded chromatophores blend together to form uniform brown cast on some portions of body in most specimens. Ventral surface of abdomen and head pale except for scattered chromatophores on abdomen in some specimens and broad band of scattered, dark chromatophores that extend from symphysis of lower jaw to opercle.

Dorsal fin pale with some dark pigmentation basally that forms somewhat diffuse spot with margin of spot in form of semicircle. Anal fin pale with scattered dark chromatophores basally. Pelvic and pectoral fins pale. Caudal fin with few scattered dark chromatophores that extend distally to at least middle of fin rays.

Maxillary barbel with scattered dark pigmentation basally and pale distally. Mental barbels pale.

Coloration in life.—Le Bail et al. (2000: 147) provided a photograph of a live specimen of the species (identified therein as *Pseudocetopsis* cf. *minutus*), photographed in an aquarium immediately after capture. The overall dark pigmentation visible in the photograph is comparable to that in the preserved specimens, but the head, body, and fins of the specimen have an overlying silvery sheen that is absent in preserved material.

Sexual dimorphism.—The presumed mature males of *P. orientale* have filaments present on the dorsal and pectoral fins and have the anal-fin margin slightly convex. Juveniles and females of the species, in contrast, lack filaments on the fins and have a straight anal-fin margin.

Distribution.—*Pseudocetopsis orientale* is known from the Atlantic coastal rivers of Suriname and French Guiana, in the region from the Corantijn River, that forms the border between Suriname and Guyana, to the Fleuve Oyapock-Rio Oiapoque along the French Guiana-Brazil border. Given the presence of this species in the Surinamese tributaries of the Corantijn River, it likely also occurs in the left-bank tributaries to that river in Guyana. Similarly it is likely that the species also occurs in the portions of the Rio Oiapoque basin within Brazil.

Etymology.—The species name, *orientale,* from the Latin for eastern, refers to the distribution of this species in the eastern most portions of the known distribution of the Cetopsinae.

Ecology.—The type locality is a rainforest stream bordered by overhanging vegetation that at the time of the collection had low (40 cm deep), clear, slowly-moving water over a sand bottom with mud along the banks. The holotype and paratypes captured with it came from holes and fissures in decaying branches submerged along the side of the stream (C. Weber, MHNG, pers. comm.). Mol et al. (2000:430) characterize the Maykaboeka Kreek as a low-gradient, second order drainage running through undisturbed rainforest. Non-type specimens from Degrad Florian in the Fleuve Iracoubo basin, French Guiana (MNHN 2002-1101), were captured in a stream approximately 3 m wide and 10–59 cm deep in clear, but slightly tea-colored waters in areas with slow current densely shaded by the gallery forest. Observations at that locality indicate that during the day *Pseudocetopsis orien-*

tale is hidden in the sediment under leaves or roots (PK).

Remarks.—The question of generic limits within the Cetopsinae has been discussed by various authors in recent years including Ferraris & Brown (1991), Lundberg & Rapp Py Daniel (1994), and Ferraris (1996). Ongoing phylogenetic studies indicate that a revamping of some generic definitions within the Cetopsinae may be necessary, but in the interim we assign the new species to *Pseudocetopsis* in keeping with the definition of that genus proposed by Ferraris & Brown (1991).

Pseudocetopsis minutus, which was originally described by Eigenmann (1912:211) as *Hemicetopsis minutus* from the Essequibo River system, has been reported by subsequent authors from a series of localities distant from that drainage basin including French Guiana (see synonymy above), the Rio Trombetas in the Amazon basin in Brazil (Ferreira, 1995:52), the Río Caroni in Venezuela (Taphorn & García Tenía, 1991, fig. 3; Lasso et al., 1990:117) and other rivers in that country (Machado-Allison et al., 1993:65, as *Hemicetopsis minimus*). Ongoing studies indicate that *P. minutus* is rather apparently endemic to the Essequibo River basin of Guyana and our comparisons herein of *P. orientale* are limited to material of *P. minutus* from that river basin.

Comparative material examined.—Pseudocetopsis minuta: British Guiana (=Guyana) Amatuk (5°18′N, 59°18′W), FMNH 53262, 1 (18 mm SL, holotype of *Hemicetopsis minutus*). *Siparuni VIII-2:* Essequibo River at Essequibo campsite (04°45′41″N, 58°45′53″W), ANSP 175839, 1 (21 mm SL).

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Literature Cited

Boujard, T., F. J. Meunier, M. Pascal, & J. F. Cosson. 1990. Les Téléostéens d'un haut bassin fluvial Guyanais, l'Arataye. 2—Inventaires des "non-Characoïdes." Cybium, 14(4):345–351.

Burgess, W. E. 1989. An atlas of freshwater and marine catfishes. A preliminary survey of the Siluriformes. T.F.H. Publications, Neptune City, New Jersey, U.S.A., 784 pp.

Eigenmann, C. H. 1912. The freshwater fishes of British Guiana, including a study of the ecological grouping of species and the relation of the fauna of the plateau to that of the lowlands.—Memoirs of the Carnegie Museum, 5:xii + 578 pages, 103 plates.

Ferraris, C. J., Jr. 1996. *Denticetopsis,* a new genus of South American whale catfish (Siluriformes: Cetopsidae, Cetopsinae), with two new species.—Proceedings of the California Academy of Sciences 49(6):161–170.

———, & B. A. Brown. 1991. A new species of *Pseudocetopsis* from the Río Negro drainage of Venezuela (Siluriformes: Cetopsidae).—Copeia 1991(1):161–165.

Ferreira, E. 1995. Composição, distribuição e aspectos ecológicos da ictiofauna de um trecho do rio Trombetas, na área de influência da futura UHE Cachoeira Porteira, Estado do Pará, Brasil.—Acta Amazonica 23(1–4, Suplemento; issue for 1993, published 1995):1–88.

Lasso, C. A., A. Machado-Allison, & R. Pérez Hernández. 1990. Consideraciones zoogeograficas de los peces de la Gran Sabana (Alto Caroni) Venezuela, y sus relaciones con las cuencas vecinas.—Memoria Sociedad de Ciencias Naturales La Salle 50(133–134):109–129.

Le Bail., P.-Y., P. Keith, & P. Planquette. 2000. Atlas des poissons d'eau douce de Guyane. Tome 2. Fascicule II. Siluriformes. Muséum National d'Histoire Naturelle, Service du Patronomie Naturel, Paris, and Institut d' Écologie et de Gestion de la Biodiversité, Paris. 307 pp.

Lundberg, J. G., & L. Rapp-Py-Daniel. 1994. *Bathycetopsis oliveirai,* gen. et sp. nov., a blind and depigmented catfish (Siluriformes: Cetopsidae) from the Brazilian Amazon.—Copeia 1994(2): 381–390.

Machado-Allison, A., C. Lasso, & R. Royero-León. 1993. Inventario preliminar y aspectos ecologicos de los peces de los Ríos Aguaro y Guariquito (Parque Nacional), Estado Guarico, Venezuela.—Memoria Sociedad de Ciencias Naturales La Salle 53(139):55–80.

Mol, J. H., D. Resida, J. C. Ramlal, & C. R. Becker. 2000. Effects of El Niño-related drought on freshwater and brackish-water fishes in Suriname, South America.—Environmental Biology of Fishes 59(4):429–440.

Oliveira, J. C. de, R. P. Vari, & C. J. Ferraris, Jr. 2001. A new species of "Whale catfish" (Siluriformes: Cetopsidae) from the western portions of the Amazon basin.—Proceedings of the Biological Society of Washington 114(3):574–578.

de Pinna, M. C. C., & R. P. Vari. 1995. Monophyly and phylogenetic diagnosis of the family Cetopsidae, with synonymization of the Helogenidae (Teleostei: Siluriformes).—Smithsonian Contributions to Zoology 51:1–26.

Ponton, D., & G. H. Copp. 1997. Early dry-season community structure and habitat use of young fish in tributaries of the River Sinnamary (French Guiana, South America) before and after Hydrodam operation.—Environmental Biology of Fishes 50:235–256.

Taphorn, D. C., & J. G. García Tenía. 1991. El Río Claro y sus peces, con consideraciones de los impactos ambientales de las presas sobre la ictiofauna del bajo Río Caroni.—Biollania 8:23–45.

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Chromosomes of Philippine mammals (Insectivora, Dermoptera, Primates, Rodentia, Carnivora)

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Abstract.—Karyotypes of nine species of Philippine mammals representing five orders are presented. Chromosomes of six species are described for the first time, including three endemic insectivores (*Podogymnura truei, Crocidura beatus, C. grayi*), the endemic dermopteran (*Cynocephalus volans*), an endemic squirrel (*Sundasciurus philippinensis*), and a widespread viverrid (*Viverra tangalunga*). Some species endemic to the oceanic Philippines have unique karyotypes whereas other endemics and widespread Asian species have karyotypes that are similar, or identical, to those of related species or conspecifics occurring outside the archipelago. These data corroborate patterns of karyotype variation previously documented for Philippine bats and murid rodents.

For more than a century, the terrestrial mammal fauna of the Philippines has been recognized as a unique assemblage (Thomas 1898). All portions of this remarkable fauna, which includes 179 species representing nine orders, are characterized by a high proportion of endemic species. More than 60% of the mammal fauna, as a whole, is endemic (Heaney et al. 1998). For bats and murid rodents, the two largest faunal components, cytogenetic studies have provided insight into how these groups have diversified within the archipelago (Rickart et al. 1989, Rickart & Musser 1993, Rickart et al. 1999, Rickart & Heaney 2002). These studies suggest that chromosomal data on other Philippine taxa may help clarify their phylogenetic and biogeographic relationships. Accordingly, this report presents karyotypes of nine species representing five orders (Insectivora, Dermoptera, Primates, Rodentia, and Carnivora).

Methods

Specimens were collected during field studies conducted in 1987 (on Leyte, Biliran and Negros islands), 1988 (Luzon Island), and 1993 (Mindanao Island). Live-trapped animals were processed and killed with sodium pentobarbital within 24 h of capture, and karyotypes prepared from bone marrow and/or spleen cells following in vivo methodology (Patton 1967, Rickart et al. 1989). Material from freshly killed animals caught in snap traps was processed in vitro (Rickart et al. 1998). Cells were processed and fixed in the field, and standard (non-differentially stained) karyotypes were prepared from stored cell suspensions. Preparations of silver-stained nucleolus organizer regions (Ag-NORs; Howell & Black 1980) and G-banded chromosomes (Seabright 1971) were made for some taxa. A minimum of 10 chromosomal spreads was examined from each preparation. Chromosome terminology follows Rickart and Musser (1993). As used herein, fundamental number (FN) refers to the total number of chromosome arms in the female karyotype (including those of sex chromosomes). Species nomenclature follows Heaney et al. (1998).

Voucher specimens were prepared as skins with partial skeletons, complete skeletons, or preserved in fluid, and are deposited in the Field Museum of Natural History, Chicago, IL (FMNH), the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and the Philippine National Museum, Manila (PNM). Microscope slides of chromosomal preparations and photomicrograph negatives cross-referenced to cataloged voucher specimens are housed at the Utah Museum of Natural History, University of Utah, Salt Lake City.

Specimens Examined

Podogymnura truei Mearns, 1905.—Mindanao Island, Bukidnon Province, Mount Kitanglad Range, 16.5 km S, 4 km E Camp Phillips, elev. 1900 m, 8°10′30″N, 124°51′E, 2 males (FMNH 147793, 147798).

Crocidura beatus Miller, 1910.—Leyte Island, Leyte Province, Mount Pangasugan, 10 km N, 4.5 km E Baybay, elev. 950 m, 10°47′N, 124°50′E, 1 male (USNM 457984).

Crocidura grayi Dobson, 1890.—Luzon Island, Camarines Sur Province, Mount Isarog, 4 km N, 22 km E Naga, elev. 1750 m, 13°40′N, 123°22′E, 1 female, 1 male (USNM 573607, 573617).

Suncus murinus (Linnaeus, 1766).—Negros Island, Negros Oriental Province, Silliman Farm, Dumaguete, elev. 5 m, 09°18′N, 123°18′E, 2 males (USNM 457996, 457997); Mount Guinsayawan, 3 km N, 17 km W Dumaguete, elev. 1470 m, 9°22′N, 123°9′E, 1 female, 1 male (USNM 458970, 458972).

Cynocephalus volans (Linnaeus, 1758).—Leyte Island, Leyte Province, 7 km N Baybay, elev. 10 m, 10°45′N, 124°47′30″E, 1 female (USNM 458982).

Tarsius syrichta (Linnaeus, 1758).—Leyte Island, Leyte Province, 7 km N, 1.5 km E Baybay, elev. 50 m, 10°45′N, 124°48′E, 1 male (PNM specimen, EAR field number 1441); Mount Pangasugan, 10.2 km N, 2.2 km E Baybay, elev. 320 m, 10°46′N, 124°49′E, 1 male (USNM 459818); Mount Pangasugan, 8.5 km N, 2.5 km E Baybay, elev. 500 m, 10°45′30″N, 124°49′30″E, 1 male (USNM 458723).

Sundasciurus philippinensis (Waterhouse, 1839).—Biliran Island, Leyte Province, 5 km N, 10 km E Naval, elev. 850 m, 11°36′N, 124°29′E, 1 male (USNM 459821).

Paradoxurus hermaphroditus (Pallas, 1777).—Leyte Island, Leyte Province, 7 km N, 1.5 km E Baybay, elev. 50 m, 10°45′N, 124°48′E, 1 male (USNM 458891); Mount Pangasugan, 10 km N, 2 km E Baybay, elev. 300 m, 10°46′N, 124°49′E, 1 male (USNM 459999).

Viverra tangalunga Gray, 1832.—Leyte Island, Leyte Province, Mount Pangasugan, 10 km N, 2 km E Baybay, elev. 300 m, 10°46′N, 124°49′E, 1 male (USNM 460000).

Results

Order Insectivora
Family Erinaceidae

Podogymnura truei. 2N = 40, FN = 76, Fig. 1A.—The karyotype of the Mindanao gymnure includes 11 pairs of small to large-sized metacentric or submetacentric autosomes, 6 pairs of medium-sized subtelocentric autosomes, and 2 pairs of small or medium-sized telocentric autosomes. The small X chromosome is submetacentric, and the minute Y chromosome appears to be telocentric.

Family Soricidae

Crocidura grayi. 2N = 38, FN = 58, Fig. 1B.—The karyotype of the Luzon shrew includes 4 pairs of small to medium-sized submetacentric autosomes, 5 pairs of small to large-sized subtelocentric autosomes, and 9 pairs of small to large-sized telocentric autosomes. The X chromosome is medium-sized and subtelocentric, and the small Y chromosome is submetacentric.

Crocidura beatus. 2N = 38(?), FN = ?, not figured.—A poor quality in-vivo prep-

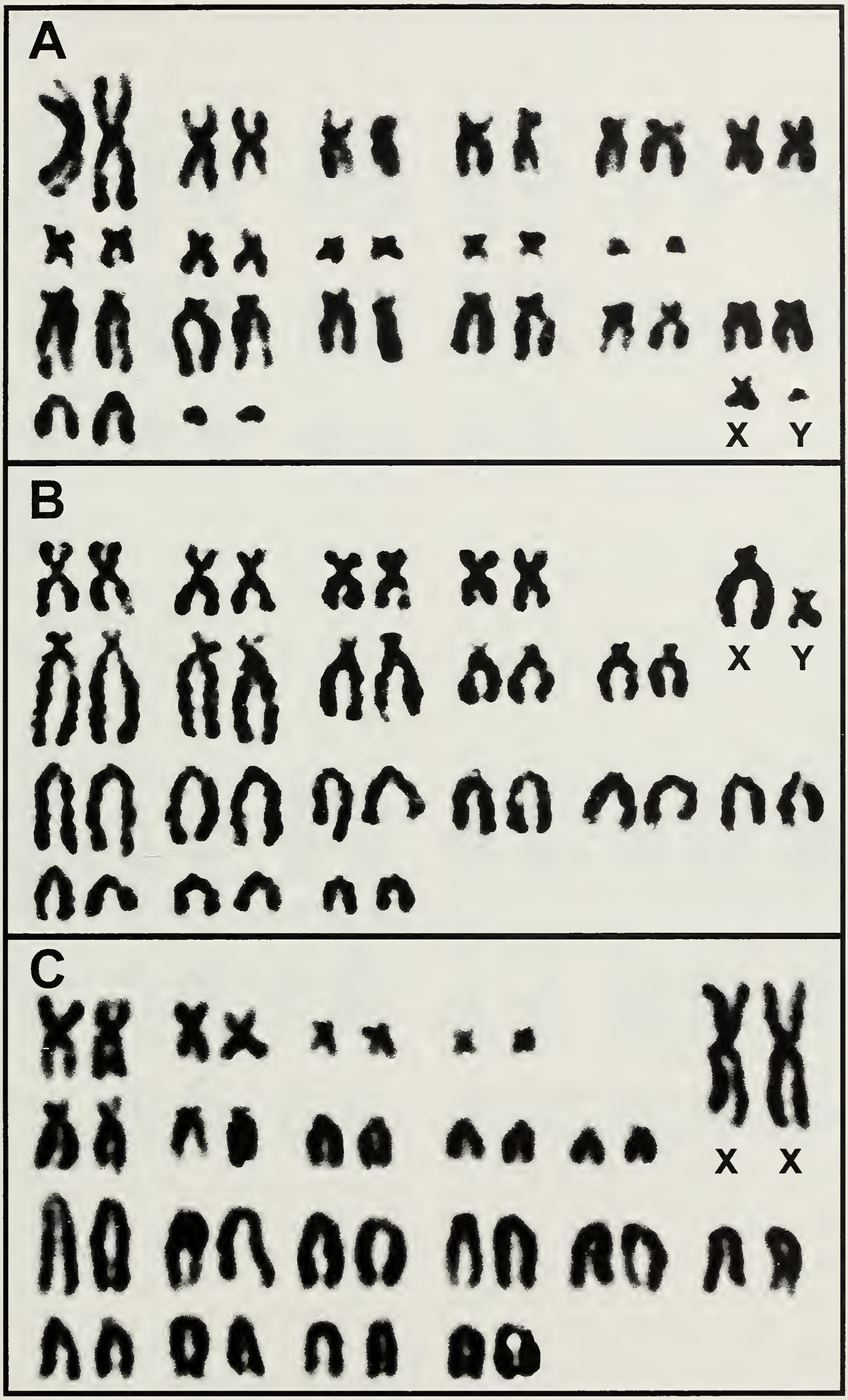

Fig. 1. Karyotypes of: A) *Podogymnura truei,* male (FMNH 147793) from in vitro preparation, 2N = 40; B) *Crocidura grayi,* male (USNM 573617), 2N = 38; C) *Suncus murinus,* female (USNM 458970), 2N = 40.

aration yielded preliminary information on the chromosomes of this species which is endemic to the Mindanao faunal region. The modal chromosome count from multiple spreads was 38, indicating a karyotype similar to that of *C. grayi* (Fig. 1B).

Suncus murinus. 2N = 40, FN = 60, Fig. 1C.—Specimens of the Asian house shrew from Negros Island have a karyotype that includes 4 pairs of small to large-sized submetacentric autosomes, 5 pairs of small to medium-sized subtelocentric autosomes, and 10 pairs of medium to large-sized telocentric autosomes. Both the X and Y chromosomes are submetacentric.

Order Dermoptera
Family Cynocephalidae

Cynocephalus volans. 2N = 38, FN = 40, Fig. 2.—The standard karyotype of a female Philippine flying lemur from Leyte Island includes 18 pairs of small to large-sized telocentric autosomes and a pair of medium-sized submetacentric X chromosomes. A G-banded preparation reveals G-positive bands on the nine largest autosomes. The X chromosome is largely G-positive. Ag-NORs are located terminally on the smallest telocentric autosomes.

Order Primates
Family Tarsiidae

Tarsius syrichta. 2N = 80, FN = 94, Fig. 3A.—Karyotypes of male Philippine tarsiers from Leyte Island include 6 pairs of small to large-sized metacentric or submetacentric autosomes and 33 pairs of small to large-sized telocentric autosomes. The submetacentric X and minute Y chromosomes are, respectively, the largest and smallest elements in the karyotype.

Order Rodentia
Family Sciuridae

Sundasciurus philippinensis. 2N = 38, FN = 72, Fig. 3B.—The karyotype of a male Philippine tree squirrel from Biliran Island includes 9 pairs of metacentric or submetacentric autosomes, 7 pairs of subtelocentric autosomes, and 2 pairs of small telocentric autosomes. The medium-sized X chromosome is submetacentric and the minute Y chromosome appears to be telocentric.

Order Carnivora
Family Viverridae

Paradoxurus hermaphroditus. 2N = 42, FN = 72, Fig. 4A.—Specimens of the common palm civet from Leyte Island have a karyotype that includes 8 pairs of small to large-sized metacentric or submetacentric autosomes, 6 pairs of small to large-sized subtelocentric autosomes, and 6 pairs of small to medium-sized telocentric autosomes. The medium-sized X chromosome is submetacentric, and the small Y chromosome is telocentric.

Viverra tangalunga. 2N = 36, FN = 64, Fig. 4B.—The karyotype of a male Malay civet from Leyte Island includes 7 pairs of small to large-sized metacentric or submetacentric autosomes, 6 pairs of small to large-sized subtelocentric autosomes, and 4 pairs of small telocentric autosomes. The X chromosome is large and submetacentric and the small Y chromosome is telocentric.

Discussion

The 2N = 40, FN = 76 karyotype of *Podogymnura truei* (Fig. 1A) is the first reported for the gymnure subfamily Hylomyinae. It differs substantially from those of hedgehogs (subfamily Erinaceinae) which have relatively uniform karyotypes of 2N = 48, FN = 90–96 and X chromosomes that are substantially larger than that of *P. truei* (Gropp 1969, Bhatnagar & El-Azawi 1978, Hübner et al. 1991, Reumer & Meylan 1986).

The widespread genus *Crocidura* displays extensive interspecific chromosomal variation (Maddalena & Ruedi 1994, Zima et al. 1998). There are seven species of *Crocidura* in the Philippines (Heaney &

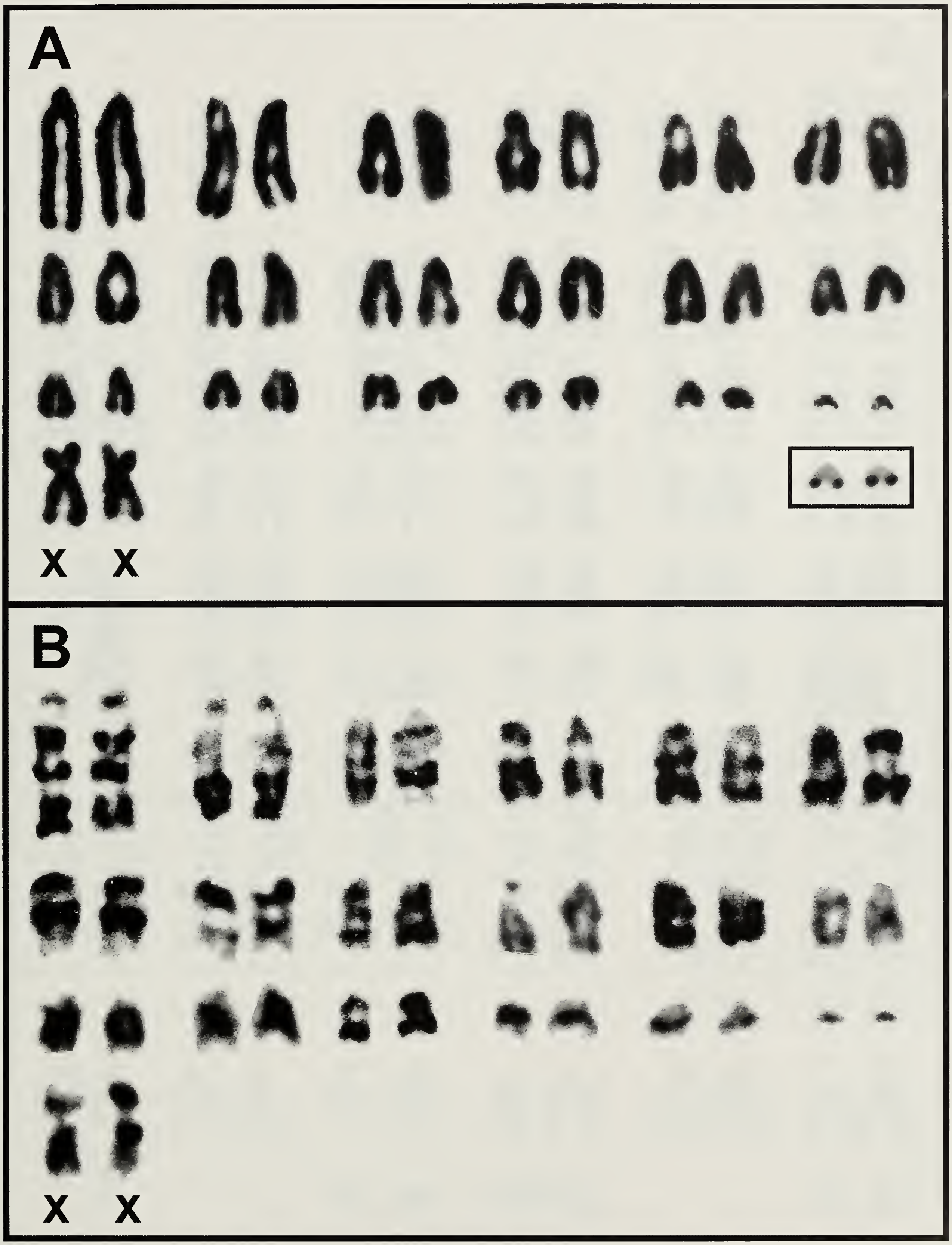

Fig. 2. Karyotypes of *Cynocephalus volans,* female (USNM 458982), 2N = 38: A) standard, inset of Ag-NOR sites; B) G-banded.

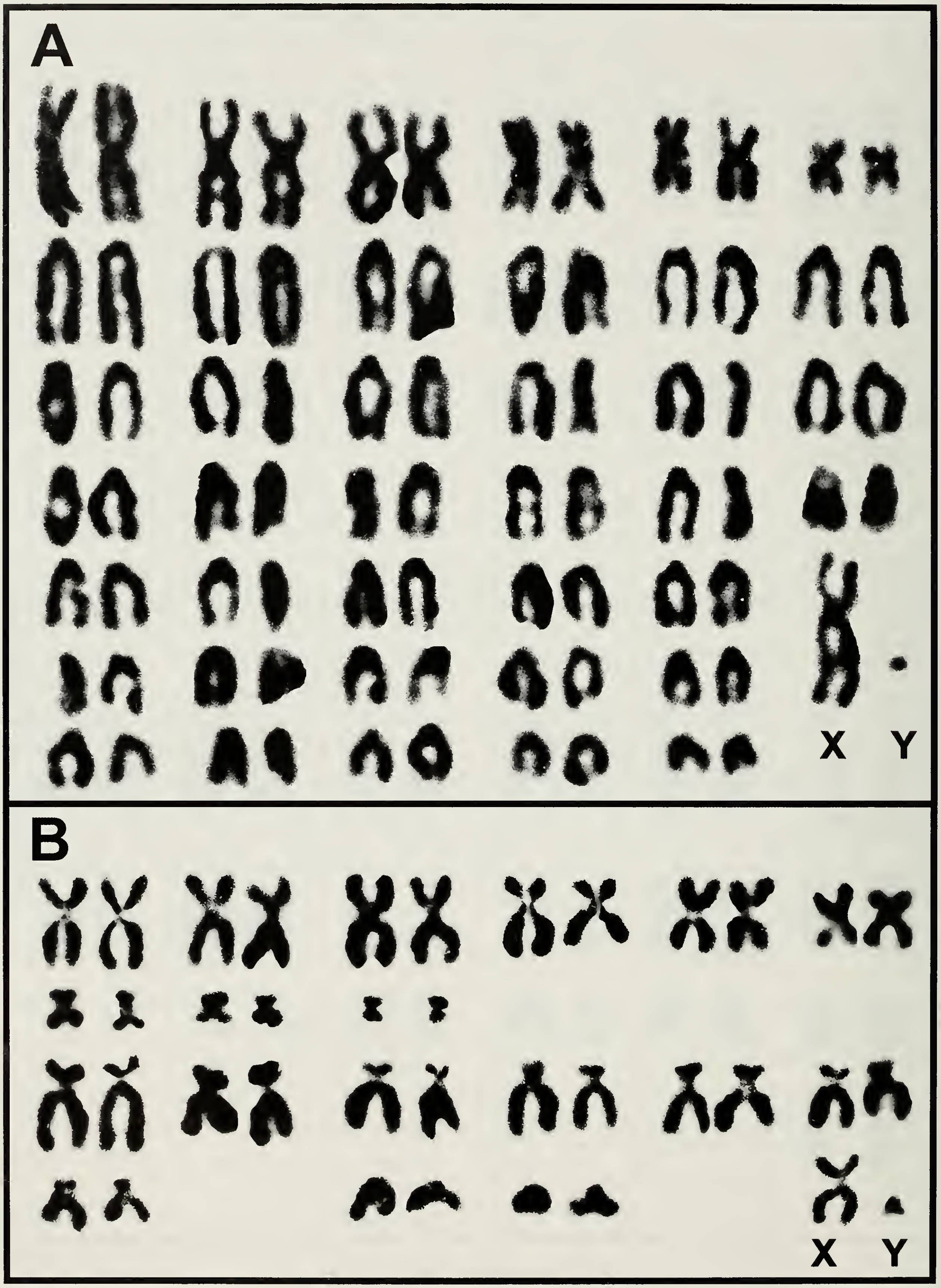

Fig. 3. Karyotypes of: A) *Tarsius syrichta,* male (EAR 1441), 2N = 80; B) *Sundasciurus philippinensis,* male (USNM 459821), 2N = 38.

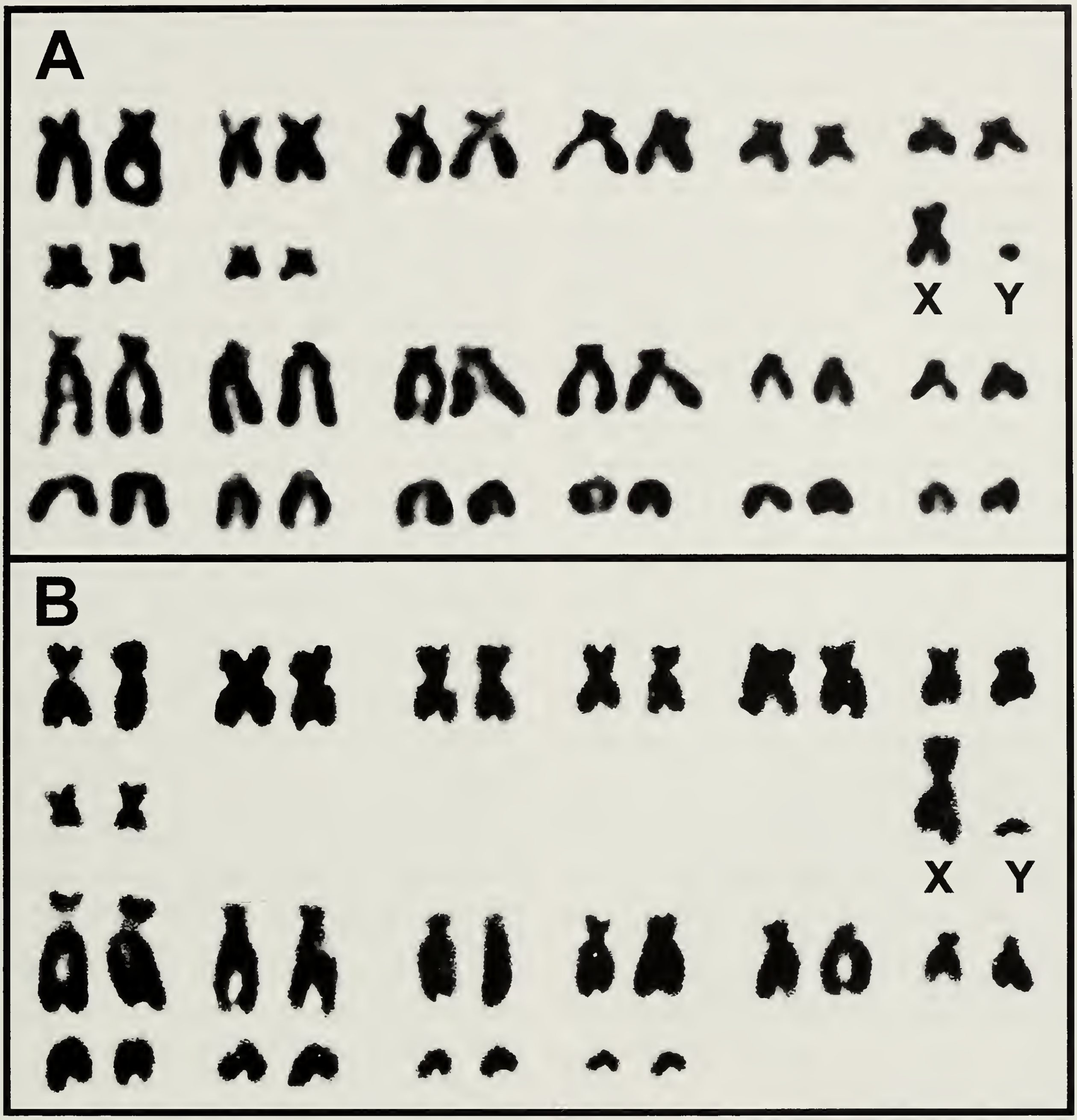

Fig. 4. Karyotypes of: A) *Paradoxurus hermaphroditus,* male (USNM 458891), 2N = 42; B) *Viverra tangalunga* male (USNM 460000), 2N = 36.

Ruedi 1994) of which two have been karyotyped (this study). The 2N = 38, FN = 58 karyotype of *C. grayi* (Fig. 1B) resembles those of several species with 2N = 38, FN = 54–58 from islands of the Sunda Shelf and from Sulewesi (Ruedi & Vogel 1995). It also is similar to the presumed ancestral arrangement for *Crocidura* (Maddalena & Ruedi 1994). The apparent similarity in the karyotypes of *C. grayi* and *C. beatus* is consistent with morphometric and allozyme data that place these species as sister-taxa (Heaney & Ruedi 1994). The limited data available suggest that the diversification of Philippine *Crocidura* has not involved major chromosomal rearrangements of the sort seen for members of the genus in Sulewesi (Ruedi & Vogel 1995), or for Philippine rodents of the genus *Apomys* (Rickart & Musser 1993, Rickart & Heaney 2002).

Suncus murinus is a chromosomally polymorphic species (2N = 30–40) found throughout much of southeast Asia (Yoshida 1985, Zima et al. 1998). It occurs throughout the Philippines as a non-native commensal (Heaney et al. 1998), and on Negros Island, it also is naturalized and abundant in primary forest habitat (Heaney et al. 1989). Both commensal and naturalized animals from Negros have identical karyotypes of 2N = 40, FN = 60 (Fig. 1C). This same arrangement has been reported for specimens from much of southeast Asia (Zima et al. 1998). Medina and Leonard (1977) reported a karyotype of 2N = 40, FN = 54 for *S. luzoniensis* (a synonym of *S. murinus*) from Luzon Island. The difference in FN compared to the Negros specimens most likely reflects variable assessment of minute secondary arms on subtelocentric autosomes.

The 2N = 38, FN = 40 karyotype of *Cynocephalus volans* (Fig. 2), one of two members of the mammalian order Dermoptera, is reported here for the first time. This also corrects an erroneous report by Hsu and Benirschke (1973). They published identical karyotypes of 2N = 56, FN = 72 for a specimen of *Galeopterus variegatus* from Malaysia and for an animal at the Lincoln Park Zoo, Chicago, originally identified as *C. volans.* After the latter died, it was sent to the Field Museum where it was accessioned and correctly identified as *Galeopterus* (FMNH 60308; W. Stanley, pers. comm.). The two dermopterans have substantially different karyotypes. *Cynocephalus* lacks nine pairs of autosomes present in *Galeopterus,* including seven pairs of small to large-sized biarmed chromosomes, and the X chromosome of the former is submetacentric whereas that of the latter is metacentric (Fig. 2; Hsu & Benirschke 1973). The Ag-NORs of *Cynocephalus* are located on the smallest autosomal pair (Fig. 2). In *Galeopterus,* this same pair bears secondary constrictions (Hsu & Benirschke 1973). This chromosomal distinctiveness is in accord with the substantial morphological and ecological differences that suggest ancient divergence of the two species and supports their placement in separate genera (Stafford & Szalay 2000).

The karyotype of *Tarsius syrichta* from Leyte Island (Fig. 3A) is identical to those previously reported for specimens from Mindanao (Boer & Boer-Van der Vlist 1973, Dutrillaux & Rumpler 1988). *Tarsius bancanus* also has 2N = 80, FN = 94 (Klinger 1963), but its karyotype differs from that of *T. syrichta* in the size and relative arm lengths of several of the biarmed autosomes. *Tarsius dianae* from central Sulawesi is the only other tarsier that has been karyotyped. Its arrangement of 2N = 46, FN = 82 (Niemitz et al. 1991) differs from those of *T. syrichta* and *T. bancanus* by multiple Robertsonian and non-Robertsonian events. Chromosomal data support phylogenetic hypotheses based on comparative morphology and behavior that associate the Philippine and Sundaic species (*T. syrichta* and *T. bancanus*) as relatively specialized forms separate from the three species of Sulawesian tarsiers (Niemitz 1977, Musser & Dagosto 1987, Dagosto et al. 2001).

The 2N = 38, FN = 72 karyotype of *Sundasciurus philippinensis* (Fig. 3B) is reported here for the first time. It is identical to that of *S. jentinki,* the only other member of the genus that has been karyotyped (Harada & Kobayashi 1980). Among callosciurine squirrels, *Dremomys rufigenis* and *Callosciurus albescens* also share this arrangement (Nadler & Hoffmann 1970, Harada & Kobayashi 1980), and several other species of *Callosciurus* have karyotypes of 2N = 40, FN = 70–74 that differ only slightly from that of *S. philippinensis* (Nadler et al. 1975, Yong Hoi-Sen et al. 1975, Oshida & Yoshida 1999). The available data suggest that callosciurines are chromosomally conservative.

A karyotype of 2N = 42, FN = 78 was reported previously for *Paradoxurus hermaphroditus* from India (Ray-Chaudhuri et al. 1966). The karyotype of Philippine specimens (Fig. 4A) is similar, but appears to have fewer subtelocentric and more telocentric elements (FN = 72). In other respects, the two karyotypes are identical.

The 2N = 36, FN = 64 karyotype of

Viverra tangalunga (Fig. 4B) is the first reported for this widespread southeast Asian species. *Viverra zibetha,* the only other member of this genus that has been examined has a substantially different karyotype of 2N = 38 and FN = 68 (Pathak 1971). Among members of the subfamily Viverrinae that have been examined, *Viverricula indica* is the only species with 2N = 36 (Wurster & Benirschke 1968). However, *Viverra tangalunga* has more telocentric and fewer subtelocentric autosomes, and a significantly smaller Y chromosome than does *Viverricula.*

Interpretation of these chromosome data is limited, in some cases, by the lack of comparative information on related taxa. Nonetheless, some general patterns of variation are apparent. Members of the endemic genera *Podogymnura* and *Cynocephalus* have karyotypes that differ substantially from those of related taxa. In contrast, endemic species of *Tarsius, Crocidura,* and *Sundasciurus,* and the widespread species *Suncus murinus* and *Paradoxurus hermaphroditus* have karyotypes that are similar, or identical, to those of closely related species or conspecifics occurring elsewhere in Asia. These results mirror patterns of chromosomal variation documented for Philippine bats and murid rodents (Rickart et al. 1999, Rickart & Heaney 2002). Most endemic taxa have karyotypes that are unique compared to relatives occurring outside of the Philippines. Some widespread species exhibit chromosomal polymorphism, in which Philippine populations have unique karyotypes. The general pattern is one of chromosomal rearrangement occurring as a result of isolation. The degree to which this pattern is expressed appears to be largely a function of how long a particular group has been present within the archipelago.

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Literature Cited

Bhatnagar, A. N., & T. F. El-Azawi. 1978. A karyotype study of two species of hedgehogs, *Hemiechinus auritus* and *Paraechinus aethiopicus* (Insectivora: Mammalia).—Cytologia 43:53–59.

Boer, L. E. M. de, & J. de Boer-Van der Vlist. 1973. The somatic chromosomes and the idiogram of *Tarsius syrichta carbonarius* Huede, 1898 (Primates: Tarsioidea).—Genen en Phaenen 16:65–71.

Dagosto, M., D. L. Gebo, & C. Dolino. 2001. Positional behavior and social organization of the Philippine tarsier (Tarsius syrichta).—Primates 42:233–243.

Dobson, G. E. 1890. Descriptions of new species of *Crocidura.*—Annals and Magazine of Natural History, series 6, 6:494–497.

Dutrillaux, B., & Y. Rumpler. 1988. Absence of chromosomal similarities between tarsiers (*Tarsius syrichta*) and other primates.—Folia Primatologica 50:130–133.

Gray, J. E. 1832. On the family of Viverridae and its generic sub-divisions, with an enumeration of the species of several new ones.—Proceedings of the Committee of Science and Correspondence of the Zoological Society of London 1832(2):63–68.

Gropp, A. 1969. Cytologic mechanisms of karyotype evolution in insectivores. Pp. 247–266 *in* Comparative mammalian cytogenetics. Springer, Berlin, 473 pp.

Harada, M., & T. Kobayashi. 1980. Studies on the small mammal fauna of Sabah, east Malaysia II. Karyological analysis of some Sabahan mammals (Primates, Rodentia, Chiroptera).—

Contributions from the Biological Laboratory, Kyoto University 26:83–95.

Heaney, L. R., & M. Ruedi. 1994. A preliminary analysis of biogeography and phylogeny of *Crocidura* from the Philippines. Pp. 357–377 *in* J. Meritt, G. Kirkland, & R. Rose, eds., Advances in the biology of shrews. Special Publication 18, Carnegie Museum of Natural History, Pittsburgh, 458 pp.

———, P. D. Heideman, E. A. Rickart, R. C. B. Utzurrum, & J. S. H. Klompen. 1989. Elevational zonation of mammals in the central Philippines.—Journal of Tropical Ecology 5:259–280.

———, et al. 1998. A synopsis of the mammalian fauna of the Philippine Islands.—Fieldiana: Zoology, n.s. 88:1–61.

Howell, W. M., & D. A. Black. 1980. Controlled silver staining of neucleolar organizer regions with a protective colloidal developer: a 1-step method.—Experientia 36:1014–1015.

Hsu, T. C. & K. Benirschke. 1973. *Cynocephalus variegatus, C. volans* (flying lemur) 2n = 56. An atlas of mammalian chromosomes. Vol. 7, Folio 303, Springer-Verlag, New York, unpaged.

Hübner, R., T. Maddalena, & W. Poduschka. 1991. The karyotype of the middle-African hedgehog *Atelerix albiventris* Wagner, 1841 and its cytotaxonomical relationships to other Erinaceinae (Insectivora: Erinaceidae).—Genetica 83:243–246.

Klinger, H. P. 1963. The somatic chromosomes of some primates (*Tupaia glis, Tarsius bancanus, Cercocebus aterrimus, Symphalangus syndactylus*).—Cytogenetics 2:140–151.

Linnaeus, C. 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis, 10th edition. Laurentius Salvius, Stockholm 1:1–824.

———. 1766. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis synonymis, locis, 12th edition. Laurentius Salvius, Stockholm 1: 1–532.

Maddalena, T., & M. Ruedi. 1994. Chromosomal evolution in the genus *Crocidura* (Insectivora: Soricidae). Pp. 335–344 *in* J. Merritt, G. Kirkland, & R. Rose, eds., Advances in the biology of shrews. Special Publication 18, Carnegie Museum of Natural History, Pittsburgh, 458 pp.

Mearns, E. A. 1905. Description of some new genera and species of mammals from the Philippine Islands.—Proceedings of the United States National Museum 28:425–460.

Medina, F. I. S., & A. Leonard. 1977. Observations sur les chromosomes de *Suncus luzoniensis* Peters.—Acta Zoologica et Pathologica Antverpiensia 69:183–188.

Miller, G. S., Jr. 1910. Descriptions of two new genera and sixteen new species of mammals from the Philippine Islands.—Proceedings of the United States National Museum 38:391–404.

Musser, G. G., & M. Dagosto. 1987. The identity of *Tarsius pumilus,* a pygmy species endemic to the montane mossy forests of central Sulawesi.—American Museum Novitates 2867:1–53.

Nadler, C. F., & R. S. Hoffmann. 1970. Chromosomes of some Asian and South American squirrels (Rodentia: Sciuridae).—Experientia 26:1383–1386.

———, ———, & M. E. Hight. 1975. Chromosomes of three species of Asian tree squirrels *Callosciurus* (Rodentia: Sciuridae).—Experientia 31: 166–167.

Niemitz, C. 1977. Zur Funktionsmorphologie und Biometrie der Gattung *Tarsius* Storr, 1780. Herleitung von Evolutionsmechanismen bei einem Primaten.—Courier der Senckenbergischen Naturforschenden Gesellschaft 25:1–161.

———, A. Nietsch, S. Warter, & Y. Rumpler. 1991. *Tarsius dianae*: a new primate species from central Sulawesi (Indonesia).—Folia Primatologica 56:105–116.

Oshida, T., & M. C. Yoshida. 1999. Chromosomal localization of nucleolus organizer regions in eight Asian squirrel species.—Chromosome Science 3:55–58.

Pallas, P. S. 1777. Pg. 426 *in* Schreber, J. C. D. von. 1774–1785. Die Saugethier in Abbildungen nach der Natur mit Beshreibungen. Erlangen Wolfgang Walden, 1112 pp.

Pathak, S. 1971. Karyotype of the Oriental Civet, *Viverra zibetha,* Linn. (Viverridae-Carnivora).—Mammalian Chromosomes Newsletter 12(2):61.

Patton, J. L. 1967. Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia: Heteromyidae).—Journal of Mammalogy 48: 27–37.

Ray-Chaudhuri, S. P., P. V. Ranjini, & T. Sharma. 1966. Somatic chromosomes of the common palm civet, *Paradoxurus hermaphroditus* (Viverridae—Carnivora).—Experientia 22:740–741.

Reumer, W. F., & A. Meylan. 1986. New developments in vertebrate cytotaxonomy IX: chromosome numbers in the order Insectivora (Mammalia).—Genetica 70:119–151.

Rickart, E. A., & L. R. Heaney. 2002. Further studies on the chromosomes of Philippine rodents (Muridae: Murinae).—Proceedings of the Biological Society of Washington 115:473–487.

———, & G. G. Musser. 1993. Philippine rodents: chromosomal characteristics and their significance for phylogenetic inference among 13 species (Rodentia: Muridae: Murinae).—American Museum Novitates 3064:1–34.

———, L. R. Heaney, & M. J. Rosenfeld. 1989. Chromosomes of ten species of Philippine fruit bats (Chiroptera: Pteropodidae).—Proceedings of the Biological Society of Washington 102:520–531.

———, J. A. Mercier, & L. R. Heaney. 1999. Cytogeography of Philippine bats.—Proceedings of the Biological Society of Washington 112:453–469.

———, L. R. Heaney, B. R. Tabaranza, & D. S. Balete. 1998. A review of the genera *Crunomys* and *Archboldomys* (Rodentia: Muridae: Murinae), with descriptions of two new species from the Philippines.—Fieldiana: Zoology, n.s. 89:1–24.

Ruedi, M., & P. Vogel. 1995. Chromosomal evolution and zoogeographic origin of southeast Asian shrews (genus *Crocidura*).—Experientia 51: 174–178.

Seabright, M. 1971. A rapid banding technique for human chromosomes.—The Lancet 1971, II: 971–972.

Stafford, B. J., & F. S. Szalay. 2000. Craniodental functional morphology and taxonomy of dermopterans.—Journal of Mammalogy 81:360–385.

Thomas, O. 1898. On the mammals collected by Mr. John Whitehead during his recent expedition to the Philippines. With field-notes by the collector.—Transactions of the Zoological Society of London 14:377–412.

Waterhouse, G. R. 1839. Description of a new species of squirrel (*Sciurus philippinensis*) from the Philippine Islands.—Proceedings of the Zoological Society of London 1839:117–118.

Wurster, D. H., & K. Benirschke. 1968. Comparative cytogenetic studies in the Order Carnivora.—Chromosoma 24:336–382.

Yong Hoi-Sen, S. S. Dhaliwal, Lim Boo-Liat, I. Mull, & The Kok-Leng. 1975. Karyotypes of four species of *Callosciurus* (Mammalia, Rodentia) from peninsular Malaysia.—Malaysian Journal of Science 3:1–5.

Yoshida, T. H. 1985. The evolution and geographic differentiation of the house shrew karyotypes.—Acta Zoologica Fennica 170:31–34.

Zima, J., L. Lukácová, & M. Macholán. 1998. Chromosomal evolution in shrews. Pp. 175–218 *in* Evolution of Shrews. Mammal Research Institute, Polish Academy of Sciences, Bialowieza, 458 pp.

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Early zoeas of *Athanas parvus* De Man, 1910 (Decapoda: Caridea: Alpheidae) reared in the laboratory

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Abstract.—Early zoeas of *Athanas parvus* De Man are described and illustrated in detail, based on laboratory-hatched eggs from females collected in Sangju, Korea. This is the first record of the genus *Athanas* Leach from Korean waters. The zoeal characteristics of *Athanas* species are compared with those of species of the other four alpheid genera for which larvae are known. Based on morphological similarity, larval characters of *Athanas* species support a close relationship between the Alpheidae and Palaemonidae.

The small shrimps of the genus *Athanas* Leach, 1814 are usually found in dead coral heads, pools under rocks, and sandy or muddy beaches. Some species are found in permanent association with sea urchins, living between the spines on the oral surface (Banner & Banner 1973). Ten species of the family Alpheidae, belonging to four genera have been recorded from Korean waters (Yang & Anker 2003). However, species of the genus *Athanas* have not been reported from Korean waters to date.

Larvae of three species of *Athanas* have been described so far: *A. djiboutensis* Coutière, 1897, first zoea obtained from Ghardaqa (Gurney 1938); *A. dimorphus* Ortmann, 1894, first zoea based on plankton material from the Red Sea (Gurney 1927) and first three zoeal stages from India (Bhuti et al. 1977); and *A. nitescens* (Leach, 1814), first three zoeal stages from the U.K. (Lebour 1932), and other descriptions based on plankton material (Sars 1906, Williamson 1915, Webb 1921, Kurian 1956, Bourdillon-Casanova 1960, Williamson 1967).

This study describes and illustrates in detail the early zoeal stages of *A. parvus* De Man, 1910, and compares morphological characteristics of the zoea of species of *Athanas* with those of the other four alpheid genera for which larvae are known.

Material and Methods

On 21 July 1997, ovigerous females of *Athanas parvus* were collected from oyster raft cultures in Sangju, Korea (34°43′00″N, 127°59′30″E). Ten newly hatched zoeas were removed and placed in each of six glass bowls containing 33.3‰ filtered seawater, and kept in a growth chamber at 25°C. Larvae were fed daily with the microalga *Dunaliella tertiolecta* Butcher, and some specimens in each stage were preserved in 7% neutral formalin. Drawings were made with the help of a camera lucida. Measurements and setal counts were based on the mean of ten specimens for each zoeal stage. Total length (TL) was measured from the rostral tip (postorbital margin for the first zoea) to the posteromedian margin of the telson, excluding posterior setae. Carapace length (CL) was measured from the postorbital margin to the posteromedian margin of the carapace. The setal armature of appendages is described from proximal to distal segments. The chromatophore pattern was determined by observation of living zoeas.

Results

Four zoeal stages were obtained. When the fourth zoea molted to the fifth zoea, the larvae died because of their inability to extricate themselves from the fourth zoeal exoskeleton. The first zoeal stage is described in detail, and for subsequent stages only main differences from previous stage are given.

First zoea
Fig. 1

Duration. 18–20 hours.

TL. 1.38 (1.26–1.46) mm; CL. 0.26 (0.24–0.32) mm.

Carapace (Fig. 1A). Rostrum absent; anterior dorsomedian papilla present; pterygostomian spine present; supraorbital and antennal spines absent; anteroventral and posteroventral denticles absent; eyes sessile.

Antennule (Fig. 1C). Peduncle unsegmented; inner flagellum with long plumose seta; outer flagellum with 3 aesthetascs, short plumose seta, and long simple seta.

Antenna (Fig. 1D). Peduncle with basal spine; endopod spine-like, less than one-third length of scale; scale 4-segmented, with 11 plumose setae and distolateral spine.

Mandibles. Rudimentary.

Maxillule (Fig. 1E). Coxal endite with subterminal seta and 3 terminal setae; basial endite with 2 stout spines and short subterminal seta; endopod segmented, with 2 terminal setae.

Maxilla (Fig. 1F). Coxal endite with 2 setae; basial endite bilobed, with 3 + 4 setae; endopod with 3 (1 basal + 2 terminal) setae and fine marginal hairs; scaphognathite with 5 plumose setae.

First maxilliped (Fig. 1G). Coxa with seta; basis unarmed; endopod segmented, with 3 terminal setae; exopod with 4 terminal natatory setae.

Second maxilliped (Fig. 1H). Coxa unarmed; basis unarmed; endopod 4-segmented, with 0, 0, 1, 3 setae; exopod with 4 terminal natatory setae.

Third maxilliped (Fig. 1I). Coxa unarmed; basis with simple seta; endopod 4-segmented, with 0, 0, 2, 2 setae; exopod with 5 (1 subterminal + 4 terminal) natatory setae.

Pereiopods (Fig. 1J). Pereiopod 1 biramous; pereiopods 2–4 absent; pereiopod 5 uniramous.

Abdomen (Fig. 1A). Composed of 5 somites, sixth somite not differentiated; all somites without spines; third somite bent; third to fifth somites with pairs of dorsomedian setae; pleopods absent.

Telson and uropods (Fig. 1B). Telson subtriangular, with 7 + 7 marginal setae; outermost 2 pairs plumose only on inner side; bases of all setae except outermost with row of minute spinules. Uropods visible.

Chromatophores (Fig. 1A). Dark red chromatophores present on peduncles of antennule and antenna, superolateral margin of each eye, anterior dorsomedian papilla of carapace, ventral margin of carapace, dorsolaterally on carapace, bases and exopods of first, second, and third maxillipeds, endopod of third maxilliped, rudiments of pereiopods 1 and 5, dorsally on second to fifth abdominal somites, ventrally on first and fourth to fifth abdominal somites, and telson. Yellow chromatophores present on peduncle of antennule and laterally on second and third abdominal somites.

Second zoea
Fig. 2

Duration. 1–2 days.

TL. 1.53 (1.52–1.54) mm; CL. 0.28 (0.26–0.32) mm.

Carapace (Fig. 2A, B). Rostrum short, not extending beyond eyes; eyes stalked.

Antennule (Fig. 2D). Peduncle 2-segmented, with 3 and 4 setae.

Antenna (Fig. 2E). Unchanged.

Mandibles (Fig. 2F). Palp absent; left and

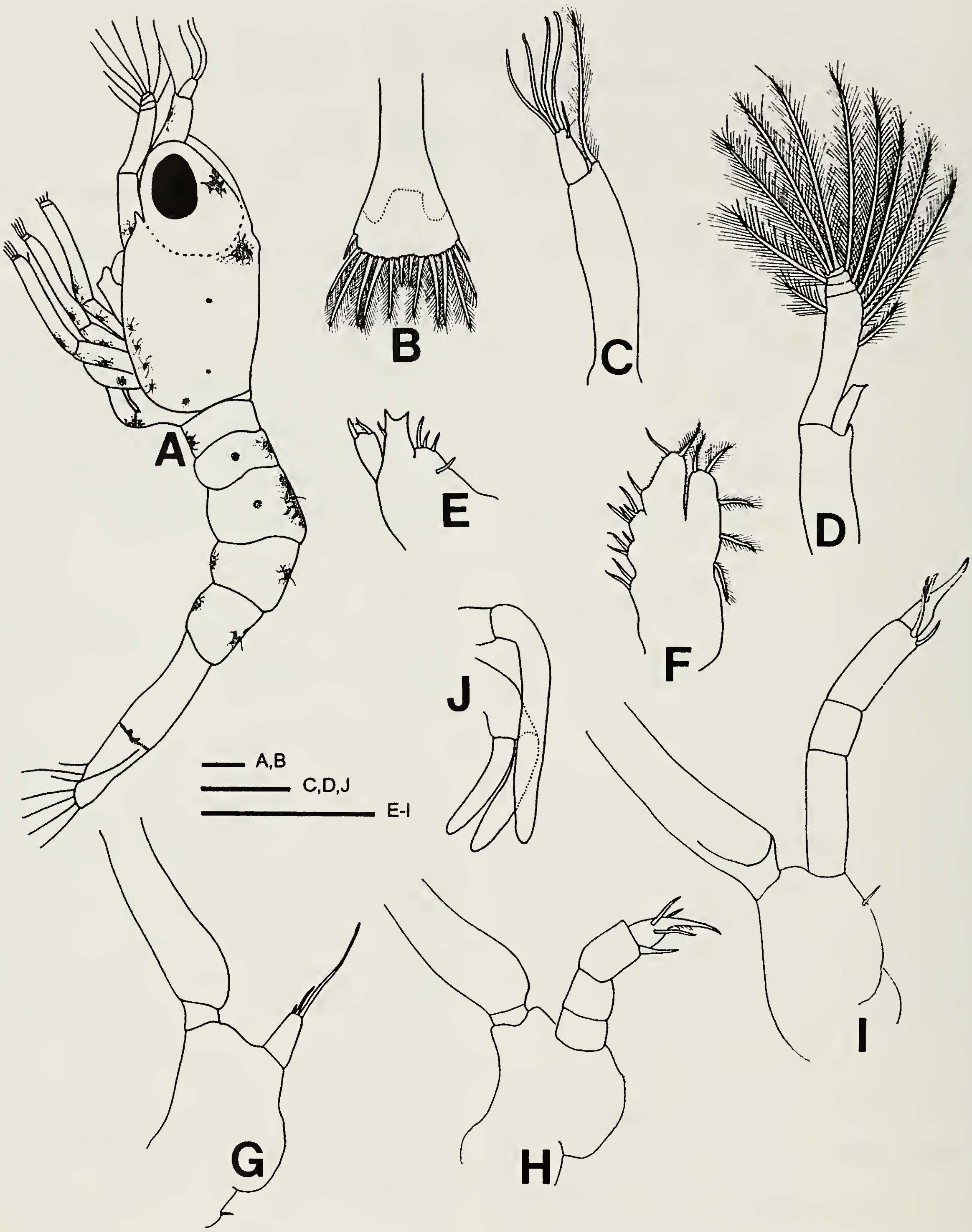

Fig. 1. First zoea of *Athanas parvus* De Man, 1910. A, habitus, lateral view; B, telson and uropods, dorsal view; C, antennule; D, antenna; E, maxillule; F, maxilla; G, first maxilliped; H, second maxilliped; I, third maxilliped; J, pereiopods 1 and 5. Exopod shown truncated in G–I. Scale bars = 0.1 mm.

right mandibles without spine between molar and incisor processes.

Maxillule (Fig. 2G). Coxal endite with 5 setae; basial endite with 2 spines and 2 setae.

Maxilla (Fig. 2H). Unchanged.

First maxilliped (Fig. 2I). Unchanged.

Second maxilliped (Fig. 2J). Basis with 2 small marginal spiniform setae; endopod 5-segmented, with 0, 0, 0, 1, 3 setae.

Third maxilliped (Fig. 2K). Unchanged.

Pereiopods (Fig. 2L). Pereiopods 1 and 5 longer; pereiopod 2 biramous as bud; pereiopod 3 uniramous.

Abdomen (Fig. 2A, B). Unchanged.

Telson and uropods (Fig. 2C). Telson

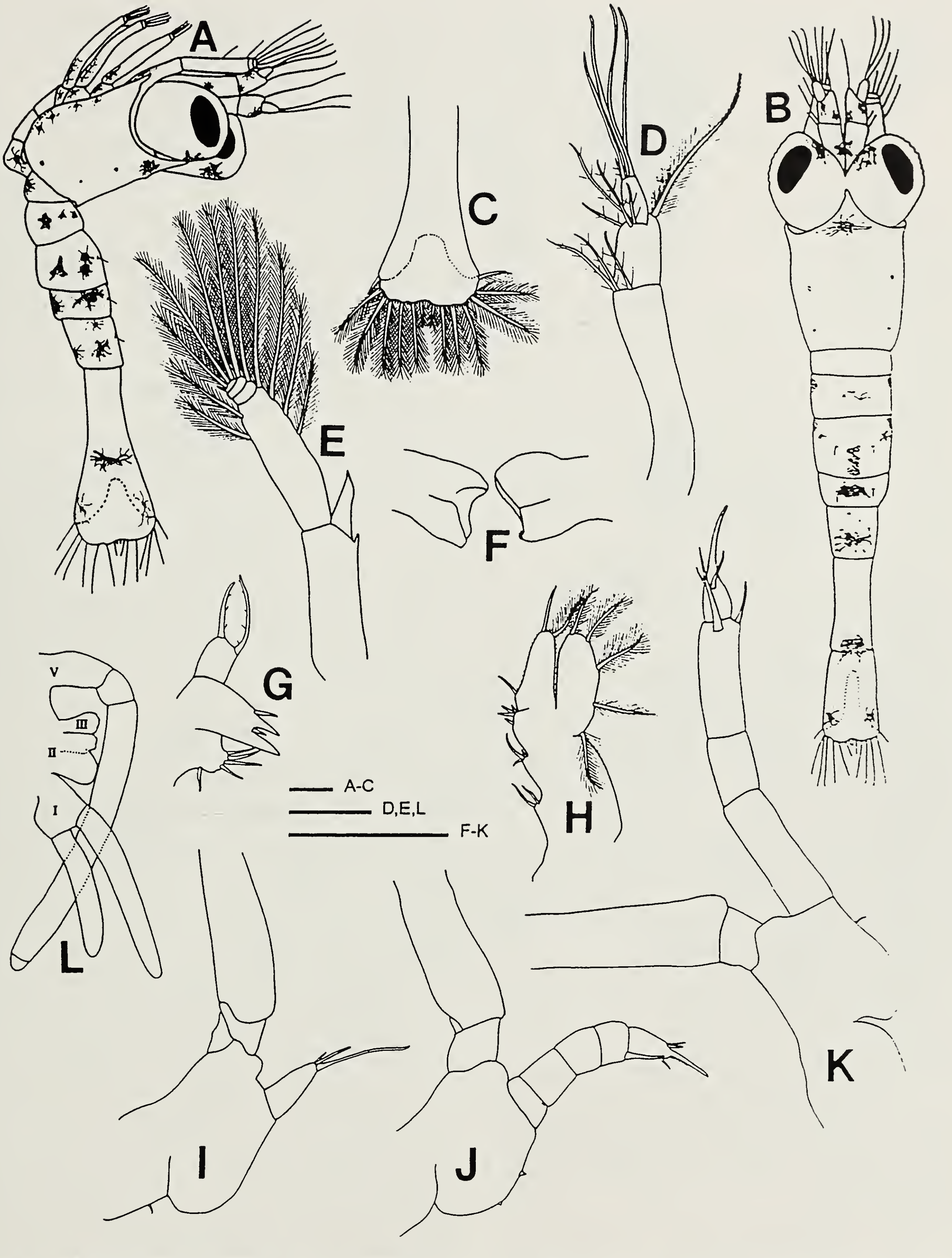

Fig. 2. Second zoea of *Athanas parvus* De Man, 1910. A, habitus, lateral view; B, habitus, dorsal view; C, telson and uropods, dorsal view; D, antennule; E, antenna; F, mandibles; G, maxillule; H, maxilla; I, first maxilliped; J, second maxilliped; K, third maxilliped; L, pereiopods 1–3 and 5. Exopod shown truncated in I–K. Scale bars = 0.1 mm.

with 8 + 8 marginal setae; outermost pair plumose only on innerside. Uropods unchanged.

Third zoea
Fig. 3

Duration. 2–3 days.

TL. 1.60 (1.56–1.62) mm; CL. 0.29 (0.28–0.32) mm.

Carapace (Fig. 3A, B). Rostrum longer.

Antennule (Fig. 3D). Peduncle with 8 and 6 setae.

Antenna (Fig. 3E). Scale 2-segmented.

Mandibles (Fig. 3F). Left mandible with 2 spines (lacinia mobilis) between molar and incisor processes; right mandible with spine at corresponding site.

Maxillule (Fig. 3G). Unchanged.

Maxilla (Fig. 3H). Unchanged.

First maxilliped (Fig. 3I). Unchanged.

Second maxilliped (Fig. 3J). Unchanged.

Third maxilliped (Fig. 3K). Unchanged.

Pereiopod 1 (Fig. 3L). Basis with simple seta; endopod 4-segmented, with 0, 0, 2, 1 setae; exopod with 4 terminal natatory setae.

Pereiopods 2–3. Unchanged.

Pereiopod 5 (Fig. 3L). Endopod 5-segmented, with 0, 0, 0, 0, 1 setae; dactylus elongated, sharply pointed, with 4 distal denticles facing mouthparts.

Abdomen (Fig. 3A, B). Sixth somite now differentiated from telson; posterolateral margin acute.

Telson and uropod (Fig. 3C). Telson with 7 + 7 marginal setae; posterior width slightly greater than anterior width. Uropod free: endopod rudimentary; exopod with 6 plumose setae.

Fourth zoea
Fig. 4

Duration. 3–4 days.

TL. 1.65 (1.62–1.67) mm; CL. 0.34 (0.27–0.36) mm.

Carapace (Fig. 4A, B). Unchanged.

Antennule (Fig. 4D). Proximal segment of peduncle with 10 plumose setae; outer flagellum with 3 aesthetascs, 2 plumose setae, and simple seta.

Antenna (Fig. 4E). Unchanged.

Mandibles (Fig. 4F). Unchanged.

Maxillule (Fig. 4G). Unchanged.

Maxilla (Fig. 4H). Basial endite with 4 + 5 setae.

First maxilliped (Fig. 4I). Unchanged.

Second maxilliped (Fig. 4J). Unchanged.

Third maxilliped (Fig. 4K). Basis with 2 setae; endopod 5-segmented, with 0, 0, 0, 2, 2 setae.

Pereiopod 1 (Fig. 4L). Basis with 2 simple setae.

Pereiopods 2–4. Unchanged.

Pereiopod 5 (Fig. 4M). Unchanged.

Abdomen (Fig. 4A, B). Unchanged.

Telson and uropod (Fig. 4C). Telson narrower, with 4 + 4 marginal setae; posterior width slightly narrower than anterior width. Uropod developed: endopod with 8 plumose setae; exopod with 12 plumose setae.

Discussion

There are larval descriptions for 17 species in seven genera of Alpheidae from the Indo-West Pacific (Yang & Kim 2002). The larval descriptions of *Alpheopsis garricki* Yaldwyn, 1971 and *Betaeopsis aequimanus* (Dana, 1852) (see Packer 1985) are not sufficiently informative for comparisons. However, useful comparison of early zoeas is possible between the remaining genera: *Alpheus* Fabricius, 1798, *Athanas, Automate* De Man, 1888, *Synalpheus* Bate, 1888, and *Vexillipar* Chace, 1988. The zoeas of species of these latter five genera can be distinguished from each other by the setation of the endopods of the maxillule, the maxilla, and the second maxilliped. In zoeas of species of *Athanas, Alpheus,* and *Vexillipar,* the endopod of the maxilla has 1 + 2 setae, while in those of *Automate* and *Synalpheus* the endopod is furnished with 0 + 4 and 2 + 3 setae, respectively. Zoeas of species of *Athanas* are readily distinguished from those of *Alpheus* and *Vexillipar* by having two setae on the endopod of the maxillule,

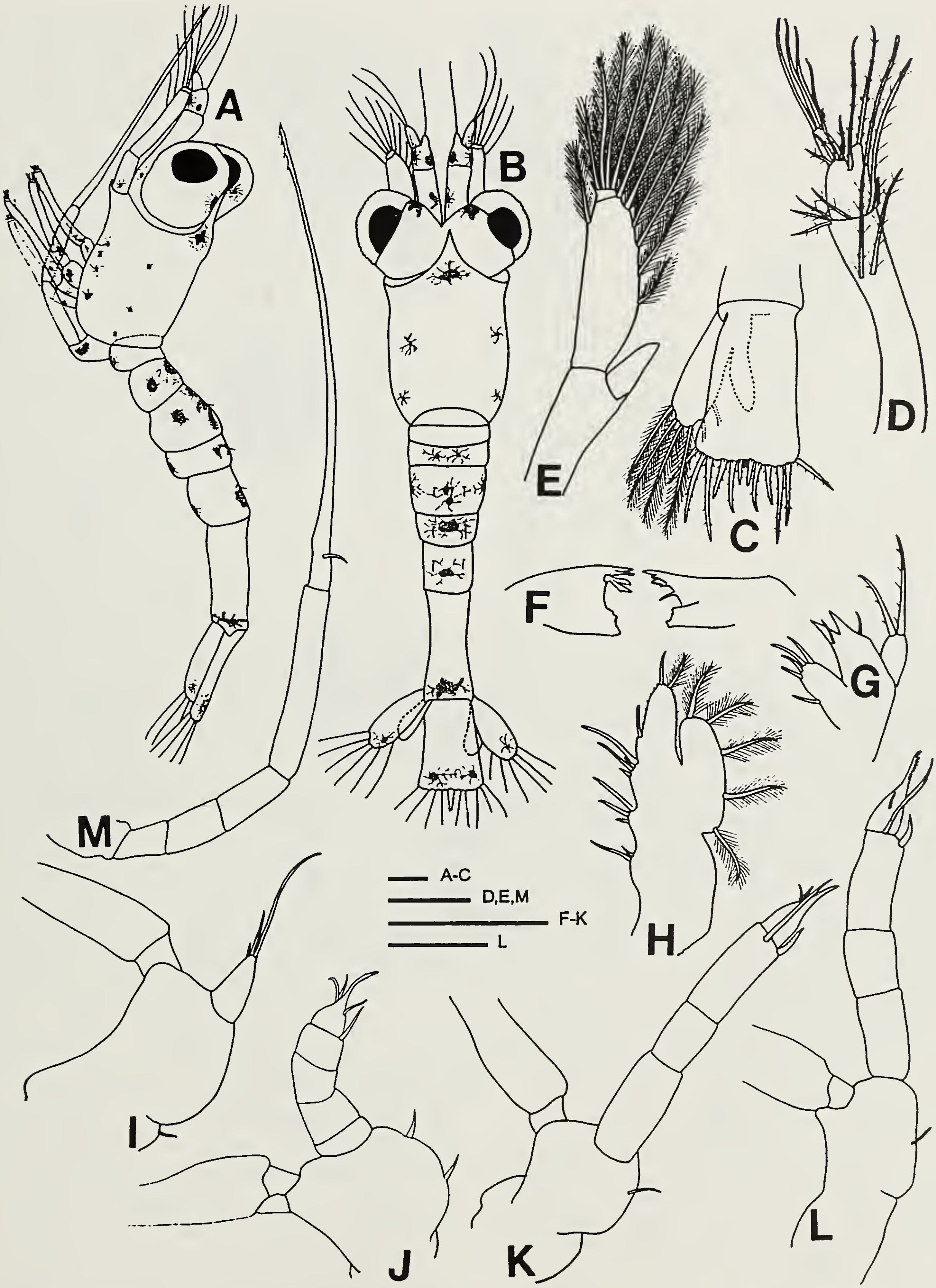

Fig. 3. Third zoea of *Athanas parvus* De Man, 1910. A, habitus, lateral view; B, habitus, dorsal view; C, telson and uropod, dorsal view; D, antennule; E, antenna; F, mandibles; G, maxillule; H, maxilla; I, first maxilliped; J, second maxilliped; K, third maxilliped; L, pereiopod 1; M, pereiopod 5. Exopod shown truncated in I–L. Scale bars = 0.1 mm.

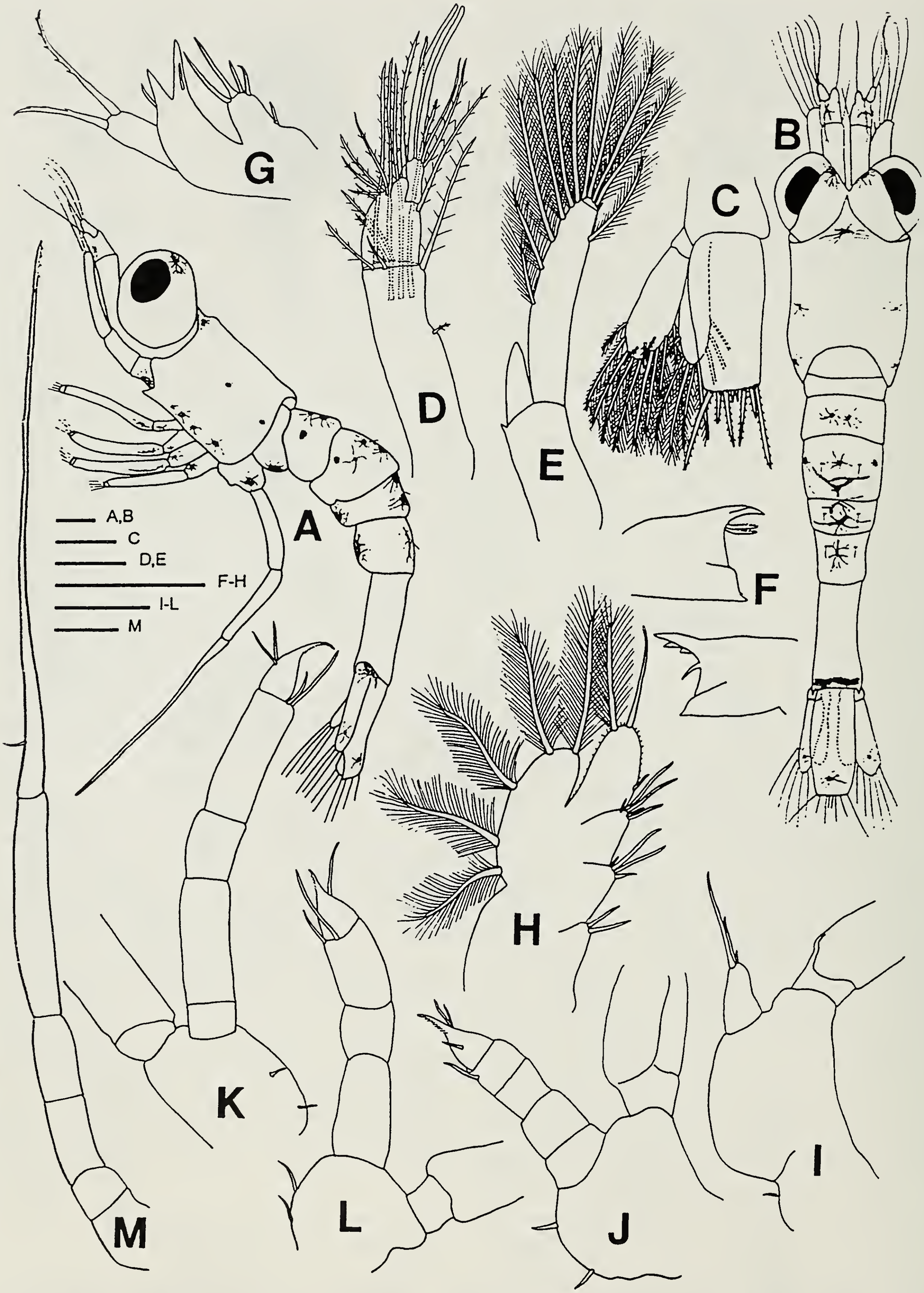

Fig. 4. Fourth zoea of *Athanas parvus* De Man, 1910. A, habitus, lateral view; B, habitus, dorsal view; C, telson and uropod, dorsal view; D, antennule; E, antenna; F, mandibles; G, maxillule; H, maxilla; I, first maxilliped; J, second maxilliped; K, third maxilliped; L, pereiopod 1; M, pereiopod 5. Exopod shown truncated in I–L. Scale bars = 0.1 mm.

and an unarmed proximal segment of the endopod of the second maxilliped.

Lebour (1932) pointed out that the differences between the larvae of *Athanas* and *Alpheus* were the length of the dactylus of the endopod of the third maxilliped in the second zoea, and the number of the exopods of the pereiopods in later stage zoeas. The dactylus of the endopod of the third maxilliped in the second zoea of *Athanas dimorphus* Ortmann, 1894 (see Bhuti et al. 1977), *A. parvus* (present study), and *Synalpheus tumidomanus* (Paulson, 1875) (see Bhuti et al. 1977) is never elongated; in species of *Alpheus* the dactylus is long, although it becomes short in the third zoea (see Yang & Kim 2002). The second zoea of *Betaeus truncatus* Dana, 1852 and *B. emarginatus* (H. Milne Edwards, 1837) (see Albornoz & Wehrtmann 1997) has the dactylus of the endopod of the third maxilliped elongated. The length of the dactylus of the endopod of the third maxilliped is, therefore, an important character of the second zoea distinguishing the larvae of *Athanas* and *Synalpheus* from those of *Alpheus* and *Betaeus*. However, it is not possible at this time to distinguish the second zoea of *Athanas* from that of *Automate dolichognatha* De Man, 1888 (see Bhuti et al. 1977) and *Vexillipar repandum* Chace, 1988 (see Saito et al. 1998) because larval descriptions of both species are limited to the first stage.

Except for *Periclimenes pandionis* Holthuis, 1951, larvae of the Alpheidae and the Palaemonidae are characterized by both the lack of a proximal endite on the maxilla, and the lack of an outer seta on the base of the maxillule, in all zoeal stages. Moreover, the flexure of the third abdominal somite in the first zoea of *Athanas* also occurs in larvae of palaemonid species of the subfamily Pontoniinae, e.g., *Coralliocaris graminea* (Dana, 1852) and *Harpiliopsis beaupresii* (Audouin, 1826) (see Gurney 1938, the latter as *Harpilius beaupresii*), and *P. pandionis* (see Gore et al. 1981). As suggested by Gurney (1938), these larval characters support the view that the Alpheidae are closely related to the Palaemonidae.

Acknowledgments

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Literature Cited

Albornoz, L., & I. S. Wehrtmann. 1997. Descripción y clave de los primeros estadíos larvales de camarones carídeos (Decapoda: Hippolytidae, Alpheidae, Rhynchocinetidae) de aguas costeras de Chile.—Investigaciones Marinas, Valparaíso 25:121–133.

Audouin, J. V. 1826. Explication sommaire des planches de Crustaceés de l'Égypte et de la Syrie, publiées par Jules-Cèsar Savingy, membre de l'Institut: offrant un expose des caractères naturelles des genres, avec la distinction des espèces. Pp. 77–98 *in* J.-C. Savingy, ed., Description de l'Égypte, Histoire Naturella, Paris 1 (4).

Banner, D. M., & A. H. Banner. 1973. The alpheid shrimp of Australia Part I. The lower genera.—Records of the Australian Museum 28:291–385.

Bate, C. S. 1888. Report on the Crustacea Macrura collected by the H.M.S. "Challenger" during the years 1873–76.—Report on the Scientific Results of the Voyage of H.M.S. "Challenger" during the Years 1873–76 24:1–942.

Bhuti, G. S., S. Shenoy, & K. N. Sankolli. 1977. Laboratory reared alpheid larvae of the genera *Automate*, *Athanas*, and *Synalpheus* (Crustacea, Decapoda, Alpheidae). Pp. 588–600 *in* Proceedings of the Symposium on Warm Water Zooplankton, Special Publication, National Institute of Oceanography, Goa, India.

Bourdillon-Casanova, L. 1960. Le méroplancton du golfe de Marseille: les larves de Crustacés Décapodes.—Recueil des Travaux de la Statation Marine d'Endoume 30:1–286.

Chace, F. A., Jr. 1988. The caridean shrimps (Crustacea, Decapoda) of the Albatross Philippine expedition, 1907–1910. Part V. Family Alpheidae.—Smithsonian Contributions to Zoology 466:1–99.

Coutière, H. 1897. Note sur quelques alphéidés nouveaux ou peu connus rapporteés de Djibouti (Afrique Orientale).—Bulletin du Muséum d'Histoire Naturelle 3:233–236.

Dana, J. D. 1852. Conspectus Crustaceorum quae in Orbis Terrarum circumnavigatione, Carolo Wilkes e Classe Republicae Foederatae Duce, lexit et descripsit.—Proceedings of the Academy of Natural Sciences of Philadelphia 1852: 10–28.

Fabricius, J. C. 1798. Supplementum entomologiae systematicae. Hafniae, 572 pp.

Gore, R. H., C. L. V. Dover, & J. R. Factor. 1981. Studies on decapod Crustacea from the Indian River region of Florida. XVIII. Rediscovery of *Periclimenes* (*Periclimenes*) *pandionis* Holthuis, 1951 (Caridea, Palaemonidae) with notes on the males and zoeal stages.—Crustaceana 40(3):253–265.

Gurney, R. 1927. Zoological results of the Cambridge expedition to the Suez Canal. Report on the larvae of the Crustacea Decapoda.—Transactions of the Zoological Society of London 22:231–286.

———. 1938. The larvae of the decapod Crustacea. Palaemonidae and Alpheidae.—Great Barrier Reef Expedition 1928–29, Scientific Reports 6: 1–60.

Holthuis, L. B. 1951. A general revision of the Palamonidae (Crustacea, Decapoda, Natantia) of the Americas. I. The subfamilies Euryrhynchinae and Pontoniinae.—Allan Handcock Foundation, Occasional Paper 11:1–332.

Kurian, C. V. 1956. Larvae of decapod Crustacea from the Adriatic Sea.—Acta Adriatica 6:1–108.

Leach, W. E. 1814. Crustaceology. Pp. 28–36 *in* D. Brewster, ed., Edinburgh Encyclopedia, 7.

Lebour, M. V. 1932. The larval stages of the Plymouth Caridea. IV. The Alpheidae.—Proceedings of the Zoological Society of London 1932:463–469.

Milne Edwards, H. 1837. Histoire naturelle des Crustacés, Comprenant l'Anatomie, La Physiologie et la Classification de ces Animaux, 2: 532 pp.

Man, J. G. de. 1888. Berichat über die von Herrn Dr. J. Brock in indischen Archipel gesammelten Decapoden und Stomatopoden.—Archiv für Naturgeschichte 53(1):215–600.

———. 1910. Diagnoses of new species of macrurous decapod Crustacea from the "Siboga-Expedition".—Tijdschrift der Nederlandsche Dierkundige Vereeniging (2)11:287–319.

Ortmann, A. 1894. Crustaceen. Pp. 3–80 *in* R. Semon, ed., Zoologische Forschungreisen in Australien und dem malayischen Archipel.—V. Denkschriften Medizinisch Naturwissenschaftliche Gesellschaft zu Jena 8.

Packer, H. A. 1985. A guide to the larvae of New Zealand shallow water Caridea (Crustacea, Decapoda, Natantia).—Zoology Publications from Victoria University of Wellington 78:1–16.

Paulson, O. 1875. Podophtalmata i Edriophtalmata (Cumacea). Chast I in Izsledovaniya Rakoobraznykh krasnago moray s zametkami otnositel'no Rakoobraznykh drugikh morei. Kiev, 144 pp. [English translation: Por, F. D. 1961 Podophtalmata and Edriophtalmata (Cumacea). Part I in Studies on Crustacea of the Red sea with notes regarding other seas. Jerusalem, Israel, 164 pp.].

Saito, T., K. Nakajima, & K. Konishi. 1998. First zoea of a rare deep-sea shrimp *Vexillipar repandum* Chace, 1988 (Crustacea, Decapoda, Caridea, Alpheidae), with special reference to larval characters of the family.—Publications of the Seto Marine Biological Laboratory 38:147–153.

Sars, G. O. 1906. Post-embryonal development of *Athanas nitescens* Leach.—Archiv für Mathematik og Naturvidenskab 27:1–29.

Webb, G. E. 1921. The larvae of the Decapoda Macrura and Anomura of Plymouth.—Journal of the Marine Biological Association of the United Kingdom 12:385–425.

Williamson, D. I. 1967. Crustacea Decapoda: Larvae IV. Caridea, Families: Pandalidae and Alpheidae.—Fiches d'Identification du Zooplancton 109:1–5.

Williamson, H. C. 1915. VI. Crustacea Decapoda: Larven.—Nordisches Plankton (6)18:315–588.

Yaldwyn, J. C. 1971. Preliminary descriptions of a new genus and twelve new species of natant decapod Crustacea from New Zealand.—Records of the Dominion Museum 7(10):85–94.

Yang, H. J., & A. Anker. 2003. New records of alpheid shrimps (Decapoda, Caridea, Alpheidae) from Korea.—Korean Journal of Systematic Zoology 19(1):1–9.

———, & C. H. Kim. 2002. Early zoeas of two snapping shrimps *Alpheus digitalis* De Haan, 1850 and *Alpheus japonicus* Miers, 1879 (Decapoda, Caridea, Alpheidae) with notes on the larval characters of the Alpheidae.—Korean Journal of Biological Sciences 6:95–105.

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Morphological variation in glochidia shells of six species of *Elliptio* from Gulf of Mexico and Atlantic Coast drainages in the southeastern United States

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Abstract.—The genus *Elliptio,* with 36 currently recognized species, is the largest genus in the family Unionidae in North America. The genus is represented by two species, *Elliptio crassidens* and *E. dilatata,* in the Interior Basin and 34 species in drainages of the eastern Gulf of Mexico and Atlantic Coast. The paucity and variation of conchological characters in the genus *Elliptio* makes it extremely difficult to define species and determine relationships. We examined glochidia from six species of *Elliptio* in an effort to determine if there are useful characteristics for species level identification and/or characters for identification of species groups. *Elliptio* species were selected to represent different morphological groups from four drainages in the southeastern United States. The glochidia from *E. crassidens, E. dariensis, E. hopetonensis, E. icterina, E. shepardiana,* and *E. mcmichaeli* were qualitatively compared, using scanning electron microscopy, with each other and with descriptions of these and other *Elliptio* glochidia described in the literature. Two groups were identified. The *crassidens* group, including *E. crassidens, E. dariensis,* and *E. mcmichaeli,* had subtriangular glochidia with a triangular styliform hook extending from the ventral margin of the valve and rough exterior valve sculpturing. Adults of this group had wrinkled or corrugated sculpturing on the posterior slope of the shell. The *complanata* group, including *E. hopetonensis, E. icterina,* and *E. shepardiana,* had subelliptical glochidia with a broad flange extending the entire ventral margin and loose-looped exterior valve sculpturing. Adults of this group lack sculpturing on the posterior slope of the shell. Differences in glochidial morphometrics were found, however, additional work is needed to determine if they are reliable for species level identification.

The genus *Elliptio,* with 36 currently recognized species, is the largest genus in the family Unionidae in North America (Turgeon et al. 1998). In the Interior Basin, this genus is represented by two species, *E. crassidens* and *E. dilatata.* The remaining 34 species are found in eastern Gulf of Mexico and Atlantic Coast drainages. These 34 species are characterized by extreme morphological variation ranging from compressed lanceolate forms (e.g., *E. shepardiana*) to those that are oval and highly inflated (e.g., *E. hopetonensis*) (Burch 1975). The paucity of conchological characters and the extreme morphological variation exhibited by most species makes it difficult to identify species and determine relationships.

Clench & Turner (1956) characterized the genus *Elliptio* as "more confusing than any other in the Unionidae of North America"—a statement which unfortunately remains true today. As the validity of some *Elliptio* species has been questioned, and some will probably be found to be synonyms, it is also likely there are valid species that are not currently being recognized. This uncertainty has resulted in reluctance on the part of conservation agencies and organizations to take appropriate actions to provide protection for some species. At least one species, the winged spike, *E. nigella,* is considered to be extinct (Brim Box & Williams 2000), and another 22 have been assigned a national conservation status of endangered, threatened, or special concern (Williams et al. 1993). While most recognized species of *Elliptio* have declined, it is still possible to protect much of the diversity represented in this genus if action is taken in the near future. Once discrete taxonomic entities are identified and their distribution accurately delineated only then can conservation and management plans be implemented.

The shells of *Elliptio* are usually moderately to greatly elongated, dark olive brown to black, often rayed in juveniles, and lack sculpturing with the exception of wrinkles or corrugations on the posterior slope and umbos of some species. Nacre color varies from white and highly iridescent to all shades of pink and red to deep purple and violet. Soft parts are whitish to flesh colored. The eggs are white. Branchial papillae are present and usually simple but dendritic papillae may be present; anal papillae are also present. The mantle margin lacks papillae anterior to branchial aperture. The glochidia are expelled from the marsupium in compacted masses called conglutinates. All species of *Elliptio* utilize only the outer gills as marsupia (Britton & Fuller 1980).

The genus *Elliptio* has been diagnosed as having hookless or spineless glochidia (Ortmann 1912, Britton & Fuller 1980). However, we found hook-like structures on the ventral margin of the glochidia of some *Elliptio* glochidia. This hook-like structure, "pseudohook," is not like those described as a diagnostic character of the subfamily Anodontinae (Clarke 1981, 1985). The pseudohook is an expansion of the flange on the ventral margin and is completely covered with microstylets of a near uniform size.

The paucity of information on *Elliptio* glochidial morphology (Hoggarth 1999) and host fish determinations (Watters 1994) is surprising considering the widespread distribution of the genus, high diversity (36 taxa), and the number of species with populations large enough to be utilized for study. Most of the work has been done on the two Interior Basin species, *E. crassidens* and *E. dilatata,* and one Atlantic Coast species, *E. complanata.* The difficulty in the identification and uncertainty surrounding their distributional limits has likely contributed to the lack of glochidial morphology and host fish research for the Atlantic Coast and eastern Gulf species.

We examined glochidia from six species of *Elliptio* in an effort to determine if there are characters useful in species and/or group identification. The *Elliptio* species were selected to represent different morphological groups from four drainages in the southeastern United States. The glochidial valve shape, lateral view, micropoints, microstyle, valve sculpturing, and hinge ligament length of *E. crassidens, E. dariensis, E. hopetonensis, E. icterina, E. shepardiana,* and *E. mcmichaeli* were compared qualitatively, using scanning electron microscopy (SEM). These species were then compared with other *Elliptio* glochidia described in published literature. Shells of adult *Elliptio* were also evaluated using museum specimens and published descriptions to determine if there were characteristics useful in identifying species groups within the genus *Elliptio.*

Materials and Methods

Gravid females representing six species of *Elliptio* were collected by hand and SCUBA. The valves were gently pried open 1 cm and the soft parts were visually inspected for swollen gills, which is usually indicative of eggs or glochidia. Three species, *E. dariensis, E. hopetonensis,* and *E. shepardiana* were collected from the Altamaha River, Appling County, Georgia, on 21 Apr 1996. A single gravid *E. crassidens* was collected from Cooleewahee Creek, Baker County, Georgia, on 2 Apr 1997, and a single gravid *E. icterina* was collected from Worthingon Springs, Dixie County, Florida, on 21 May 1996. Fifteen *E. mcmichaeli* were collected from the Choctawhatchee River on 5 May 1986.

The gravid mussels were transported in coolers with ambient temperature creek water to the U.S. Geological Survey, Center for Aquatic Resources Studies, Gainesville, Florida, where they were held in 4-liter jars until they released their glochidia. Female mussels released their glochidia within two weeks of their capture date. All of the glochidia were collected from females that released their glochidia in captivity, except for *E. mcmichaeli.* Glochidia of *Elliptio mcmichaeli* were removed from specimens that had been fixed in a 10% buffered solution of formalin and stored in 70% ethanol. Glochidia collected alive were determined viable when a snapping response was observed after a few salt crystals were added to a small subsample of 50 to 100 individual glochidia (Zale & Neves 1982). The viable glochidia were stored in 70% ethanol and were later used to describe glochidial morphology using *SEM.*

Tissue inside the glochidial shell was removed by soaking them in a 5% sodium hypochlorite solution for about 10 minutes. The shells were then rinsed several times with tap water and preserved in 70% ethanol (Kennedy et al. 1991). Several hundred preserved shells were mounted on a double-sided sticky carbon tape, air dried for 15 minutes, coated with gold, and examined using *SEM.* Photos were taken of the valve (250–500×), flange region (300–3,000×), hinge ligaments (500–1,000×), and shell sculpturing (15,000–30,000×) of the glochidia from the six *Elliptio* species. The flange is defined as a flattened area along the ventral margin of glochidial valve with microstylets, often referred to as micropoints (small tooth-like projections located along the flange). Measurements of the glochidia were determined by averaging the height (dorsal to ventral edge), length (anterior to posterior edge) and dorsal margin (long edge) length measurements of the glochidia under a stereo microscope with an ocular micrometer (10×). The number of glochidia used to determine average measurements varied because some of the glochidia samples collected were small.

Shells of adult *Elliptio* in the Florida Museum of Natural History collection were examined to determine the presence or absence of wrinkled sculpturing on the posterior slope. This character ranges in its development from the obvious to the obscure and may be absent in some individuals. It is often best developed on the upper portion of the slope nearest the umbo, which is often eroded, obscuring or removing any trace of the sculpturing. We examined lots of *E. congarea, E. crassidens, E. dilatata, E. hopetonensis, E. dariensis, E. fraterna, E. mcmichaeli,* and *E. shepardiana* to evaluate this character.

Results

Glochidial shell descriptions.—Elliptio crassidens (Lamarck, 1819). Glochidium subtriangular (Fig. 1a) with a length of 134 ± 2.8 μm (130–138 μm), a height of 150 ± 6.9 μm (141–160 μm), and a hinge length of 85 ± 4.5 μm (80–92 μm) (Table 1). A triangular, styliform flange (hook), covered with microstylets, extends from the ventral aspect of each valve (Fig. 1b, f). Microstylets are arranged in complete vertical rows. The microstylets are longer toward the middle and ventral margins of the valve and smaller toward the distal edge and the lateral margins of the valve. Valve outline is asymmetric with the anterior margin slightly more expanded than the posterior margin (Fig. 1a). Ventral margin produced into a nipple-like extension giving the valve

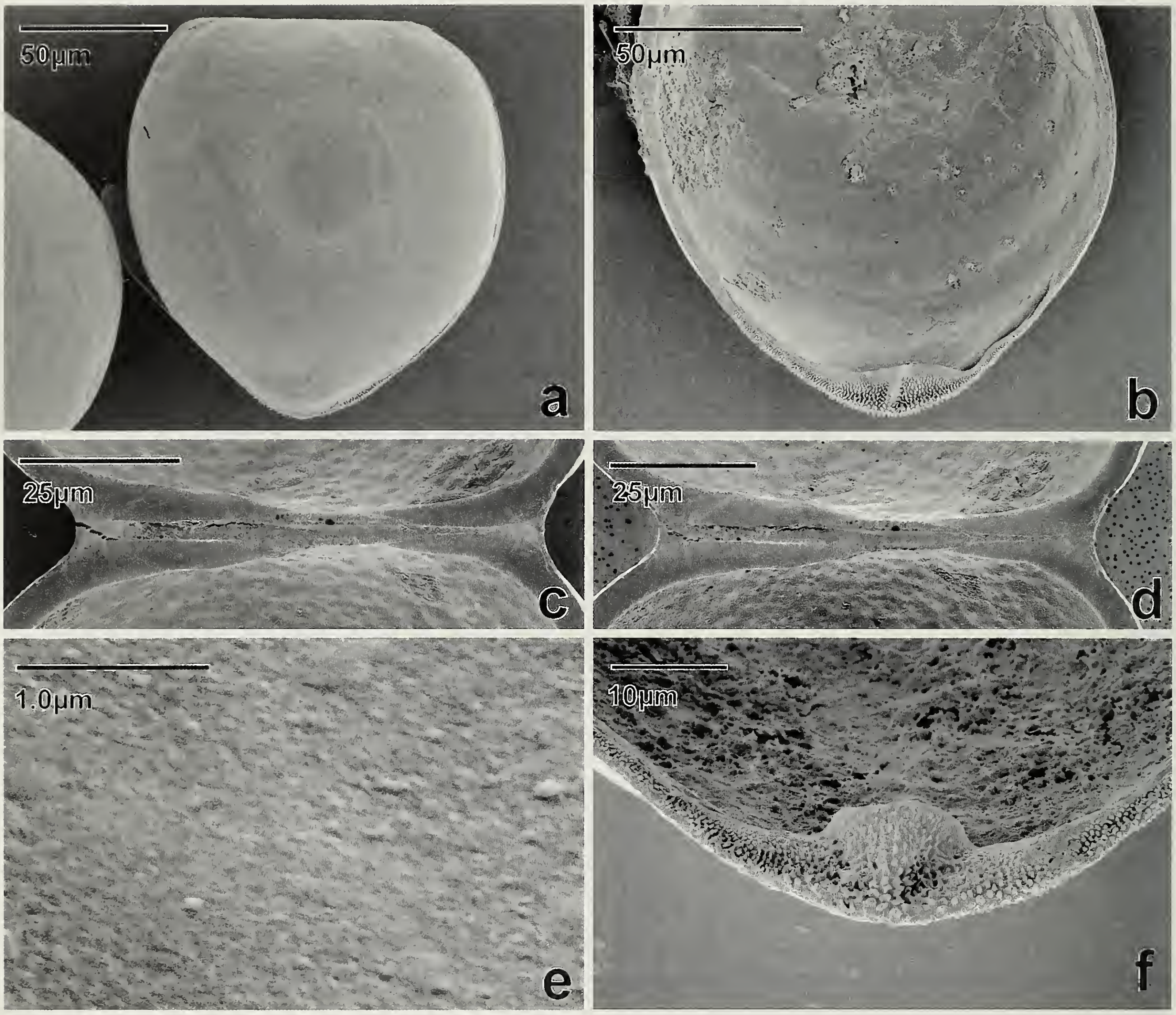

Fig. 1. *Elliptio crassidens.* Scanning electron micrographs (*SEM*) of glochidium. a, exterior valve; b, interior valve showing styliform hook; c, d, hinge; e, exterior valve sculpture; f, flange region with triangular styliform hook.

its triangular shape (Fig. 1a). The hinge ligament is located nearer the posterior margin (Fig. 1c, d) than the anterior margin and the valve is covered with rough exterior valve sculpturing (Fig. 1e).

Elliptio dariensis (Lea, 1842). Glochidium subtriangular (Fig. 2a) with a length of 142 ± 5.5 μm (135–151 μm), a height of 166 ± 6.4 μm (157–172 μm), and a hinge length of 88 ± 5.0 μm (81–95 μm) (Table 1). Anterior and posterior margins subequal with the anterior margin slightly more fully rounded than the posterior margin. Ventral margin produced into a nipple-like extension (Fig. 2a, e) giving the valve its triangular shape. A triangular, styliform flange extends from the ventral aspect of each valve to form a hook (Fig. 2b, e). Microstylets are arranged in complete vertical rows on the flange (Fig. 2b). They are larger toward the center of the flange and toward the proximate edge of the flange, and smaller near the distal edge of the hook and toward the lateral margins of the valve. The hinge ligament is slightly posterior of center (Fig. 2c) and the valve is covered with rough exterior valve sculpturing (Fig. 2d).

Elliptio mcmichaeli (Clench & Turner, 1956). Glochidium subtriangular (Fig. 3a) with a length of 146 ± 7.9 μm (130–157 μm), a height of 153 ± 5.8 μm (149–161 μm), and a hinge length of 90 ± 9.4 μm

Table 1.—The number of glochidia used to determine the measurements and standard deviation for six species of *Elliptio*.

Species	Number of glochidia	Number of females	Mean measurement ± *SD*		
			Length	Height	Hinge
(Triangular shape)					
Elliptio crassidens	6	1	134 ± 3 (130–138 μm)	150 ± 7 (141–160 μm)	85 ± 5 (80–92 μm)
Elliptio dariensis	6	3	142 ± 6 (135–151 μm)	166 ± 6 (157–172 μm)	88 ± 5 (81–95 μm)
Elliptio mcmichaeli	10	5	146 ± 8 (130–157 μm)	153 ± 6 (149–161 μm)	90 ± 9 (80–110 μm)
(Subelliptical shape)					
Elliptio hopetonensis	10	4	206 ± 6 (197–215 μm)	226 ± 4 (222–231 μm)	137 ± 5 (130–145 μm)
Elliptio icterina	10	1	203 ± 6 (195–215 μm)	216 ± 11 (195–234 μm)	141 ± 9 (125–148 μm)
Elliptio shepardiana	10	2	241 ± 3 (238–245 μm)	284 ± 6 (279–295 μm)	148 ± 6 (140–160 μm)

(80–110 μm) (Table 1). Anterior and posterior margins subequal with the anterior margin slightly more fully rounded than the posterior margin. The ventral margin is produced into a nipple-like point (Fig. 3a–c) giving the valve a triangular appearance. Extending from the ventral margin of each valve is a triangular, styliform hook (collapsed in Fig. 3c). Microstylets cover the hook in complete vertical rows. The microstylets are longer near the center of the hook and become smaller laterally where they intergrade into micropoints (Fig. 3c). The hinge ligament is located slightly posterior of center (Fig. 3d) and the valve is covered with rough exterior valve sculpturing (Fig. 3c).

Elliptio hopetonensis (Lea, 1838). Glochidium depressed subelliptical (Fig. 4a) with a length of 206 ± 5.8 μm (197–215 μm), a height of 226 ± 3.9 μm (222–231 μm), and a hinge length of 137 ± 5.0 μm (130–145 μm) (Table 1). Anterior and posterior margins equal, but only slightly rounded to a more fully rounded ventral margin (Fig. 4a). A broad flange extends from the ventral margin (Fig. 4b). This flange is covered with microstylets in complete vertical rows (Fig. 4d). These microstylets are larger near the midpoint of the ventral margin and grade into micropoints laterally. The dorsal margin is straight, long, and the hinge ligament is located much nearer the posterior than the anterior margin (Fig. 4c). The surface of the valve is covered with loose-looped exterior valve sculpturing (Fig. 4e).

Elliptio icterina (Conrad, 1834). Glochidium depressed subelliptical (Fig. 5a) with a length of 203 ± 6.4 μm (195–215 μm), a height of 216 ± 10.5 μm (195–234 μm), and a hinge length of 141 ± 8.8 μm (125–148 μm) (Table 1). Anterior and posterior margins equally, but only slightly rounded to a more fully rounded ventral margin. A wide ventral flange extends from the margin (Fig. 5b). The flange is covered in microstylets, (Fig. 5b, d) which are longer near the midpoint of the flange and grade into micropoints laterally. The dorsal margin is straight with the hinge ligament located much nearer to the posterior margin of the valve (Fig. 5c). Loose-looped exterior valve sculpturing covers the exterior surface of each valve (Fig. 5e) and that sculpturing can even be seen extending onto the surface of the microstylets on the flange (Fig. 5d).

Elliptio shepardiana (Lea, 1834). Glochidium subelliptical (Fig. 6a) with a length

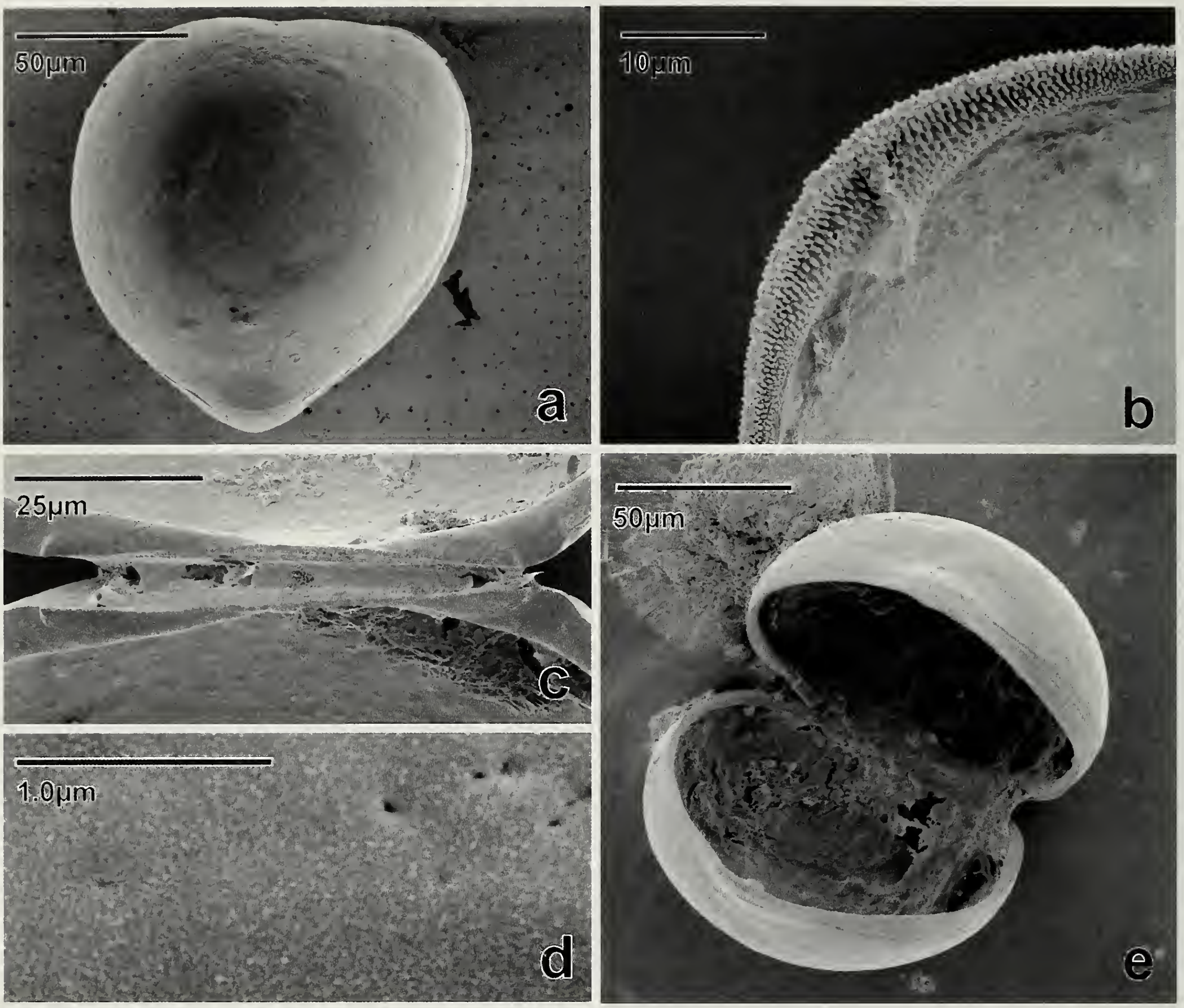

Fig. 2. *Elliptio dariensis. SEM* of glochidium. a, exterior valve; b, interior valve showing styliform hook; c, hinge; d, surface sculpturing; e, internal view.

of 241 ± 3.3 µm (238–245 µm), a height of 284 ± 5.8 µm (279–295 µm), and a hinge length of 148 ± 6.3 µm (140–160 µm) (Table 1). Anterior and posterior margins more or less equal and only slightly rounded. The ventral margin is strongly arched and supports a wide ventral flange (Fig. 6b). The ventral flange is widest near the middle of the ventral margin and tapers to both anterior and posterior margins. The flange supports numerous microstylets arranged in complete vertical rows which grade into micropoints distally on the flange and laterally toward the anterior and posterior margins of the flange (Fig. 6c, d). The hinge is straight and the hinge ligament is positioned nearest the posterior margin of the valve (Fig. 6c). Loose-looped valve sculpturing covers the exterior surface of each valve (Fig. 6e), and this sculpturing is seen extending onto the ventral flange and covering the microstylets (Fig. 6d).

Adult shell morphology.—Elliptio crassidens is widespread in the Interior Basin and eastward along the Gulf Coast from the Amite River in Louisiana to the Ochlockonee River drainage in Florida (Brim Box & Williams 2000). Populations in the Apalachicola and Ochlockonee have been referred to as a distinct subspecies, *E. incrassatus.* However, this taxon is generally not recognized as valid. *Elliptio crassidens* is large (length of 150 mm) and has a moderate to thick shell with a prominent pos-

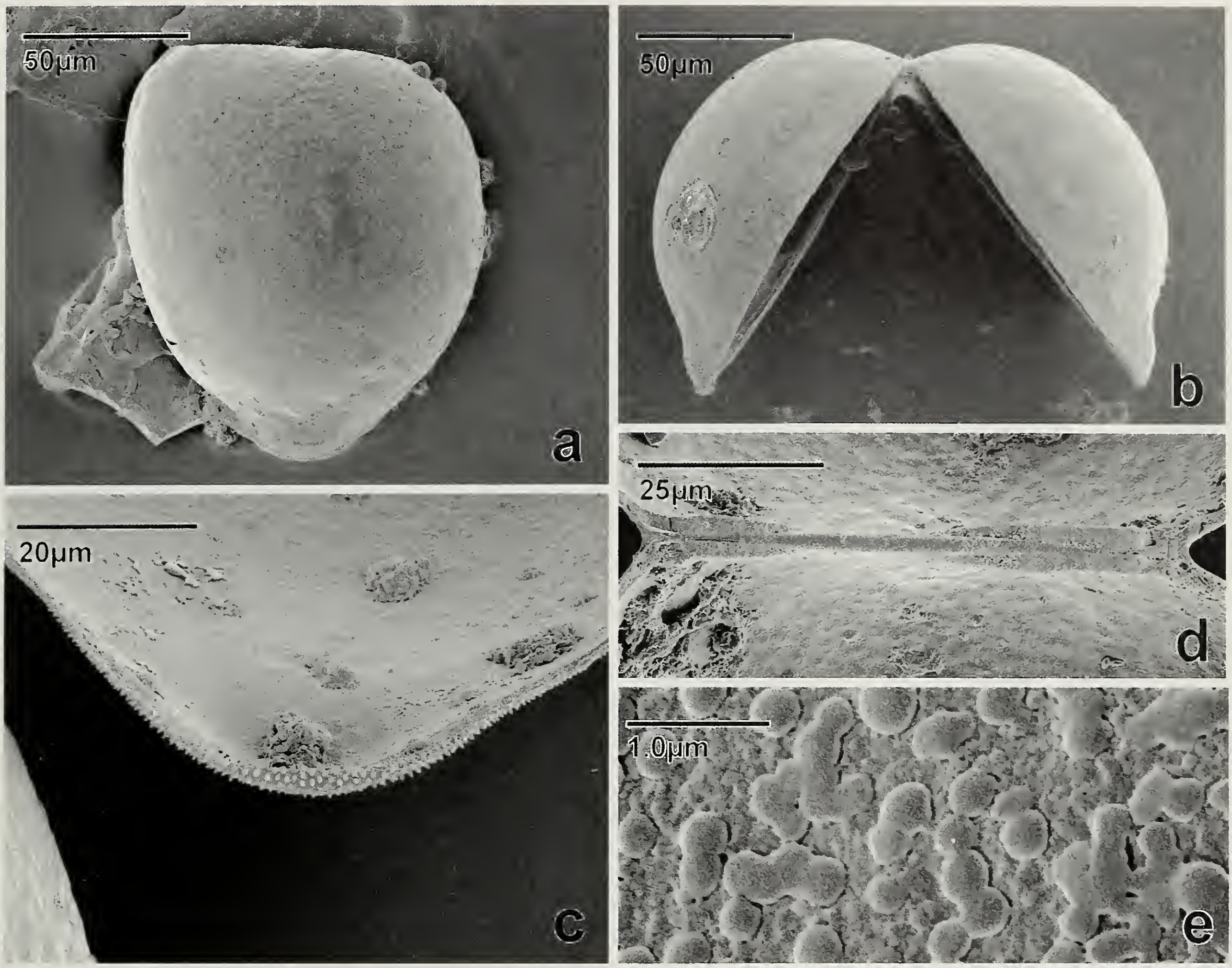

Fig. 3. *Elliptio mcmichaeli. SEM* of glochidium. a, exterior valve; b, side view of valve; c, flange; d, hinge; e, exterior valve sculpture.

terior ridge. It typically has sculpturing on the posterior slope consisting of distinct wrinkles or corrugations.

Elliptio dariensis is endemic to the Altamaha River drainage, including the Ohoopee and Ocmulgee rivers in Georgia. Johnson (1970, 1972) considered the distribution of this species to extend southward into the St. Johns River system in peninsular Florida. The shell is thin, large (length to 135 mm), and moderately inflated. The posterior ridge is well defined with a broad posterior slope. Similar to *E. crassidens,* the posterior slope typically has sculpturing in the form of numerous wrinkles.

Elliptio mcmichaeli is endemic to the Choctawhatchee River system (Gulf of Mexico drainage) in Alabama and Florida. The shell is thin, moderately large (>110 mm in length), with a poorly developed biangulated posterior ridge. The posterior slope is broad, somewhat concave, with sculpturing in the form of wrinkles that radiate from the posterior ridge across the slope to the dorsal margin.

Elliptio hopetonensis is endemic to the Altamaha River drainage in Georgia. The shell is moderately thin and large (155 mm in length). The posterior ridge is broad and rounded dorsally, but terminates in a biangulation near the ventral margin. The posterior slope is broad, somewhat concave, and lacks any wrinkled or corrugated sculpturing.

Elliptio icterina is found in coastal drainages from the Escambia River system in Alabama and Florida, east to peninsular Florida and north on the Atlantic Slope to

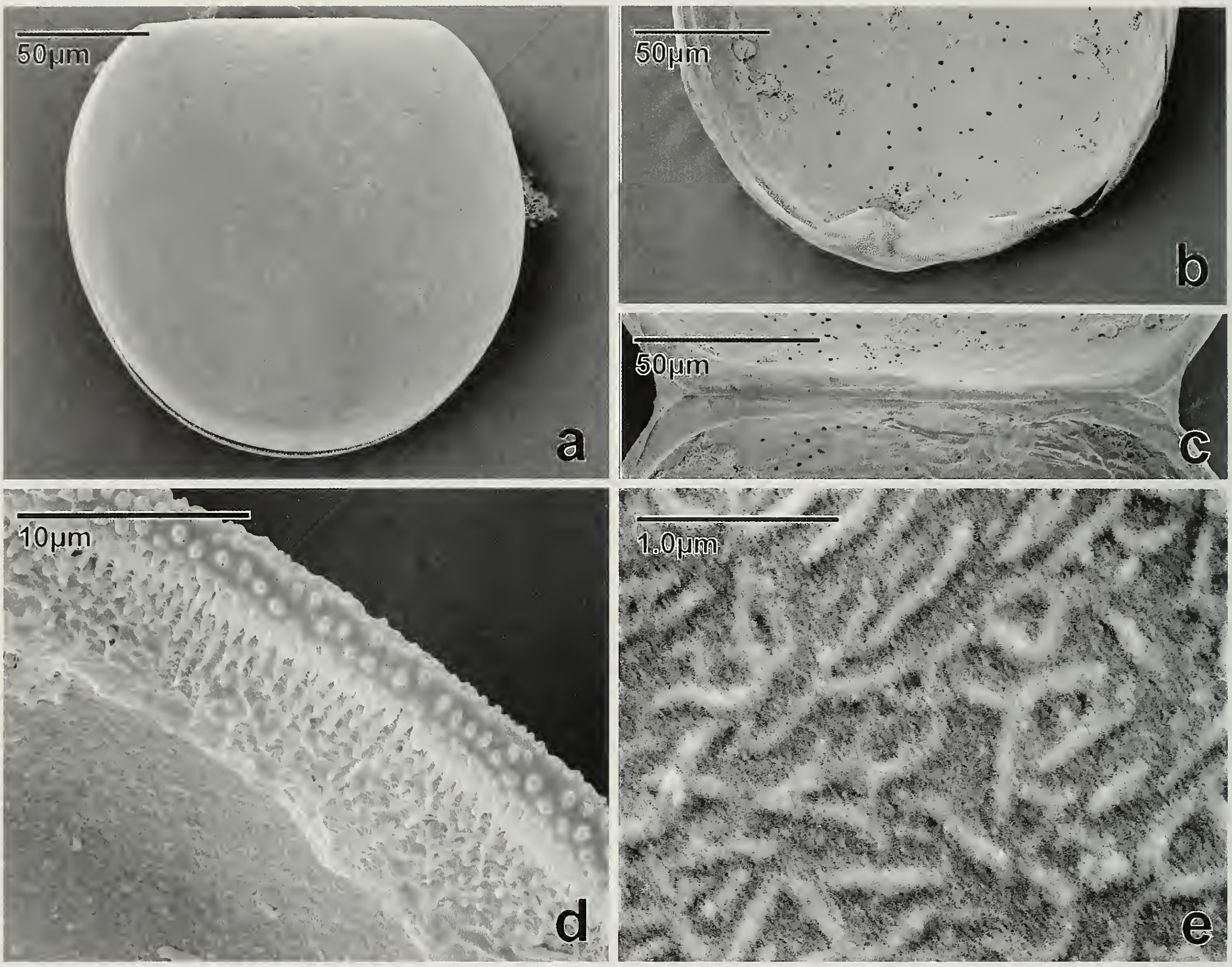

Fig. 4. *Elliptio hopetonensis. SEM* of glochidium. a, exterior valve; b, interior valve showing expanded flange of ventral margin; c, hinge; d, flange region showing rows of microstylets; e, exterior valve sculpture.

White Oak River in North Carolina (Johnson 1970). The shell of *E. icterina* is moderately compressed and small (length to approximately 85 mm). The posterior ridge is low, somewhat rounded, with a broad posterior slope. Wrinkled sculpturing is absent from the posterior slope.

Elliptio shepardiana is endemic to the Altamaha River system in Georgia, including the Ocmulgee, Oconee, and Ohoopee rivers. The shell is long (length to 190 mm), moderately compressed, rounded anteriorly, and somewhat pointed posteriorly. The posterior ridge is broadly rounded with a secondary ridge above it, which often results in a slight biangulation at the posterior end. The posterior slope is devoid of wrinkled sculpturing.

Discussion

Based on glochidial and adult shell morphology of the six species described above we have identified what appears to be two clades within the genus *Elliptio.* While the six species represent less than 20% of the genus, the nature and consistency of the characters would appear to be indicative of two distinct groups. As glochidia of the remaining 28 species of *Elliptio* are examined it should be easy to assign them to one of the two groups described above. It is also possible that one or more additional clades may be found in the remaining 26 species of Atlantic Coast and eastern Gulf of Mexico drainage *Elliptio.*

Elliptio crassidens *group.*—The glochidium of *Elliptio crassidens* was first figured

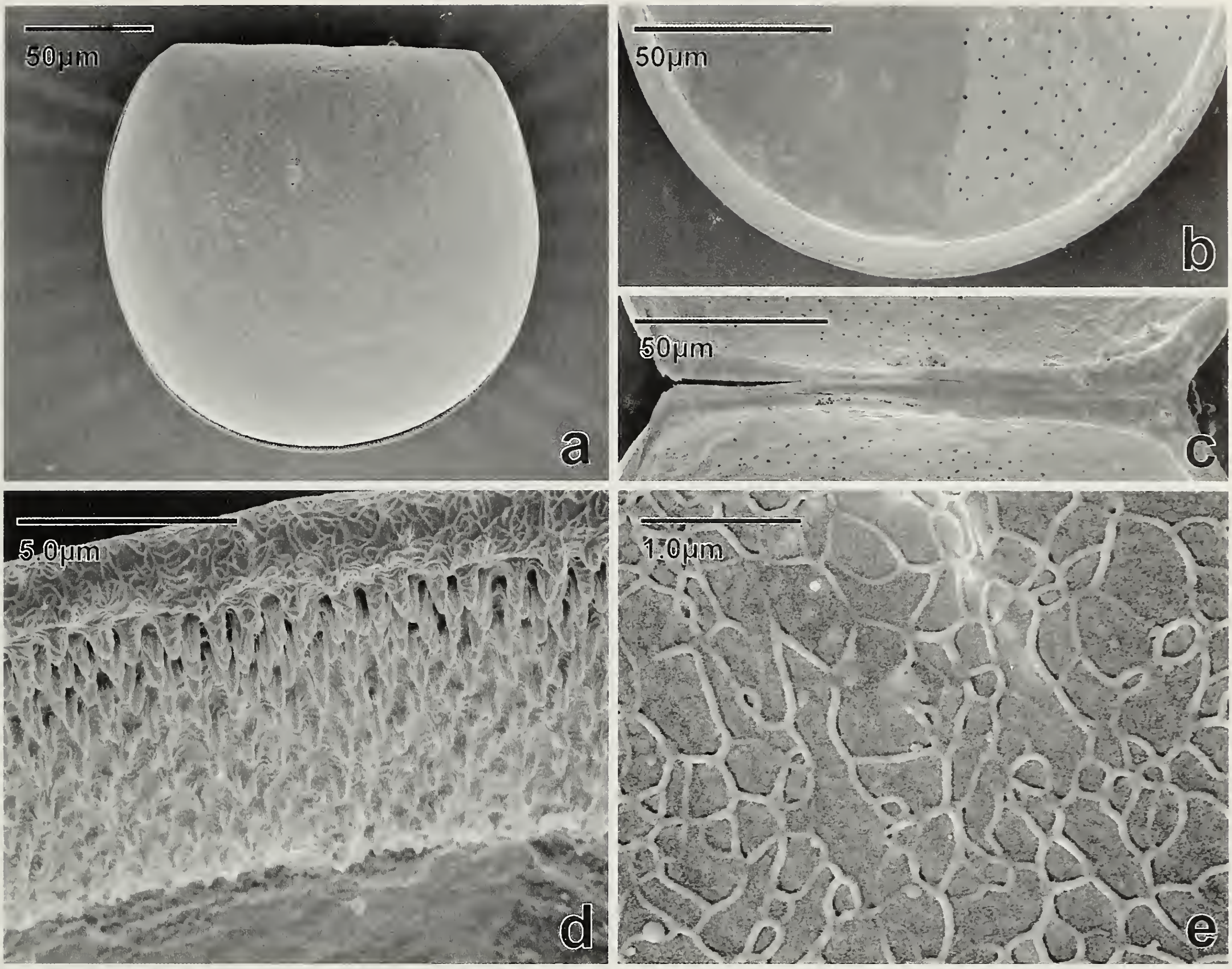

Fig. 5. *Elliptio icterina. SEM* of glochidium. a, exterior valve; b, interior valve; c, hinge; d, flange showing microstylets; e, exterior valve sculpture.

(Ortmann 1911) and subsequently described (Ortmann 1912) illustrating its subtriangular shape (Fig. 6, plate 89, page 346–347). Ortmann (1912) and Utterback (1915–1916) described the glochidium as small, suboval, without hooks. Ortmann and Utterback gave identical dimensions of 0.13 by 0.15 mm in length and height, respectively. Likewise, other reports (Surber 1912, 1915; Coker et al. 1921) generally describe the glochidium of *E. crassidens* (or its synonyms) as small, suboval, and spineless or hookless. Surber (1915) described the glochidium as subtriangular and somewhat intermediate between that of *Alasmidonata calceola* (= *viridis*) and *Quadrula* (= *Fusconaia*) *ebena.* He did not identify the glochidium of *E. crassidens* as having a hook on the ventral margin and he gave the size of this glochidium as larger, 0.15 by 0.16 mm.

We found the glochidium of *Elliptio crassidens* to be subtriangular with a definite hook-like structure at the terminus of the ventral margin. While our measurements generally agree with those of Ortmann and Utterback, their description does not mention the presence of a "hook." It is possible that they did not see the hook due to lack of magnification. The glochidial shells of the *crassidens* group were the only Lampsiline-Amblemine species observed to possess subtriangular glochidia (Hoggarth 1999).

The three species examined during this study which are assigned to the "*Elliptio crassidens*" group are *E. crassidens, E. dariensis,* and *E. mcmichaeli.* The glochidia

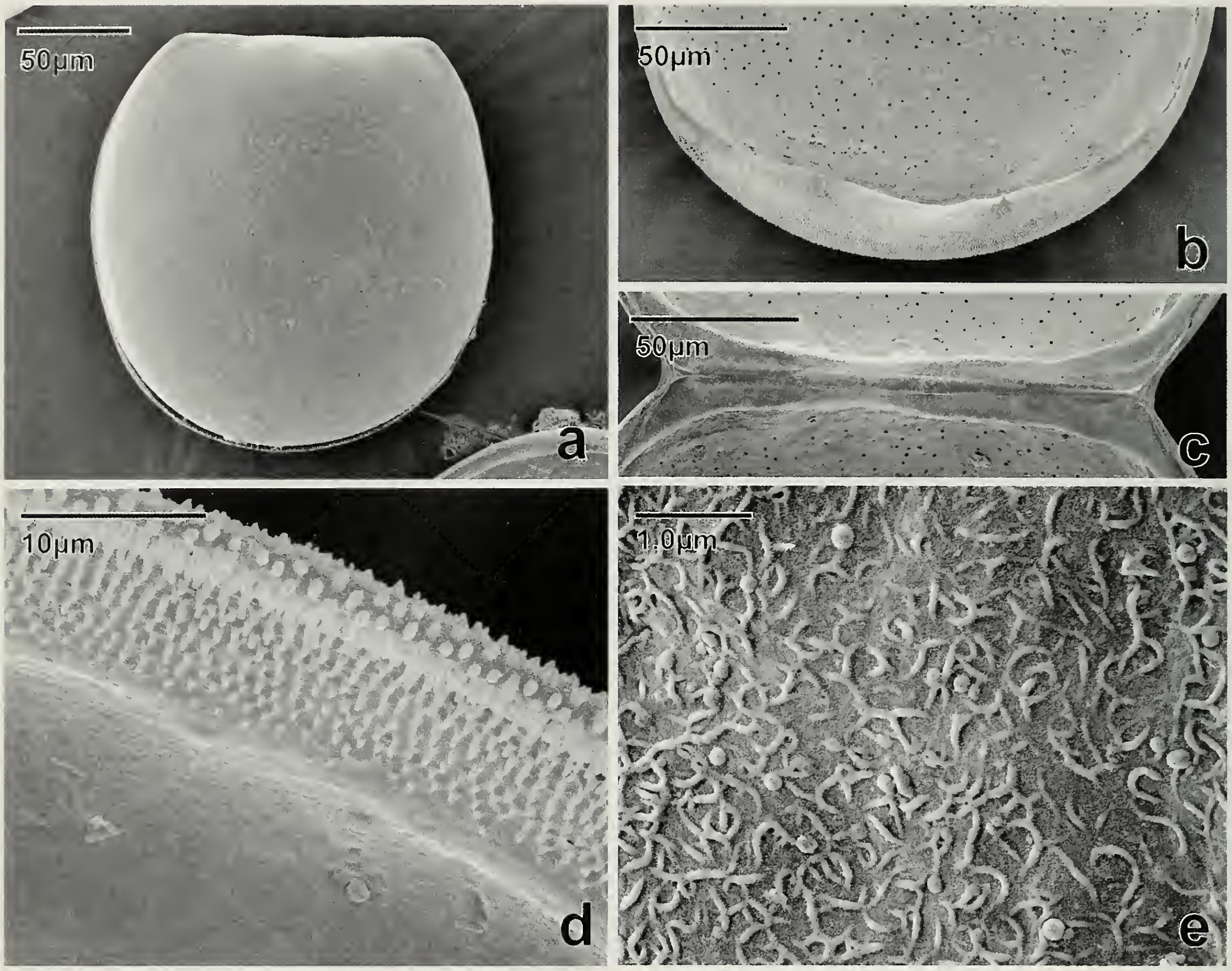

Fig. 6. *Elliptio shepardiana. SEM* of glochidium. a, exterior valve; b, interior valve showing wide ventral flange; c, hinge; d, flange region showing microstylets; e, exterior valve sculpture.

of these species share subtriangular valve shape, the presence of a small styliform hook at the terminus of the ventral margin, and rough exterior valve sculpturing. The shells of adults of this group also share the wrinkled or corrugated sculpturing on the posterior slope.

Elliptio complanata *group*.—The glochidium of *Elliptio dilatata* was first described by Lea (1863) (as *Unio gibbosus*). He described the glochidium as pouch-shaped, without hooks, and very much like that of *Ptychobranchus fasciolaris.* In fact, this glochidium is not similar to *fasciolaris,* except that both are subelliptical (Hoggarth 1999). Lefevre & Curtis (1910, 1912) provide the first measurements for this glochidium (0.22 by 0.19 mm in length and height) and Ortmann (1911, 1919) adds that the glochidium of *dilatata* is small, suboval, and without hooks.

Hoggarth (1999) described this glochidium as subelliptical with equal lateral margins and equal length and height (0.22 mm). He found that the glochidium was covered in loose-looped valve sculpturing and that lanceolate micropoints cover the narrow ventral flange. He noted that only Ortmann (1919) found the dimensions of this glochidium to be equal (0.20 mm), while Lefevre and Curtis (see above) described this glochidium as longer than high, and all other authors found this glochidium to have a length of 0.20 mm and a height of 0.22 mm (Ortmann 1912, Surber 1912, Utterback 1915–1916).

The light microscope photographs of the glochidia of *Elliptio complanata* in Matteson (1948) clearly show the shape to be subelliptical and hookless. The low magnification of the glochidial photographs is such that details of the sculpturing of the shell surface and micropoints are not visible. However, based on the subelliptical outline it appears to be identical to the glochidia of *E. dilatata, E. hopetonensis, E. icterina,* and *E. shepardiana.* These glochidia are all higher than long with *E. shepardiana* the largest and *E. icterina* and *E. hopetonensis* having almost identical dimensions with *E. complanata.* Furthermore, glochidia of all three species possess similar ventral margins (hookless and micropoint structure) and loose-looped external valve sculpturing, except for *E. complanata,* which is yet to be determined. These are characteristics they share with *E. dilatata* reported by Hoggarth (1999). Based on the subelliptical shape of the glochidia of *E. buckleyi* (D. S. Ruessler, pers. comm.), it also belongs to the *E. complanata* group. Adult shells of the species in the *E. complanata* group are characterized by the absence of sculpturing on the posterior slope.

Host fish.—Host fish data for most species of *Elliptio* is incomplete. Of the 36 currently recognized species in the genus, only five, *E. buckleyi, E. crassidens, E. complanata, E. dilatata* and *E. icterina,* have any published information on host fish (Watters 1994, Keller & Ruessler 1997). This may be explained in part by the fact that most species of *Elliptio* occur in Atlantic and eastern Gulf Coast streams where there are no commercially important species. The lack of economic interest resulted in very little research into the reproductive biology and host fish utilization by early mussel biologists, who concentrated their efforts on the commercially valuable Mississippi Basin species.

Howard (1914) reported finding *Elliptio crassidens* encysted on a skipjack herring, *Alosa chrysochloris.* This is the only host fish information available for *E. crassidens* (Watters 1994). The host fish for *E. dariensis* and *E. mcmichaeli* remain unknown. However, *E. dariensis* failed to produce juveniles when exposed to bluegill, *Lepomis macrochirus,* during a laboratory host fish experiment (C. O'Brien, pers. obs.). During the same laboratory host fish experiment, eastern mosquitofish, *Gambusia holbrooki,* and *L. macrochirus* were identified as host fishes for *E. hopetonensis,* but the largemouth bass, *Micropterus salmoides,* failed to produce juvenile mussels.

While the host for *Elliptio mcmichaeli* is unknown, there are data that suggest the host is a migratory fish. There are historic records of *E. mcmichaeli* from the upper Pea River, a tributary of the Choctawhatchee River, in southeast Alabama (Blalock-Herod, pers. comm.). The middle portion of the Pea River was impounded in the early 1900s, totally eliminating upstream access to native migratory fishes, including two migratory shads, Alabama shad, *Alosa alabamae,* and skipjack herring, *A. chryssoclorris.* During a recent survey of the entire watershed, *E. mcmichaeli* was found at numerous stations below the dam on the Pea River and elsewhere in the Choctawhatchee watershed, except it was absent in the Pea River above the dam (Blalock-Herod, pers. comm.). Since the Pea River above the dam currently supports a mussel community, which formerly included *E. mcmichaeli,* its absence today may be due to the lack of suitable migratory host fish that are blocked by the dam. Although circumstantial, we think this evidence strongly suggests a migratory host fish for *E. mcmichaeli.*

Matteson (1948) found yellow perch, *Perca flavescens,* as a host fish for *Elliptio complanata* via laboratory infestations and Wiles (1975) found *E. complanata* glochidia encysted on banded killifish, *Fundulus diaphanus.* Other fishes reported as hosts for *E. complanata* include green sunfish, *Lepomis cyanellus,* orangespotted sunfish, *L. humilis,* largemouth bass, *Micropterus salmoides,* and white crappie, *Pomoxis annularis* (Young 1911). Keller & Ruessler (1997) reported *L. machrochirus, M. salmoides,* and Florida gar, *Lepisosteus platy-*

rhincus as host fishes for *E. buckleyi*. They also identified *L. macrochirus* and *M. salmoides* as the host fishes for *E. icterina*. These were the only fish species tested with *E. icterina* during their study. The host fish for *E. shepardiana* remains unknown. Host fishes for the spike, *E. dilatata*, include six fishes representing four families: flathead catfish, *Pylodictus olivaris*, and sauger, *Stizostedion canadense* (Howard 1914); gizzard shad, *Dorosoma cepedianum*, and white crappie, *P. annularis* (Wilson 1916); black crappie, *P. nigromaculatus*, and yellow perch, *Perca flavescens* (Clarke 1981).

Based on host fish information available, it is not possible to make any definitive statements regarding possible association between species groups of *Elliptio* and particular host fish usage. However, based on glochidial shell morphology and host fish information presented above, this could be the case. It appears that species of the *crassidens* group, triangular-shaped glochidia, may only use the highly migratory fishes of the genus *Alosa* (family Clupeidae), while species of the *complanata* group, subelliptical-shaped glochidia, may use a variety of fishes, 12 species representing 6 families. None of the host fishes used by the *E. complanata* group are highly migratory. If future host fish research confirms this pattern this would provide an additional characteristic to distinguish these two species groups of *Elliptio*. It would also suggest a very early evolutionary divergence within the genus *Elliptio*.

Species level identification for many species of the genus *Elliptio* remains problematic and their evolutionary relationships remain a mystery. The proper identification of mussel species is a very important part of any management plan. However, conchological differences may not be the only tool needed to identify species of the complex *Elliptio* group. More research is needed to explore the genetic and host fish usage differences between these two *Elliptio* groups identified and any other groups that might become apparent.

Literature Cited

Brim Box, J., & J. D. Williams. 2000. Unionid mollusks of the Apalachicola Basin in Alabama, Florida, and Georgia.—Bulletin of the Alabama Museum of Natural History 21:1–143.

Britton, J. C., & S. L. H. Fuller. 1980. The freshwater bivalve mollusca (Unionidae, Sphaeriidae, Corbiculidae) of the Savannah River Plant, South Carolina. Savannah River Plant Publication SRO-NERP-3. Department of Energy, Aiken, South Carolina, 37 pp. + 5 maps.

Burch, J. B. 1975. Freshwater Unionacean clams (Mollusca: Pelecypoda) of North America, Rev. edition. Malacological Publication, Hamburg, Michigan, 204 pp.

Clarke, A. H. 1981. The tribe Alasmidontini (Unionidae: Anodontinae), part I. *Pegias, Alasmidonta,* and *Arcidens*.—Smithsonian Contributions to Zoology 326:1–101.

———. 1985. The tribe Alasmidontini (Unionidae: Anodontinae), part II: *Lasmigona* and *Simpsonaias*.—Smithsonian Contributions to Zoology 399:1–75.

Clench, W. J., & R. D. Turner. 1956. Freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River.—Bulletin of the Florida State Museum of Biological Sciences 1:97–239.

Coker, R. E., A. F. Shira, H. W. Clark, & A. D. Howard. 1921. Natural history and propagation of fresh-water mussels.—Bulletin of the U.S. Bureau of Fisheries 37(1919–1920):77–181, 17 pls. Separately issued as Bureau of Fisheries Document 893.

Conrad, T. A. 1834. Descriptions of some new species of fresh water shells from Alabama, Tennessee, etc.—American Journal of Science and Arts 25: 338–343, 1 pl. [Reprinted in Sterkiana 9(1963): 49–50.]

Hoggarth, M. A. 1999. Descriptions of some of the glochidia of the Unionidae (Mollusca: Bivalvia).—Malacologia 41:1–118.

Howard, A. D. 1914. Experiments in propagation of freshwater mussels of the *Quadrula* group. Report of the U.S. Commissioner of Fisheries for 1913, Appendix IV, pp. 1–52. Issued separately as Bureau of Fisheries Document 801.

Johnson, R. I. 1970. The systematics and zoogeography of the Unionidae (Mollusca: Bivalvia) of the southern Atlantic Slope region.—Bulletin of the Museum of Comparative Zoology 140:263–449.

———. 1972. The Unionidae (Mollusca: Bivalvia) of peninsular Florida.—Bulletin of the Florida State Museum of Biological Science 16:181–249.

Keller, A. E., & D. S. Ruessler. 1997. Determination or verification of host fish for nine species of unionid mussels.—American Midland Naturalist 138:402–407.

Kennedy, V. S., S. C. Fuller, & R. A. Lutz. 1991. Shell hinge development of young *Corbicula fluminea* (Muller) (Bivalvia: Corbiculoidea).—American Malacological Bulletin 8:107–111.

Lamarck, J. B. P. A. 1815–1822. Histoire des Animaux sans Vertébres. 8 volumes.

Lea, I. 1834. Observations on the naïades; and descriptions of new species of that, and other families.—Transactions of the American Philosophical Society 5[New Series]:23–119, pls. 1–19.

———. 1838. Description of new freahwater and land shells.—Transactions of the American Philosophical Society 6[New Series]:1–154, pls. 1–24.

———. 1842. Description of new freahwater and land shells.—Transactions of the American Philosophical Society 8[New Series]:163–250, pls. 5–27.

———. 1863. Descriptions of the soft parts of one hundred and forty-three species and some embryonic forms of Unionidae of the United States.—Journal of the Academy of Natural Sciences, Philadelphia 5(N.S.):401–456.

Lefevre, G., & W. C. Curtis. 1910. Experiments in the artificial propagation of fresh-water mussels.—Bulletin of the U.S. Bureau of Fisheries 28(1908):615–626. Issued separately as Bureau of Fisheries Document No. 671.

———, & ———. 1912. Studies on the reproduction and artificial propagation of freshwater mussels.—Bulletin of the U.S. Bureau of Fisheries 30(1910):105–201. Issued separately as Bureau of Fisheries Document No. 756.

Matteson, M. R. 1948. Life history of *Elliptio complanatus* (Dillwyn, 1817).—American Midland Naturalist 40:690–723.

Ortmann, A. E. 1911. A monograph of the najades of Pennsylvania, parts I and II. Anatomical Introduction. The Systems of the North American Najades.—Memoirs of the Carnegie Museum 4: 279–347.

———. 1912. Notes upon the families and genera of the najades.—Annuals of the Carnegie Museum 8:222–365.

———. 1919. A monograph of the naiades of Pennsylvania, part III. Systematic account of the genera and species.—Memoirs of the Carnegie Museum 8:1–385.

Surber, T. 1912. Identification of the glochidia of freshwater mussels. Report of the U.S. Commissioner of Fisheries for 1912 and Special Papers, pp. 1–10. Issued separately as Bureau of Fisheries Document No. 771.

———. 1915. Identification of the glochidia of freshwater mussels. Report of the U.S. Fisheries for 1914, Appendix V, pp. 1–9. Issued separately as Bureau of Fisheries Document No. 813.

Turgeon, D. D. et al. 1998. Common and scientific names of aquatic invertebrates from the United States and Canada: mollusks, 2nd edition. American Fisheries Society Special Publication 26, 526 pp.

Utterback, W. I. 1915–1916. The naiades of Missouri.—American Midland Naturalist 4(3):41–53, (4):97–152, (5):181–204, (6):244–273, (7):311–327, (8):339–354, (9):387–400, (10):432–464.

Watters, G. T. 1994. An annotated bibliography of the reproduction and propagation of the Unionoidea (primarily of North America).—Ohio Biological Survey Miscellaneous Contributions No. 1, 158 pp.

Wiles, M. 1975. Parasites of *Fundulus diaphanus* (LeSueur) (Pisces: Cyprinodontidae) in certain Nova Scotian freshwaters.—Canadian Journal of Zoology 53:1578–1580.

Williams, J. D., M. L. Warren, Jr., K. S. Cummings, J. L. Harris, & R. J. Neves. 1993. Conservation status of freshwater mussels of the United States and Canada.—Fisheries 18:6–22.

Wilson, C. B. 1916. Copepod parasites of fresh-water fishes and their economic relations to mussel glochidia.—Bulletin of the U.S. Bureau of Fisheries 34:333–374. Issued separately as Bureau of Fisheries Document 824.

Young, D. 1911. The implantation of the glochidium on the fish.—University of Missouri Bulletin, Sciences Series 2:1–16.

Zale, A. V., & R. J. Neves. 1982. Fish hosts for four species of lampsiline mussels (Mollusca: Unionidae) in Big Moccasin Creek, Virginia.—Canadian Journal of Zoology 60:2535–2542.

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First fossil record of a finfoot (Aves: Heliornithidae) and its biogeographical significance

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Abstract.—The distal end of a humerus from the Lee Creek Mine in North Carolina is identified with the modern Neotropical species as *Heliornis* aff. *fulica* and provides the first fossil record for the family Heliornithidae. The fossil was determined to come from the Middle Miocene (14 Ma) Pungo River Formation based on sedimentary, preservational, and other lines of evidence. This in turn implies that *Heliornis* did not spread into South America until after the isthmian land connection about 3 Ma and that the interchange of Heliornithidae between the Old and New World probably took place through the Northern Hemisphere in the Paleogene.

The finfoots or sungrebes (Heliornithidae) comprise 3 species, each in a monotypic genus, that are placed in the traditional avian order Gruiformes. On the basis of both morphology and molecular data, the family is probably most closely related to rails, Rallidae (Houde 1994, Livezey 1998). The species are sedentary, swimming and diving birds of forested streams in the tropics of the New World, Africa, and southeast Asia. Hitherto, there has been no fossil record of the family (Brodkorb 1967, Houde 1994, Tommy Tyrberg, Kimstadt, Sweden, pers. comm.). This has changed with the discovery of the distal end of a humerus in spoil piles of the Lee Creek phosphate mine near Aurora, North Carolina, from which tens of thousands of fossil bird bones had been recovered previously (Olson and Rasmussen 2001).

Systematics

Class Aves
Order Gruiformes
Family Heliornithidae

The fossil humerus is characterized by its short, curved overall shape, which at first suggests a medium-sized species of one of the "higher" orders of arboreal land birds (Olson 1985). It differs from all of these in the very rounded, hemispherical condylus ventralis (ulnar condyle), which contrasts markedly with the narrow, transversely ovoid, and often proximally flattened condyle in the traditional orders Coliiformes, Trogoniformes, Coraciiformes, Piciformes, and Passeriformes. Another highly distinctive character is the extension of the epicondylus ventralis distally well past the margins of the distal condyles. These two features (Fig. 1) in combination with the overall size and shape are diagnostic of the Heliornithidae.

Genus *Heliornis* Bonnaterre, 1791

There is little in the way of qualitative differences in the distal half of the humerus to distinguish the three genera of Heliornithidae. *Podica* and *Heliopais* differ from *Heliornis* and the fossil in their much larger size, so that on size and geographical grounds it is more reasonable to assign the fossil to the type-genus of the family, *Heliornis.*

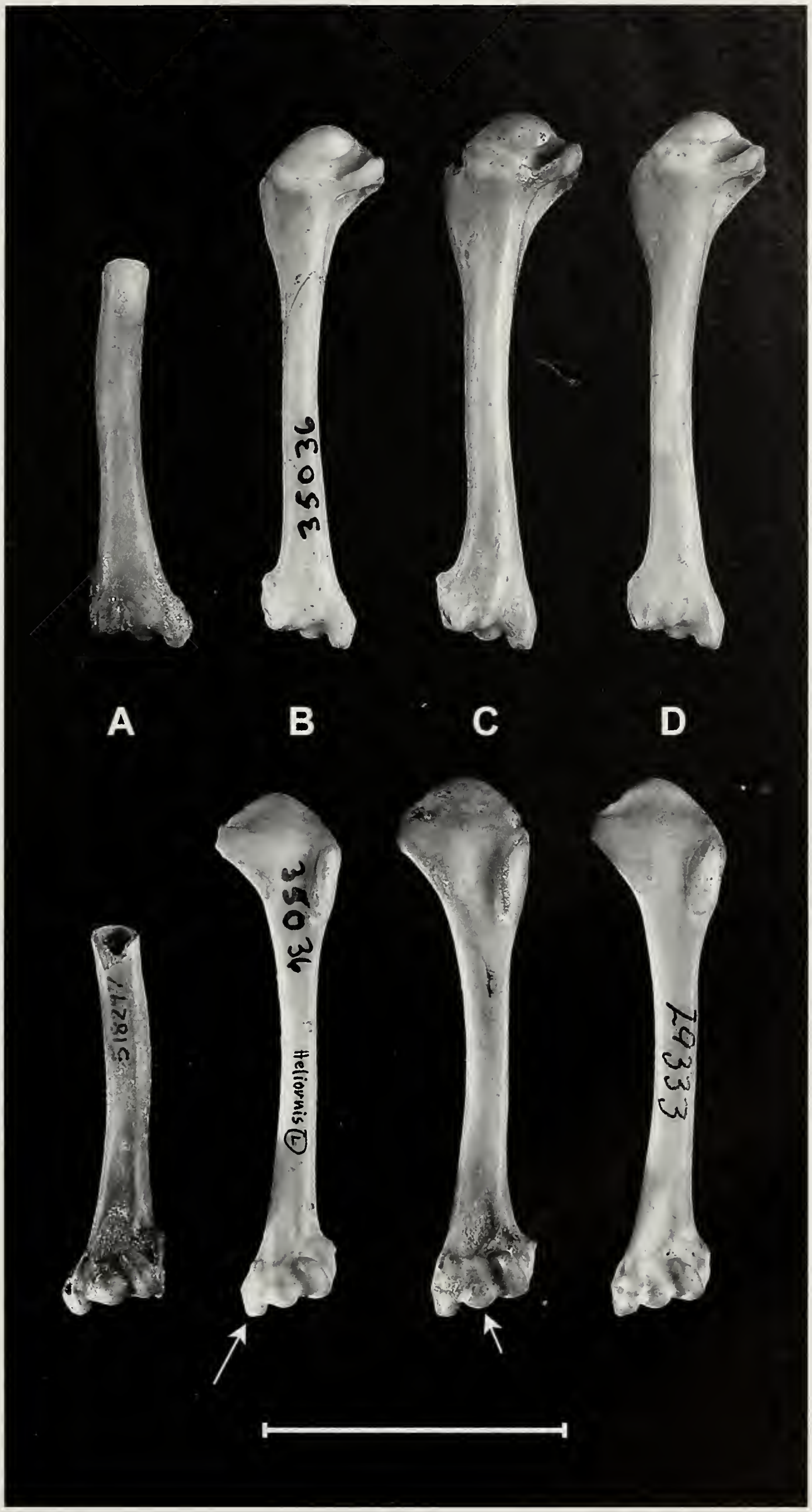

Fig. 1. Left humeri of *Heliornis* (top row anconal view; bottom row palmar view): A, fossil *Heliornis* aff. *fulica* from Lee Creek Mine, North Carolina; B, C, modern *Heliornis fulica* (UF 38828 = PB 35036; USNM 321493; UF 33412 = PB 29333). The distally projecting epicondylus ventralis (long arrow) and the very rounded, hemispherical condylus ventralis (short arrow) are diagnostic features of the Heliornithidae.

Table 1.—Measurements (mm) of the humerus of modern *Heliornis fulica* (Heliornithidae) compared with fossil humerus of *Heliornis* aff. *fulica* (USNM 518297) from the Miocene of North Carolina.

	Heliornis fulica (N = 13) Range (mean) *SD*	*Heliornis* aff. *fulica* fossil
Distal width	6.2–7.0 (6.8) 0.24	6.9
Shaft width	2.4–3.2 (2.8) 0.19	3.2
Shaft depth	2.4–2.8 (2.6) 0.12	2.9

Heliornis aff. *fulica* (Boddaert, 1783)

Referred specimen.—Distal half of left humerus, National Museum of Natural History, Smithsonian Institution, USNM 518297, collected 13 June 2001 by Geoff Keel.

Locality.—Lee Creek Mine, south side of Pamlico River, near Aurora, Beaufort County, North Carolina (35°23′22″N, 76°47′06″W).

Horizon.—Pungo River Formation, Middle Miocene; Langhian stage, ca. 14 Ma (Gibson 1983). Fossil birds at the Lee Creek Mine come from deposits of two ages separated by an unconformity—the Middle Miocene Pungo River Fm and the Lower Pliocene Yorktown Fm (Olson and Rasmussen 2001). Assignment of the present fossil is based on several lines of evidence. It was recovered from a spoil pile that was topped by sediments of the Pungo River Fm; the preservation is excellent, the bone having a hard, shiny surface, unlike the etched appearance of many of the bones from the Yorktown Fm; blackish phosphatic sand characteristic of the Pungo River Fm was adherent to the fossil; and no strictly tropical elements occur in the Yorktown Fm but are known from the Pungo River and equivalent formations.

Comparisons.—In size, the fossil falls within the range of modern *Heliornis fulica* in two measurements, though near the high end, and is very slightly larger in shaft depth (Table 1). Although the shaft of USNM 518297 is thus generally somewhat more robust, this character varies considerably in the modern series. Qualitatively, the only apparent differences are the somewhat more curved shaft, the relatively larger condylus ventralis, and the wider sulcus musculo humerotricipitalis in the fossil. These differences may indicate slight differences in flight capability, but given the time disparity they are very minor. There is nothing in this single fossil to suggest that it represents a divergence from the lineage leading to the modern species *Heliornis fulica.* This perception might be altered if more of the skeleton were available.

Discussion

The Heliornithidae are among the classic examples pantropical families of birds (Fig. 2), such as barbets (Capitonidae) and trogons (Trogonidae), which likewise occur in the Old and New World tropics, but not in Australasia. This pattern invites the question of whether their distribution is the result of vicariant events or dispersal.

Modern *Heliornis fulica* extends practically throughout the Neotropics from Mexico to northern Argentina. The fossil record from North Carolina is more than 2600 air line km NE of the nearest occurrence of *Heliornis* in Veracruz, Mexico. The specimen comes from deposits about 14 Ma, whereas a land connection was established between North and South America only about 3 Ma, with mammalian overland dispersal having taken place in both directions before about 2.5–2.8 Ma (Marshall 1985).

Finfoots, being weak fliers and with very specific aquatic habitat requirements, are almost certainly incapable of dispersing over an oceanic barrier. Thus, the evidence now at hand suggests that *Heliornis fulica* must have spread into South America from North America after the isthmian land connection formed, and perhaps considerably after that, given that it has no recognized subspecies (Hellmayr and Conover 1942).

Heliornis differs from other finfoots in having altricial young that are carried in axillary marsupia (Houde 1994), so that it is

Fig. 2. Modern distribution of the three species of Heliornithidae (solid) and the only fossil record (arrow). Map modified from Fisher and Peterson (1964).

presumably the most derived of the three species. Houde (1994) found *Heliornis* to be closer genetically to the Asian genus *Heliopais,* than to the African genus *Podica,* although the quality of the DNA of *Heliopais* may have been equivocal. He also found that the degree of genetic divergence between *Heliornis* and the African genus *Podica* was too small to be compatible with a trans-Atlantic origin of the former and subsequent separation via sea-floor spreading, which would have necessitated a common distribution across what is now Africa and South America well back into the Cretaceous (Smith et al. 1994).

Assuming finfoots to require tropical environments and to be incapable of crossing marine water barriers, interchange of finfoots between the Old and New World must have taken place early in the Tertiary across the Northern Hemisphere, because *Heliornis* was already in North America by the Middle Miocene. There is abundant floral and faunal evidence for interchange between North America and both Europe and Asia in the Eocene (Manchester 1999) and in particular for invasions of mammals from Asia in the late Eocene (Woodburne and Swisher 1995). Thus, fossils of Heliornithidae might be anticipated in Paleogene deposits of the northern continents.

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Literature Cited

Brodkorb, P. 1967. Catalogue of fossil birds. Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes).—Bulletin of the Florida State Museum, Biological Sciences 11:99–220.

Fisher, J., and R. T. Peterson. 1964. The world of birds. Doubleday and Co., Garden City, New York, 288 pp.

Gibson, T. G. 1983. Stratigraphy of Miocene through Lower Pleistocene strata of the United States Central Atlantic Coastal Plain; pp. 35–80 *in* C. E. Ray, ed., Geology and paleontology of the Lee Creek mine, North Carolina, I.—Smithsonian Contributions to Paleobiology 53.

Hellmayr, C. E., and B. Conover. 1942. Catalogue of birds of the Americas, part 1, number 1. Zoological Series Field Museum of Natural History 13, 636 pp.

Houde, P. 1994. Evolution of the Heliornithidae: reciprocal illumination by morphology, biogeography and DNA hybridization (Aves: Gruiformes).—Cladistics 10:1–19.

Livezey, B. C. 1998. A phylogenetic analysis of the Gruiformes (Aves) based on morphological characters, with an emphasis on the rails (Rallidae).—Philosophical Transactions of the Royal Society B 353:2077–2151.

Manchester, S. R. 1999. Biogeographical relationships of North American Tertiary floras.—Annals of the Missouri Botanical Garden 86:472–522.

Marshall, L. G. 1985. Geochronology and land-mammal biochronology of the transamerican faunal interchange. Pp. 49–85 *in* F. G. Stehli and S. D. Webb, eds., The great American biotic interchange. Plenum Press, New York, 532 pp.

Olson, S. L. 1985. The fossil record of birds. Pp. 9–238 *in* D. S. Farner, J. R. King, and K. C. Parkes, eds., Avian biology, vol. 8. Academic Press, New York, 256 pp.

Olson, S. L., and P. C. Rasmussen. 2001. Miocene and Pliocene birds from the Lee Creek Mine, North Carolina. Pp. 233–365 *in* C. E. Ray and D. J. Bohaska, eds., Geology and paleontology of the Lee Creek mine, North Carolina, III.—Smithsonian Contributions to Paleobiology 90.

Smith, A. G., D. G. Smith, and B. M. Fussell. 1994. Atlas of Mesozoic and Cenozoic coastlines. Cambridge University Press, 99 pp.

Woodburne, M. O., and C. C. Swisher III. 1995. Land mammal high-resolution geochronology, intercontinental overland dispersals, sea level, climate, and vicariance. Pp. 335–364 *in* W. A. Berggren, D. V. Kent, M.-P. Aubrey, and J. Hardenbol, eds., Geochronology, time scales and global stratigraphic correlations.—SEPM (Society for Sedimentary Geology) Special Publication 54.

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The type specimen of *Anoura geoffroyi lasiopyga* (Chiroptera: Phyllostomidae)

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Abstract.—In 1868, Wilhelm Peters described *Glossonycteris lasiopyga,* based on a specimen provided by Henri de Saussure and collected in México. The type specimen was presumed to be among those housed in the collections of the Zoologisches Museum of the Humboldt Universität in Berlin, Germany. Our study of one of Saussure's specimens from México, discovered in the collections of the Museum d'Histoire Naturelle, Geneva, Switzerland, demonstrates that it and not one of the Berlin specimens is the holotype.

Henri de Saussure (Saussure 1993) wrote several reports on the animals he collected during his intensive explorations of central México at the middle of the 19th Century. Among Saussure's specimens, which included several mammals and birds he described as new to science (Baud 1977), was a bat he identified as *Anoura ecaudata* Geoffroy (Saussure, 1860). He described the specimen, provided some measurements, and said it occurred in temperate and warm regions of México. The specimen was deposited in the mammal collections of the Museum d'Histoire Naturelle in Genève, Switzerland.

The same specimen was redescribed by Peters (1868) as the basis of a new genus and species he named *Glossonycteris lasiopyga.* A translation of Peters' description follows:

B. Medial upper incisors smaller than outer ones; lower incisors deciduous [p. 364].
   a. Zygomatic arch developed.
      [. . . .]
   b. Zygomatic arch absent.
      6. *Glossonycteris* nov. gen.

Teeth: 3.3/3.3 1/1 2-2/2-2 1/1 3.3/3.3, molars having distinct W-shaped [p. 365] formation, the cingulum of the two next-to-last upper cheek teeth more developed. Interfemoral membrane very short, having hair on both sides, calcar very short. Tail?

On the only dried specimen that I was able to examine, through the kind efforts of Mr. H. de Saussure, there was no trace of tail to be seen, and it is probably absent, however this can only be determined with certainty from fresh or alcohol specimens. Both zygomatic arches were lacking on the skull and this appeared natural, but I am not entirely sure of this point since I have had no chance to examine an intact skull.

I. *Glossonycteris lasiopyga* n. sp. (Pl. fig. 2.)
   ?1844. *Choeronycteris peruana* Tschudi, *Fauna Peruana.* I. P. 71. Pl. 3. Fig. 1. 2.—*Archiv f. Naturgesch.* I. p. 247.
   1860. *Anoura ecaudata* Geoffroy, H. de Saussure, *Guèrin Rev. et Mag. Zool.* p. 81.

The specimen examined by Mr. de Saussure is the only one available to me for inspection, while *Choeronycteris peruana* Tschudi, which is perhaps identical with it, cannot be decided upon exactly, since Mr. Coulon of the Neuchatel Museum informs me that this species cannot be found among the Chiroptera given to the museum by Mr. von Tschudi. The description and drawing given in *Fauna Peruana* are not adequate for an exact opinion.

I give here the measurements of the dried specimen from Mexico, sent to me by Mr. de Saussure, as far as these could be determined.

Forearm	41
L. of 1 finger: mtcp. 3.0; 1st ph. 3.3; 2nd ph. 2.0	8.0
L. of 2 finger: mtcp. 32.3; 1st ph. 2.0	34.5

L. of 3 finger: mtcp. 39.5; 1st ph. 13.7; 2nd ph. 21.0; 3rd ph. 0.011; cartilage 3.7
L. of 4. fing. mtcp. 37.3; 1st ph. 1.0; 2nd ph. 13.3; cartilage 1.5
L. of 5. fing. mtcp. 33.0; 1st ph. 8.0; 2nd ph. 11.5; cartilage 1.5

Tibia	3.0
Foot	11.5
Calcar	3.0

Although there is no clear statement of the kind of specimen preservation, from Peters' (1868) text we know that he had at hand only one specimen. The specimen was a dried skin and nearly complete skull because his description of *Glossonycteris lasiopyga* contains diagnostic characters from both the skin and the skull, and he illustrated the skull as Fig. 2 in the accompanying Plate.

The dental formula Peters (1868) gave for *Glossonycteris* includes three upper and three lower incisors. However, *Anoura* has only two upper incisors on each side and lacks lower incisors. We interpret this discrepancy as indicating that Peters was attempting to provide a more complete dental formula that included the deciduous teeth. We reached this conclusion because Peters stated that the lower incisors were deciduous (see beginning sentence of translation) and, as evident from his Fig. 2, the type of *Glossonycteris lasiopyga* lacked lower incisors. Peters also indicated three upper and lower incisors in the dental formulae for *Lonchoglossa* Peters, 1868 (another junior synonym of *Anoura*) and for *Choeronycteris* Tschudi, 1844, a taxon that also has only two upper incisors on each side and lacks lower incisors.

Clearly, the specimen described by Peters is the holotype. Thomas (1893) treated *Glossonycteris lasiopyga* as a junior synonym of *Anura* [= *Anoura*] *geoffroyi.* Sanborn (1933) was the first to use the current name combination *Anoura geoffroyi lasiopyga* to refer to the subspecies whose range he gave as México, Guatemala, and El Salvador. He gave the type locality as southern México.

Carter and Dolan (1978) discussed two specimens of *Anoura geoffroyi lasiopyga* that Carter examined at the Zoologisches Museum der Humboldt-Universität zu Berlin (ZMB), Berlin, Germany. These specimens, an adult male (ZMB 3565) and an adult whose sex is unknown (ZMB 3564), had been collected in Cuernavaca, Morelos, México, by Boucard in August 1866. Both specimens are labeled as "typus", and were considered by Carter and Dolan (1978) to be syntypes. However, a review of the museum catalog (handwritten by Peters himself), and of the specimens labels (secondary ones), resulted in no confirmation of any kind of type status (R. Angermann, in litt., 28 November 2000).

These specimens are not syntypes because Peters (1868) mentioned only the specimen he borrowed from Saussure and which had been collected before 1860. Dr. Renate Angermann (in litt., 28 November 2000) was kind enough to examine copies of two letters in the archives of the Zoologisches Museum der Humboldt-Universität from Wilhelm Peters to H. de Saussure. One is dated 28 December 1865, in which Peters requested the loan of six specimens collected in México, including the specimen Saussure (1860) had identified as *Anoura ecaudata.* The other five specimens were those described by Saussure as new: *Vespertilio mexicanus, Molossus aztecus, Stenoderma tolteca, Tylostoma mexicana,* and *Macrotus mexicanus.* The other letter is from March 1866, in which Peters said he was sending back the five specimens mentioned above with his opinion about their taxonomic status, and which he indicated as: *Vespertilio mexicanus* Sauss. = *V. lucifugus* Leconte; *Molossus aztecus* Sauss. = *Nyctinomus brasiliensis* Geoffroy; *Stenoderma tolteca* Sauss. = *Dermanura cinereum* Gervais; *Tylostoma mexicana* Sauss. = *Trachyops* (*Vamp.*) *cirrhosus* Spix; and *Macrotus mexicanus* Sauss. = *Macr. waterhousii* Gray. Apparently the specimen Saussure had identified as *Anoura ecaudata* was not returned at that time.

Recently, a nearly complete skull of *An-*

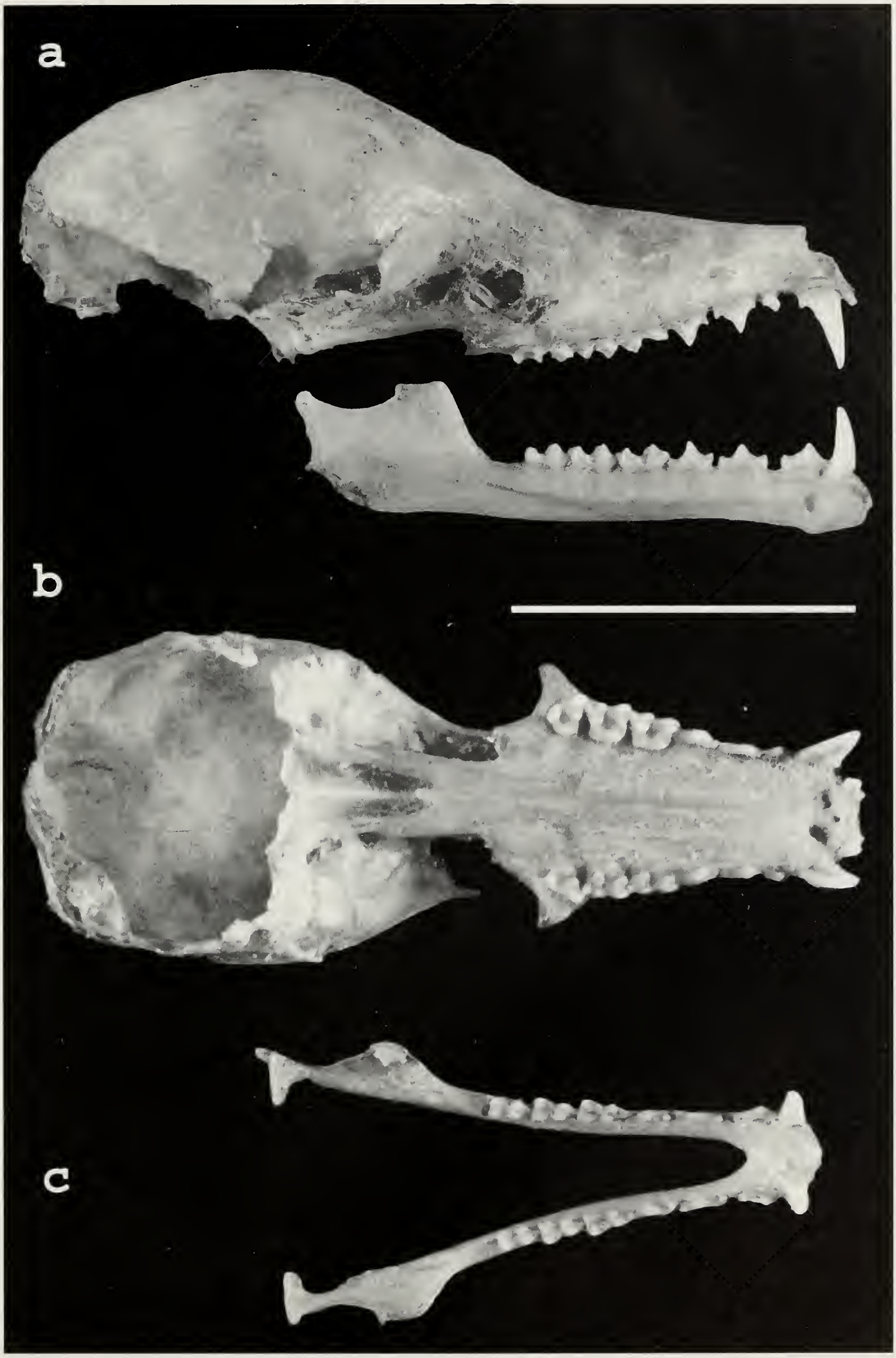

Fig. 1. Photographs of the cranium and mandibles of MHNG 515.88, holotype of *Anoura geoffroyi lasiopyga*: a) lateral view of cranium and mandible, b) ventral view of cranium, and c) dorsal view of mandible; horizontal bar = 10 mm.

oura geoffroyi was found in the mammal collections of the Museum d'Histoire Naturelle, Genève, Switzerland (Fig. 2). It is of an adult individual cataloged as MHNG 515.88 and bears a label linking it to Henri de Saussure. The skull is missing both bullae; part of the right temporal bone; and part of the exoccipital region including the basioccipital and basisphenoid. The dental formula is 2/0-1/1-3/3-3/3. The skull label contains the following information: *Obverse*—Museum Geneve/No. 515-88/Glossonycteris geoffroyi Gray/Localite Mexique, ach. Sumichrast. *Reverse*—Saussure 1860 VII L.49?/monto M.L [written in pencil and difficult to read].

Cranial measurements (in mm) are as follows: greatest length of skull, 24.8; interorbital breadth, 4.9; braincase breadth, 9.5; palate length, 13.2; maxillary toothrow length, 9.4; width across M2, 3.4; dentary length, 17.3; mandibular toothrow length, 9.7; condylocanine length, 16.6; condylomolar length, 6.6; coronoid height, 3.8; dentary depth below M1, 1.4; mandibular condyle length, 1.6.

Photographs (Fig. 1) of the skull and mandibles of this specimen essentially duplicate the illustrations that Peters (1868: Fig. 2 and 2b) provided of the holotype of *Glossonycteris lasiopyga*; although the skull appears to have had additional damage since the original description. The similarities, augmented by the label information, support our conclusion that specimen MHNG 515.88 is the holotype of *Glossonycteris lasiopyga* Peters, 1868. Although this specimen was not documented by Baud (1977) in his catalogue of type specimens at the Genève museum, it was recently identified as a potentially significant specimen by Claude Weber (pers. comm., 1999). To date, the skin has not been located.

We have been unable to determine the actual type locality of *Glossonycteris lasiopyga.* Saussure (1860:494) simply said the specimen came from ". . . les régions chaudes et tempérées. . . ." (warm and temperate regions) of México, and there is no further information in the museum catalogue. Saussure's field collector was François Sumichrast, and there is no information in Saussure's notes (Saussure 1993) suggesting that either he or Sumichrast collected in or near Cuernavaca, Morelos (the locality Carter and Dolan [1978] provided for the specimens they identified as syntypes in the Berlin museum), during Saussure's expedition to México. Sumichrast collected in Orizaba, Puebla, México City, Tampico, and in a few other small villages in between (Boucard 1884, Sumichrast 1881). Of course, Sumichrast also collected extensively at Santa Efigenia, his finca and famous collecting locality located in Oaxaca near the border with Chiapas. However collecting at this site did not begin until after 1867 following the Mexican civil war (1855 to 1860; Panni 2001a) and the brief reign from 1861 to 1867 of the Austrian Archduke Ferdinand Maximilian as Emperor of México (Panni 2001b). In addition, we know that the holotype of *Glossonycteris lasiopyga* is not the specimen from San Gerónimo (Isthmus of Tehuantepec) later recorded by Sumichrast (1881). The type specimen must have been collected during Saussure's trip to México between 1855 and 1856. It definitely was not collected later than 1860 when Saussure (1860) reported the specimen Peters (1868) later described as a new taxon. Although not helpful to us for locating the type locality of *Glossonycteris lasiopyga,* Alvarez (1963) provided a valuable discussion on the importance of Sumichrast's (1881) report for determining some of the actual type localities for several of the species Saussure described from México. Based on the knowledge that the specimen probably came from somewhere along the Atlantic slope of central México where Saussure did most of his field work, we further restrict the type locality to the State of Veracruz.

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Literature Cited

Alvarez, T. 1963. The type locality of *Nyctomys sumichrasti* Saussure.—Journal of Mammalogy 44: 582–583.

Baud, F. 1977. Catalogue des types de mammifères et d'oiseaux du Muséum d'Histoire naturrelle de Genève.—Revue suisse de Zoologie 84:201–220.

Boucard, A. 1884. Notice sur François Sumichrast.—Bulletin de la Société Zoologique de France 9: 305–312.

Carter, D. C., & P. G. Dolan. 1978. Catalogue of type specimens of Neotropical bats in selected European museums.—Special Publication, The Museum, Texas Tech University 15:1–136.

Panni, E. 2001a. La Guerra Civil, 1858–1860. Pp. 21–40 *in* J. Garciadiego, coord., Gran Historia Ilustrada de México. IV. De la Reforma a la Revolución, 1857–1920. Editorial Planeta Mexicana, México, 400 pp.

Panni, E. 2001b. La Intervención y el Segundo Imperio, 1861–1867. Pp. 41–60 *in* J. Garciadiego, coord., Gran Historia Ilustrada de México. IV. De la Reforma a la Revolución, 1857–1920. Editorial Planeta Mexicana, México, 400 pp.

Peters, W. 1868. Über die zu den Glossophagae gehörigen Flederthiere und über eine neue Art der Gattung Colëura.—Monatsberichte der Königlich-Preussischen, Akademie der Wissenschaften zu Berlin 1869:361–368.

Sanborn, C. C. 1933. Bats of the genera Anoura and Lonchoglossa.—Field Museum of Natural History, Zoological Series 20:23–27.

Saussure, H. de. 1860. Note sur quelques mammifères du Mexique.—Revue et Magasin de Zoologie Pure et Appliquée, Série 2, 12:1–11. 53–57, 97–110, 241–254, 281–293, 377–383, 425–431, 479–494, 4 pls. [Also printed as an independently-paginated, 82-page separate.]

Saussure, H. de. 1993. Voyage aux Antilles et au Mexique 1854–1856. Présenté par Louis de Roguin et Claude Weber. Editios Olizane, Genève, Suisse, 513 pp.

Sumichrast, F. 1881. Enumeración de las especies de mamíferos, aves, reptiles y batracios observados en la parte central y meridional de la República.—Mexicana. La Naturaleza 5:199–213.

Thomas, O. 1893. On some mammals from central Peru.—Proceedings of the Zoological Society of London 1893:333–341, plates 28–29.

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Observations on the structure of the mandibular gnathobase in some American *Mesocyclops* (Copepoda: Cyclopidae)

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Abstract.—The mandibular edge of males and females of several American species of the cyclopoid genus *Mesocyclops* was examined. The general structure, arrangement, and size of teeth was assessed for each species and shown to be variable among them. We used a modified version of a previous index, the Gnathal Index (GI) plus the Mandibular Size Index (MSI), and the Mandibular Power Index (MPI) which, together are expected to 1) provide a quantitative measure of morphologic variation amongst species and 2) suggest the feeding habits of these species. All species showed different values in terms of teeth number, size, and arrangement, as indicated by results of these indices. Known predatory species (i.e., *M. edax, M. longisetus,* and *M. aspericornis*) showed high values of MSI and MPI. The MSI values were positively correlated to the total body length. Our data suggest a predatory capability for these two species. *Mesocyclops yutsil, M. reidae,* and *M. chaci* had the lowest MPI and MSI values; they represent a group that probably are detritivores. The remaining species, all with lower MPI values, are probably omnivores. For the species examined here, most males are smaller than females but their mandibles tend to be similar in relative size and structure. Experimental observations support our conclusions about the predatory forms. Feeding experiments are needed to determine the limits of these indices for most species in the second and third groups.

Knowledge of the mandibular structure in the species of the freshwater copepods genus *Mesocyclops* is limited to the basic descriptions. There are no previous comparative studies about the morphology and specific variation of the mandible structures in freshwater copepods. Mandibles, together with other cephalic appendages, are directly involved in food handling and ingestion; hence, different feeding habits may be expected to correlate with particular mandible types.

Most species of the freshwater cyclopid genus *Mesocyclops* are omnivorous. However, the role of some *Mesocyclops* as predators of mosquito larvae and consequently as biological controls has been studied for several years in the neotropical and nearctic regions (Marten 1989; Marten et al. 1989, 1994a, 1994b), and in several Asian countries (Sinh Nam 2000) suggesting that these species may be carnivores. However, there are no surveys dealing with the morphological bases of their capacity for carnivory in terms of the structure and size of their mouthparts, particularly of their mandibles. The morphological structure of marine calanoid copepod feeding appendages (i.e., the cutting edges of the mandible or the structure of the maxillar setae) is a tool useful to infer their feeding habits (Itoh 1970). This aspect has not been explored in freshwater cyclopoid copepods, a group found in a wide range of continental environments and with different feeding habits.

There are ten species and one subspecies

Table 1.—Gnathal Index (GI), Mandibular Size Index (MSI), and Mandibular Power Index (MPI) obtained from the analysis of females and males of some American species of *Mesocyclops*. Species arranged alphabetically; numbers between parentheses indicate the rank of the MPI value.

Species	GI	MSI	MPI
M. aspericornis (Daday, 1906) (♀)	67.9	4.16	282.4 (2)
M. brasilianus Kiefer, 1936 (♀)	63.6	2.79	177.4 (10)
M. brasilianus (♂)	60.6	2.92	176.9 (11)
M. chaci Fiers, 1996 (♀)	51.2	2.05	104.5 (15)
M. edax (Forbes, 1891) (♀)	82.4	4.51	371.6 (1)
M. evadomingoi Gutiérrez-Aguirre, 2001a (♀)	75.6	2.41	182.1 (8)
M. longisetus s.str. (Thiébaud, 1912) (♀)	62.5	3.26	203.7 (5)
M. longisetus curvatus Dussart, 1987 (♀)	73.2	2.54	186.4 (7)
M. pescei Petkovski, 1986 (♀)	85.0	2.56	217.5 (4)
M. pescei (♂)	63.1	2.79	176.1 (12)
M. residae Petkovski, 1986 (♀)	75.0	2.02	151.5 (13)
M. reidae (♂)	80.2	2.23	178.4 (9)
M. thermocyclopoides (Harada, 1931) (♀)	72.9	2.63	191.7 (6)
M. thermocyclopoides (♂)	87.0	2.79	234.8 (3)
M. yutsil Reid, 1996 (♀)	77.9	1.92	149.5 (14)

of *Mesocyclops* known to be distributed in Mexico (Suárez-Morales & Reid 1998, Gutiérrez-Aguirre & Suárez-Morales 2001a, 2001b; Fiers et al. 2000), representing close to 60% of the species currently known from the neotropics (Gutiérrez-Aguirre & Suárez-Morales 2001b). In this work, analyzes the structure of the mandibular edge of ten species and one subspecies of *Mesocyclops,* all of them known to be distributed in Mexico and Central America, and some found also in North America. The mandible edge structure and relative size are determined for the species of *Mesocyclops* examined, and variations among species are discussed in relation to their feeding habits. A quantitative aspect of this question is analyzed through different indexes, one of them derived from a formula first proposed by Itoh (1970) for the evaluation of the mandible structure of marine calanoid copepods.

Methods

Specimens were obtained from field collections of zooplankton in different freshwater environments of Mexico. The methods of collection and sampling sites in Mexico are described in Suárez-Morales et al. (1996) and in Gutiérrez-Aguirre and Suárez-Morales (2001a). Additional type and non-type material was requested on loan to different museums harboring collections of American *Mesocyclops,* the National Museum of Natural History, Smithsonian Institution at Washington, D.C. (USNM), the Museum National d' Histoire Naturelle, Paris (MNHN-Cop), and El Colegio de la Frontera Sur, Unidad Chetumal, Chetumal, Mexico (ECO-CHZ) (see Suárez-Morales & Gutiérrez-Aguirre 2001). Female specimens of eleven species or subspecies plus males of four species of *Mesocyclops* recognized in Mexico and Central America were analyzed (see Table 1). Examination followed dissection of the mandibles and included camera-lucida illustrations of the mandibular edge detailing the teeth width, height, number, and separation.

Mandibular morphology.—In general, the morphological interpretation proposed by Huys & Boxshall (1991) was followed. The gnathobase is a ventral extension of the coxa; it has a variable number of non-articulation elements, that are the teeth. The mandible edge bears a proximal seta and in some cases an inner, flexible setiform extension (named "inner" proximal tooth). Both elements, the proximal seta and the

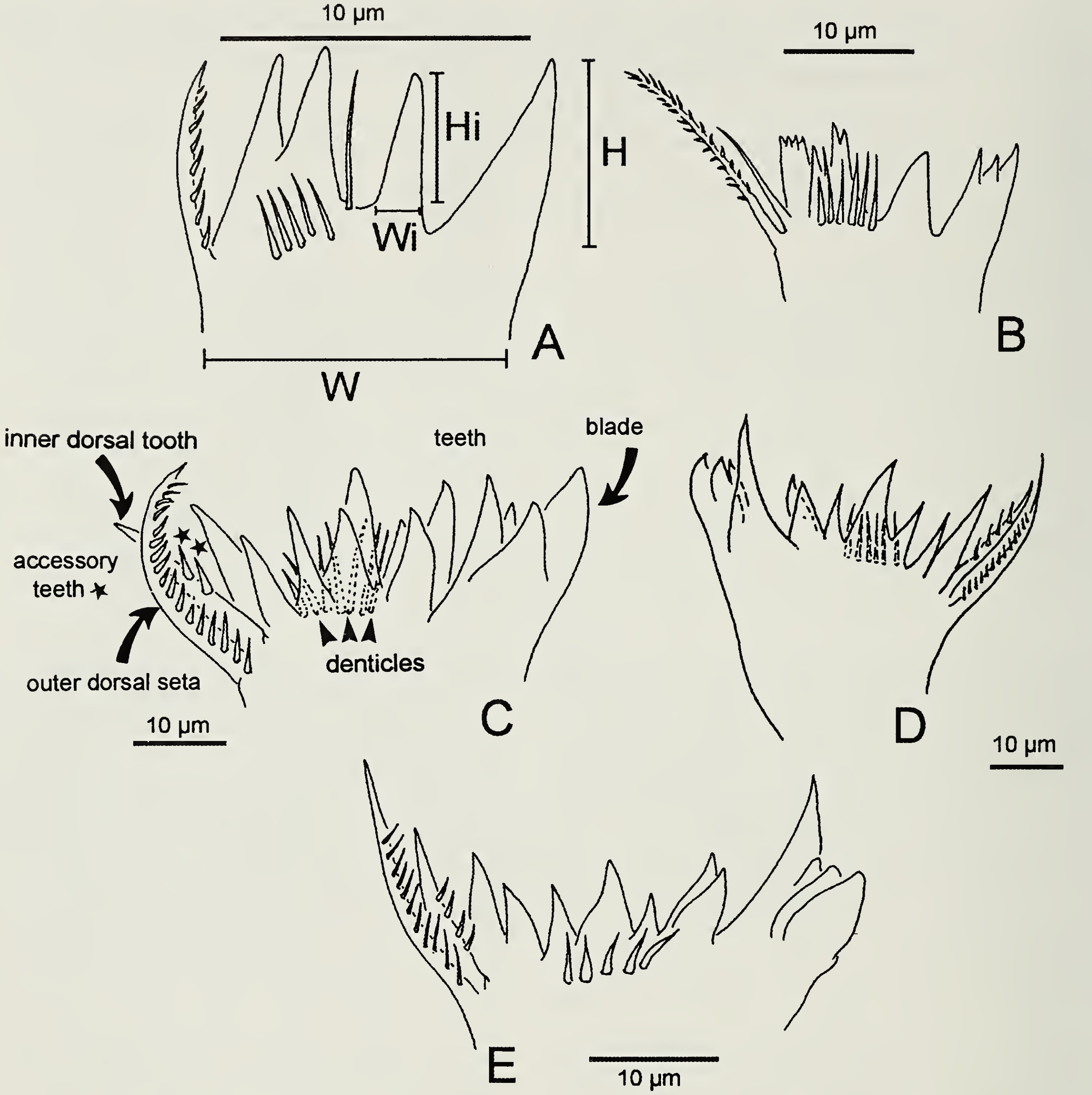

Fig. 1. Structure and nomenclature of the mandibular edge of males and females of species of *Mesocyclops* from Mexico: A) *M. yutsil* (♀), showing factors used in index formulae; B) *M. chaci* (♀); C) *M. edax* (♀), showing nomenclature of mandibular structures. Outer dorsal seta and inner dorsal tooth are proximal; blade is distal; D) *M. aspericornis* (♀); E) *M. evadomingoi* (♀).

inner tooth, can have epicuticular extensions (such as setules or as pinnate elements mostly uniserially arranged). In some species these extensions are noticeably strong, we named these structures "accessory teeth" (see Fig. 1C). In *Mesocyclops,* the distal edge of the gnathobase has a noticeably larger tooth; it can be simple (as in Fig. 1A) or formed by a cluster of two or more teeth (see Fig. 1C, E). This structure is known herein as the blade (see Fig. 1C), but it was counted as one tooth and also is used as a reference for measurements of the other teeth. There are setiform structures along the mandible edge, arising near the base of the teeth; these are not true setae, and are named denticles for the purposes of this work (Fig. 1C). The same nomenclature was used in the descriptions of the mandibular structure.

Formulae.—The mandibular elements (teeth number, edge width, height) were evaluated with an index based on the Edge Index (EI) proposed by Itoh (1970) for marine calanoid copepods. The original formula of this EI is as follows:

$$EI = \Sigma\ (wi/W \times hi/H \times 10^4) \times 1/N$$

where W is the width of the edge of the gnathobase, measured from distal tooth to proximal seta, and wi the width of the space between each pair of adjacent teeth, respectively. Factor H is the height of the main tooth (blade) and hi the height of each remaining tooth, respectively (Itoh 1970), and N is the number of teeth. We modified this formula substituting the meaning of wi by the actual width of the teeth (not the space between each tooth as in the Itho's formula) and rearranged the factors. The name of the resulting value was changed herein to gnathal index (GI), the resulting formula as:

$$GI = \Sigma\ ((wi/W \times 1/N)(hi/H \times 1/N)) \times 1000$$

where wi is the width of each tooth, not the space between them and W is the width of the edge of the gnathobase; hi is the height of each tooth and H is the maximum height of the blade tooth (see Fig. 1A). The first factor indicates the width of each tooth compared to the total edge width, the sum of all individual tooth widths gives an idea of the how much of edge of the gnathobase is take up by teeth. A value of 1 would imply that all the available edge is covered by teeth. However, for some species the factor figure is over 1, if teeth are arranged in more than one row. Dividing the result of this factor by the number of teeth, we obtain the average tooth width. The second factor iss designed to indicate how high teeth are when compared to the highest one (the blade); dividing this product by the number of teeth provides an average tooth height. The overall product of multiplying the average height and width is an idea on how strong each tooth is in the mandible, the higher and wider, the stronger. Additionally, we formulated a mandibular size index (MSI) to quantify the length of the edge of the gnathobase as it relates to the total body length of the specimen. This index is obtained from the following formula: MSI = W/TL × 100, where W is the width of the mandible edge (in μm) and TL the length of the species (in μm) including the caudal rami. This index is expected to provide a comparative estimation on how large are the mandibles with respect to the size of the copepod. The figure obtained is a percentage, scaled to 100. The relation between TL and MSI was analyzed statistically by determining the correlation factor (*r*). Finally, by multiplying GI by MSI, the mandibular power index (MPI) is obtained, which provides a measure of the strength-size combination of the mandibles of each species. That is, a species with a high GI will not necessarily have a high strength-size combination, if the width of the blade is small relative to the length of the specimen (as indicated by the MSI).

Results

Material examined.—Mesocyclops aspericornis: 3 adult ♀♀ from small reservoir near km 90 of the highway Culiacán-Los Mochis, Sinaloa, Mexico (25°17′N, 107°47′W); 1 adult ♀ from Anapoima, Cundinamarca, Colombia (04°33′N, 074°32′W), USNM-216634; *M. brasilianus*: 6 adult ♀♀, 2 adult ♂♂ from Sayaxché, Guatemala (16°31′57″N, 90°11′18″W). 1 adult ♀, Mantecal, Venezuela, Collection of B. Dussart, MNHN Cp 821, 1 adult ♂, Lago Valencia, Venezuela (10°10′N, 0.67°45′00″W), USNM-204662; *M. chaci*: 1 adult ♀, 1 adult ♂, Gruta Tza-Ma, Yucatán, Mexico (USNM-274244); *M. edax,* 2 adult ♀♀ from Cranes Pond, North Carolina, USA, 1 adult ♀, Cenote Viejo, central Quintana Roo, Yucatan Peninsula, Mexico, USNM-259699; *M. evadomingoi,* holotype specimen, pond at km 45 of the Jonuta-Villahermosa federal road, Tabasco, Mexico (17°58′44″N, 92°14′11″W), slides ECO-CHZ 01157 (♀), paratype ECO-CHZ 01159 (♂); *M. longisetus* s. str.: 4 adult ♀♀ from small temporal pond near Comitán city, Chiapas, Mexico

(16°09′57″N, 92°05′23″W), 2 adult ♀♀, 2 adult ♂♂, pond at Km 51 Jonuta-Villahermosa federal road, Tabasco, México (18°23′16″N, 92°47′0″W); *M. longisetus curvatus*: 3 adult ♀♀ from small pond at km 45, Jonuta-Villahermosa federal road, Tabasco, Mexico (17°58′44″N, 92°14′11″W), 3 adult ♀♀, Cenote Catedrales, central Quintana Roo, Yucatan Peninsula, Mexico, USNM-259687; *M. pescei*: 11 ♀♀, 5 ♂♂ from small pond km 45, Jonuta-Villahermosa federal road, Tabasco, Mexico (17°58′44″N, 92°14′11″W); *M. reidae*: 1 adult ♀, 1 adult ♂ from Tabano, Cuba; *M. thermocyclopoides*: 3 adult ♀♀, 1 adult ♂ from Pulsar, Tabasco, Mexico (17°39′10″N, 91°33′23″W), 2 adult ♀♀, 2 adult ♂♂, from small pond at km 45 of the Jonuta-Villahermosa federal road, Tabasco, Mexico (17°58′44″N, 92°14′11″W); *M. yutsil*: 2 adult ♀♀ (USNM-259843, USNM-259846)) from cenote Yuncú, Yucatan Peninsula, Mexico; 1 adult ♀, Cenote Mucuyché, Yucatan, Mexico (USNM-259848).

Structure of mandibles.—The mandibular edge in this genus follows a general pattern, with a strong blade which is, in most cases, the largest and strongest one on the gnathal edge (Fig. 1). In some species such as *M. evadomingoi* (♀), *M. pescei* (♂, ♀), and *M. thermocyclopoides* (♀), the blade is formed by a cluster of two or more teeth. A row or rows of smaller teeth follow toward the proximal end. Teeth may be bicuspidal or multicuspidal. Teeth have a variable basal width and may have groups or rows of small denticles at their base. In some species, the inner proximal tooth is quite strong and armed with two or more internal accessory teeth (i.e., *M. edax*, *M. longisetus* s.str.). The structure of the blade showed some range of variation in the species of *Mesocyclops* studied (Figs. 1, 2). A brief description of the mandibular morphology of each species and sex examined is given below together with the percent variability of the indexes estimated; this is provided only for those species in which we could evaluate these variation. Total number of teeth includes the blade and the inner proximal tooth. GI, MSI, MPI are given in Table 1. When material was available to determine the variability of the indices, the percentage range of variation from the average is indicated in each case for the species.

Mesocyclops aspericornis (♀): Gnathobase with 10–11 wide-based teeth, all monocuspidal. Distal blade of three teeth. A single row of 6 denticles inserted near base of teeth on central part of gnathal edge. Proximal seta spinulated; inner proximal tooth with row of four accessory teeth (Fig. 1D). Variability in percent with respect to average: GSI (11.9%), MSI (8.8%), MPI (18.4%).

Mesocyclops brasilianus (♀): Gnathobase with 8 wide-based teeth, all teeth monocuspidal. Two paired sets of denticles inserted near base of teeth on central part of gnathobase. Proximal seta slender, long, with row of setules on inner margin (Fig. 2B). Inner proximal tooth naked. Variability in percent with respect to average: GSI (14.1%), MSI (9%), MPI (5.1%).

Mesocyclops brasilianus (♂): Gnathobase with 4 wide-based teeth, all teeth monocuspidal. Blade a cluster with two distal teeth. Two groups of denticles inserted near base of teeth on central part of gnathobase. Proximal seta short, lightly setulated (Fig. 2A). Variability in percent with respect to average: GSI (12.3%), MSI (8.7%), MPI (19.3%).

Mesocyclops chaci (♀): Gnathobase forming cluster of 3–4 wide-based teeth, proximal seta biserially pinnate. Inner proximal tooth slender, setiform, next proximal tooth tetracuspidal, next one monocuspidal, next one bicuspidal, distal monocuspidal, blade formed by a cluster of three teeth. Row of six denticles inserted near base of bicuspidal tooth on central part of gnathobase (Fig. 1B).

Mesocyclops evadomingoi (♀): Gnathobase wide, with 12 wide-based teeth, all monocuspidal. Distal cluster of three teeth partially fused to blade. Row of five den-

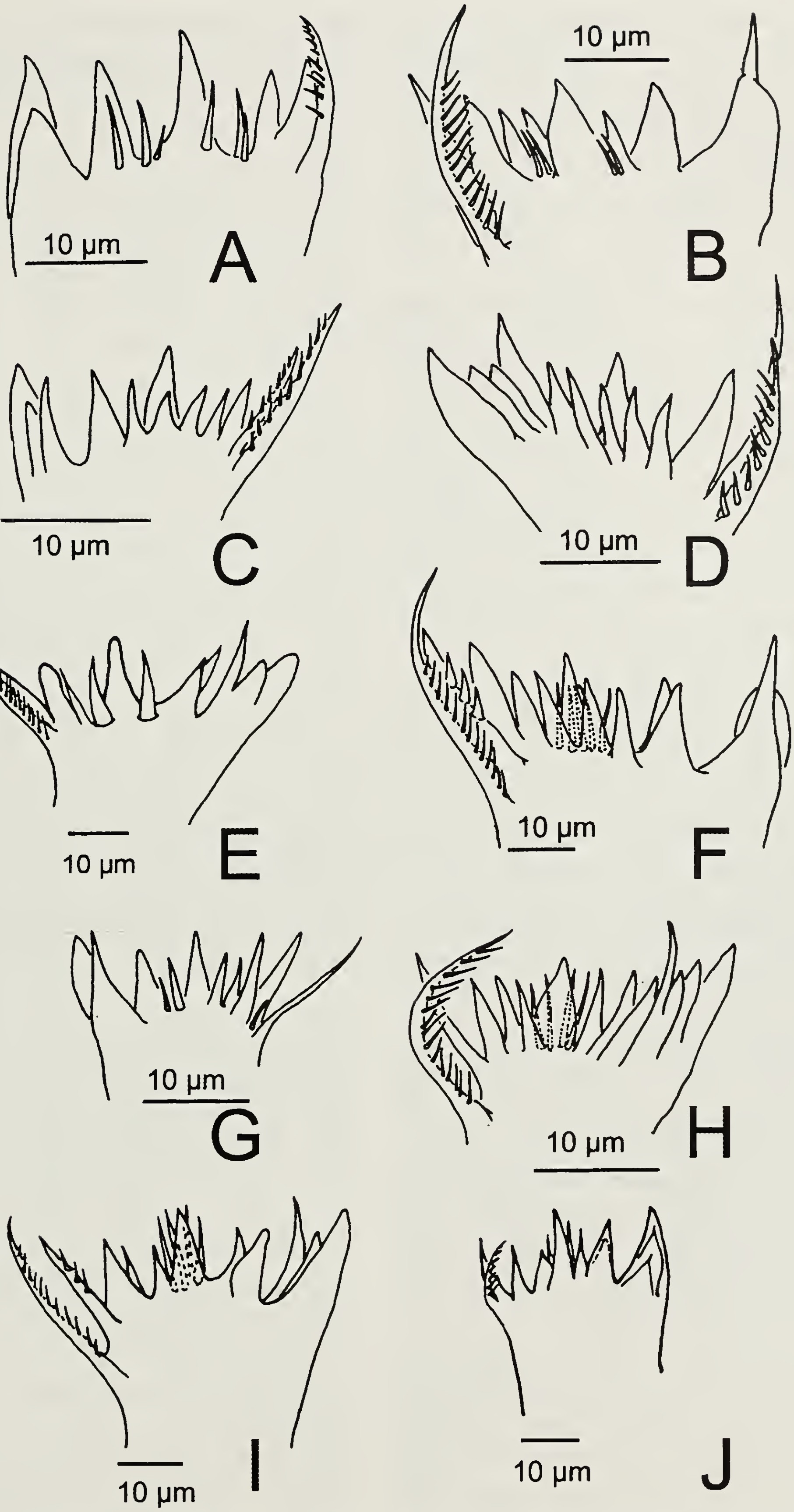

Fig. 2. Structure of the mandibular edge of males and females of species of *Mesocyclops* from Mexico; A) *M. brasilianus* (♂); B) *M. brasilianus* (♀); C) *M. pescei* (♂); D) *M. pescei* (♀); E) *M. longisetus curvatus* (&femlae;); F) *M. longisetus* s.str. (♀); G) *M. thermocyclopoides* (♂); H) *M. thermocyclopoides* (♀); I) *M. reidae* (♀); J) *M. reidae* (♂).

ticles inserted near base of teeth on central part of gnathobase. Outermost proximal seta long, with uniserial row of spinules along inner margin; inner proximal tooth relatively short, with row of 3–4 secondary teeth on inner margin (Fig. 1E). Variability in percent with respect to average: GSI (4.4%), MSI (3.4%), MPI (0.3%).

Mesocyclops edax (♀): Gnathobase with 13 wide-based teeth, all monocuspidal. A single row of 6–7 denticles inserted near base of the teeth on central part of the gnathal edge. Distal cluster of three strong teeth clustering partially with blade. Proximal seta heavily spinulated along inner margin only. Inner proximal tooth with 2–3 strong accessory teeth (Fig. 1C). Variability in percent with respect to average: GSI (4.7%), MSI (2.3%), MPI (4.5%).

Mesocyclops longisetus s.str. (♀): Gnathobase with 8–10 wide-based teeth, all teeth monocuspidal. Row of five denticles inserted near base of teeth on central part of gnathobase. Proximal seta relatively long, slender, with inner row of short setules. Inner proximal tooth with three strong accessory teeth (Fig. 2F). Variability in percent with respect to average: GSI (20.6%), MSI (2.9%), MPI (22.3%).

Mesocyclops longisetus curvatus (♀): Gnathobase with 10–11 wide-based teeth, all teeth monocuspidal. Blade with blunt tip. Proximal seta relatively long, slender, with inner row of short spinules. Inner proximal tooth naked, shorter than the proximal seta (Fig. 2E). Variability in percent with respect to average: GSI (14.4%), MSI (16.4%), MPI (27.4%).

Mesocyclops pescei (♀): Gnathobase with 12 teeth, all monocuspidal. Base of teeth unornamented. Distal cluster of four teeth partially fused with blade. Proximal seta long, strongly spinulated along inner margin. Inner proximal tooth slender, naked, slightly longer than proximal seta (Fig. 2D). Variability in percent with respect to average: GSI (15%), MSI (6.9%), MPI (16.2%).

Mesocyclops pescei (♂): Gnathobase with 11 wide-based teeth, all monocuspidal. Base of teeth unornamented. Blade partially fused to two adjacent teeth. Proximal seta relatively long, with row of spinules along inner margin. Inner proximal tooth slender, slightly shorter, with row of small, weak accessory teeth along inner margin (Fig. 2C). Variability in percent with respect to average: GSI (37.4%), MSI (15.5%), MPI (29.5%).

Mesocyclops reidae (♀): Gnathobase with 10 wide-based teeth, all monocuspidal. Base of teeth with single row of four denticles inserted on central surface of base. Distal cluster of 2–3 teeth with blade. Proximal seta relatively long, with row of short spinules along inner margin. Inner proximal tooth slender, slightly shorter than proximal seta, with three accessory teeth on inner margin (Fig. 1I).

Mesocyclops reidae (♂): Gnathobase with 9 wide-based teeth, all monocuspidal. Base of teeth with row of 2–3 denticles. Distal cluster of three teeth with blade. Proximal seta with row of short setules along inner margin. Inner proximal tooth slightly shorter, naked (Fig. 1J).

Mesocyclops thermocyclopoides (♀): Gnathobase with 12–13 wide-based teeth, all teeth monocuspidal. Row of four denticles inserted near base of teeth on central part of gnathobase. Distal cluster of 3–4 teeth partially fused with blade. Proximal seta relatively long, slender, with inner row of strong spinules. Inner proximal tooth slender, naked (Fig. 2H). Variability in percent with respect to average: GSI (10.3%), MSI (17.9%), MPI (7.6%).

Mesocyclops thermocyclopoides (♂): Gnathobase with 8 teeth, all teeth monocuspidal. Blade clustered with one tooth. Two or three denticles inserted near base of teeth on central part of gnathobase. Proximal seta relatively long, slender, naked. Inner proximal tooth absent or reduced (Fig. 2G).

Mesocyclops yutsil (♀): Gnathobase with 4 wide-based teeth, including large blade; all moncuspidal. Row of five denticles in-

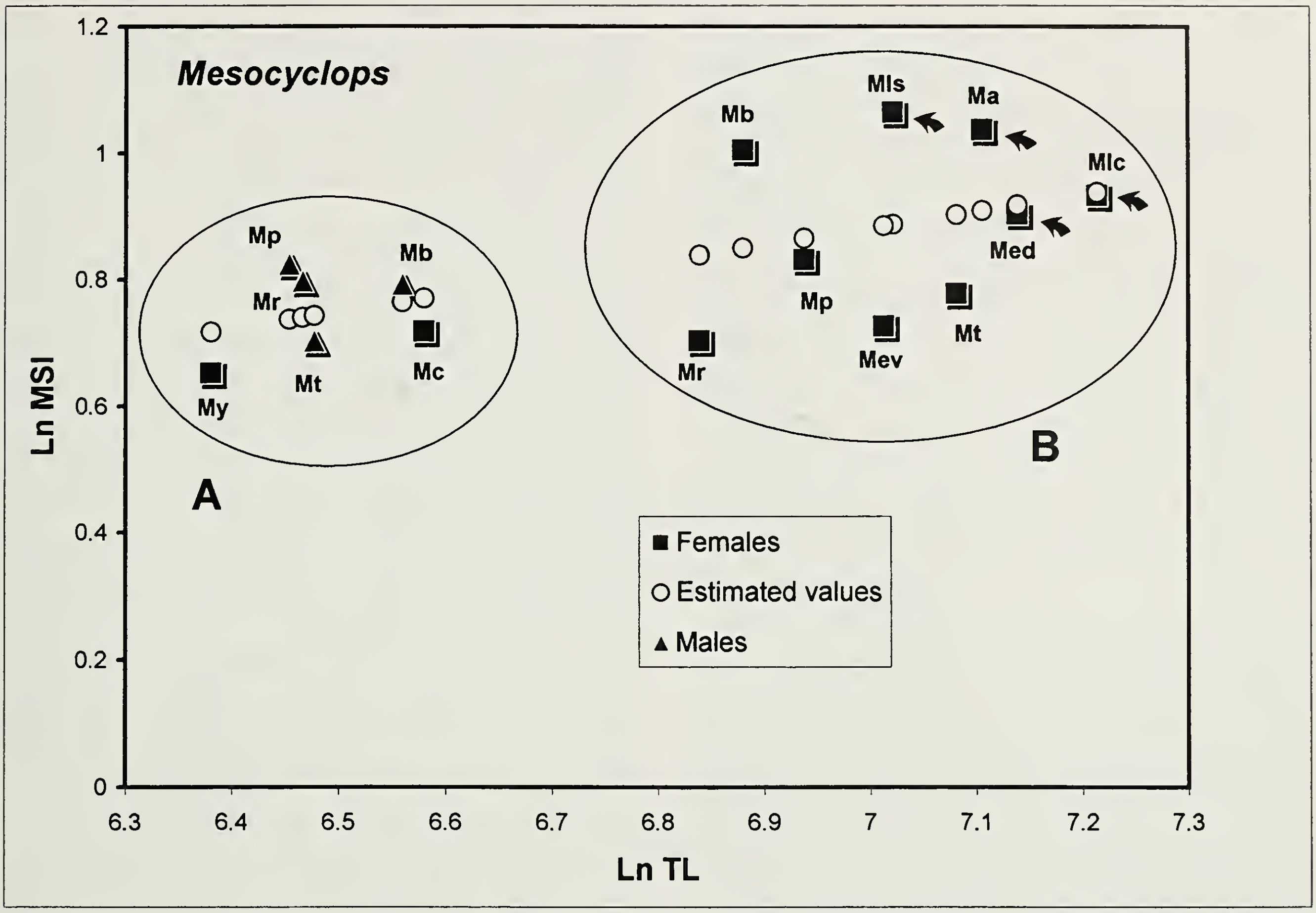

Fig. 3. MSI vs. TL logarithmic (ln) regression. Ellipses indicate two major groups with distinct features (see text por explanation) including both males (triangles) and females (squares). Arrow indicate the species with highest TL and MSI values. Species abbreviations as: Ma = *M. aspericonis*; Mb = *M. brasilianus*; Mc = *M. chaci*; Med = *M. edax*; Mev = *M. evadomingoi*; Mls = *M. longisetus* sensu stricto; Mlc = *M. longisetus curvatus*; Mp = *M. pescei*; Mr = *M. reidae*; Mt = *M. thermocyclopoides*; My = *M. yutsil*.

serted diagonally near base of teeth on central part of gnathobase. Proximal seta relatively short, as long as adjacent teeth, with inner row of short spinules (Fig. 1A).

Discussion

The Mandibular Power Index (MPI) of species of *Mesocyclops* comparable numerical data which are presented in Table 1. The highest MPI value was that of *Mesocyclops edax,* followed by *M. aspericornis,* whereas the lowest figure was shown by the females of *M. yutsil* and *M. chaci.* Additional differences were detected between males and females of the same species. Out of the four species with both sexes evaluated, males of two (*M. reidae, M. thermocyclopoides*) had higher MPI values than females; females of *M. brasilianus* and *M. pescei* had an MPI figure higher than their males (see Table 1).

The Mandibular Size Index (MSI), size of the gnathal edge relative to body length of the specimen, yielded interesting differences among the species. Females *M. edax* have the largest mandibular edge (MSI = 4.5), followed by females of *M. aspericornis* (4.16), and females of *M. longisetus* s.str. (MSI = 3.26) (see Table 1). Females of *Mesocyclops yutsil, M. chaci,* and *M. reidae* have the smallest mandibles, relative to body size, of all the species examined herein (MSI = 1.92 and 2.05, respectively).

The TL vs. MSI graphic analysis, which used the logarithm (ln) of both factors, showed two distinct groups (see Fig. 3) with a positive correlation ($r = 0.598$, $p = >0.05$) which is slightly higher if only females are considered (r = 0.62, p = >0.05). Group A includes the females of most species and group B contains the four males examined and the females of *M. chaci* and *M. yutsil.* The forms with highest values in terms of MSI and TL were the females of *M. aspericornis, M. edax, M. longisetus* s.str., and *M. longisetus curvatus* (arrowed in Fig. 3). Overall, the morphology of the mandibular edge of the studied *Mesocyclops* shows a relatively wide range of variation in terms of tooth structure.

Itoh's (1970) Edge Index was modified due to the differences between the calanoid teeth/mandibular pattern and the cyclopoid pattern (see Huys & Boxshall 1991), mainly with respect to the distribution of teeth along the gnathal edge. The two main factors (width and height), when combined, provide an idea of the strength of the the teeth. Then, when divided by the number of teeth (N), a quantitative measure is obtained about the strnngth of each tooth, which is the actual interpretation of this index for *Mesocyclops.* These figures also provide a quantitative estimation of the morphological differences found in the species examined. Although the taxonomic value of the mandible edge remains unexplored in *Mesocyclops* or in any other freshwater genus, this work reveals the many different characters with potential use for identification purposes, and that most of them can be evaluated quantitatively. Mandibles are one of the most heavily chitinized structures in the copepods; therefore, these appendages could be used to identify these crustaceans at the species level from stomach contents in trophic or ecological surveys.

The size of the body (LT) is a key factor for a copepod used in mosquito control, but one of the largest species of Cyclopidae known (*Homocyclops ater* (Herrick)) can not be used as a mosquito predator (see Marten et al. 1994b). Therefore, the use of the MSI together with the TL was considered necessary to infer the trophic habits of the species of *Mesocyclops.* The MSI vs. TL graphic (Fig. 3) yielded some interesting facts: the relative size of the mandibular edge tends to be proportional to the total length of the species; males are smaller but at least in two of the males evaluated (*M. pescei, M. reidae*), mandibles are at least as large as those of their females. The value of males as potential predators of mosquito larvae is undetermined, although in this study the male of *M. thermocyclopoides* ranked higher (MPI) than the female.

The females of *Mesocyclops longisetus, M. aspericornis,* and *M. edax* are unique in showing a proximal seta with 2–4 strong, wide-based accessory teeth. They had the highest MSI values which, complemented with their body size (1.0–1.2 mm) suggests they are the most well-equipped species for predation within the examined group (see Fig. 3). Overall, these results agree with those of field and laboratory experiments testing the predation capabilities of *M. aspericornis* and *M. longisetus* (see Marten et al. 1994b, Suárez 1992) and of *M. edax* (Marten 1989). *Mesocyclops thermocyclopoides,* recorded in Honduras, Costa Rica, and Mexico, has been successfully used as a mosquito control (Marten et al. 1994a, 1994b). Only recently were the neotropical records of this species confirmed with Asian specimens (Gutiérrez-Aguirre et al. 2003). *M. thermocyclopoides* ranked sixth in the MSI; its size (comparable to that of *M. aspericornis* and *M. longisetus curvatus*) suggests that this species might be capable of attacking a mosquito larva. Our results on this species agree entirely with the observations obtained from experimental works by Kumar & Rao (1999a, 1999b) establishing this species as an omnivorous form feeding on rotifers, ciliates, and algae.

A second group of probably omnivorous species was found based on MSI vs TL values and MPI, i.e., the females of *M. evadomingoi, M. thermocyclopoides, M. pescei,* and *M. brasilianus* (see Fig. 3). MSI values range between 2.2 and 2.8; they are medium to large-sized forms (0.75 mm–1.00 mm), most with small to medium-sized mandibles (except for *M. brasilianus,* a species with a mandible size equal to that of predator species). These omnivorous species may be capable of predation upon small prey items when conditions are appropriate to such behavior, but they may also ingest other food sources. Males of these species, some even with MSI values higher than their females, may not be able to feed on large prey (i.e., mosquito larvae) because of their relatively small size. Finally, the females of *M. chaci* and *M. yutsil* are slender, probably planktic forms (Fiers et al. 1996). In terms of size of the mandibular edge and teeth structure, these two species represent the diametral opposite end with respect to the predator group. Their mandibles are built quite differently, they probably handle algae, suspended organic matter along the water column, or even the heavily chitinized edge with these short, very solid teeth (shown by the top GI values of all the examined group) could be used to scrape off food from littoral surfaces or vegetation (if they are epibenthic forms).

According to our results, the examined species of American *Mesocyclops* exhibit a wide variation of the mandibular size and armament. We speculate that at least the morphological extremes (*M. yutsil–M. aspericornis*) are on correspondence with different feeding habits and prey sizes. Therefore, not all the species of *Mesocyclops* are suitable to be developed or cultured as potential biological controls of mosquitoes.

It is clear that the evaluation of the teeth strength through the GI alone could be misleading, a species with very strong teeth will rank relatively high in this index (i.e., *M. yutsil*) but this does not necessarily imply a predatorial capacity. This is why the GI should be complemented with the MSI and the MPI. A MSI value over 3 would represent a species conveniently armed for predation. We recognize, however, that the relatively reduced number of observations (see the Material examined section) is a drawback of this analysis, but still, our results seem to make sense in terms of 1) the estimated high capacity of three well-known predator species and their consistent tendency to cluster together in the three indices used, 2) the distinction of different and even contrasting structural-morphological patterns within the genus, 3) the relation of this pattern with experimentally tested feeding habits (for predators and one omnivorous species), and 4) the relative body and mandibular size differences among the species examined herein. Of course, these patterns and estimations should be complemented with additional observations in order to have a more robust numerical analysis.

Using the detailed drawings provided in redescriptions by Dahms & Fernando (1993), we extended our results of mandibular indices to other species and genera for which feeding habits are known or inferred. *Mesocyclops leuckarti* (Claus, 1857) is a predator species (Marten 1994). The MSI estimated for this species is 4.06 and the MPI is 315.8; these values are within the range value of other predator species we have detected in this work. Although these indices were designed for *Mesocyclops,* we tested our methods on *Acanthocyclops brevispinosus* (Herrick, 1884) of the "*robustus-vernalis*" group complex (Dodson 1994). Recently, it was redescribed by Dahms & Fernando (1997). It has a MSI of 3.82, a value which suggests predating habits. *Eucyclops conrowae* Reid, 1992), a supposedly herbivore, had a GI of 65.1, a MSI of 2.7, and a MPI of 175; these figures categorize this species within the omnivorous forms. In these or in the other instances, experimental observations will provide valuable data to find a link between the mandible structure and the feeding habits of freshwater copepods. It is probable that the differences among the species categorized here as omnivorous forms, regardless of the genus, rely mainly on the size of the potential prey they are able to capture and handle (either protozoans, planktonic algae, or insect larvae).

Literature Cited

Deday, E. von. 1906. Untersuchungen uber die Copepodenfauna von Hinterindien, Sumatra und Java, nebst einem Beitrag zur Copepodenkenntnis der Hawaii-Inseln. (Reise von Dr. Walter Volz). Zoologischer Jahrbuch, Abt. Syst., Geogr. Biol. Thiere 24(3):175–206.

Dahms, H. U., & C. H. Fernando. 1993. Redescription of *Mesocyclops leuckarti* (Copepoda, Cyclopoida), including a study of its naupliar development.—Internationale Revue der gesamten Hydrobiologie 78:589–609.

———. 1997. Redescription of *Acanthocyclops brevispinosus* (Herrick, 1884) (Copepoda, Cyclopoida) from Ontario.—Crustaceana 70:129–144.

Dodson, S. 1994. Morphological analysis of Wisconsin (U.S.A.) species of the *Acanthocyclops vernalis* group (Copepoda: Cyclopoida).—Journal of Crustacean Biology 14:113–131.

Dussart, B. H. 1987. Sur quelques *Mesocyclops* (Crustacea, Copepoda) d' Amerique du Sud.—Amazoniana 10:149–161.

Fiers, F., J. W. Reid, T. M. Iliffe, & E. Suárez-Morales. 1996. New hypogean cyclopoid copepods (Crustacea) from the Yucatán Peninsula, Mexico.—Contributions to Zoology 66:65–102.

———, V. Ghenne, & E. Suárez-Morales. 2000. New species of continental cyclopoid copepods (Crustacea, Cyclopoida) from the Yucatán Peninsula.—Studies of Neotropical Fauna & Environment 35:209–251.

Forbes, S. A. 1890 [1891]. On some Lake Superior Entomostraca. Annual Report for the Commission of Fish and Fisheries 1887. Government Printing Office, Washington, D.C., 701–718, pls. I–IV.

Gutiérrez-Aguirre, M., & E. Suárez-Morales. 2001a. A new species of *Mesocyclops* (Copepoda, Cyclopoida, Cyclopidae) from southeastern Mexico.—Journal of Limnology 60:143–154.

———. 2001b. Distribution and taxonomy of the tropical American *Mesocyclops* Sars, 1914 (Copepoda, Cyclopoida).—Crustaceana 74:477–487.

———, J. W. Reid & E. Suárez-Morales. 2003. An Afro-Asian species of *Mesocyclops* (Copepoda: Cyclopoida) in Central America and Mexico.—Journal of Crustacean Biology 23. (in press).

Harada, I. 1931. Studien über Süsswasserfauna Formosas.—Annotationes Zoologicae Japonenses 13:149–168.

Itoh, K. A. 1970. A consideration on feeding habits of planktonic copepods in relation to the structure of their oral parts.—Bulletin of the Plankton Society Japan 17:1–10.

Kiefer, F. 1936. Brasilianische Ruderfusskrebse (Crustacea, Copepoda), gesammelt von Herrn Dr. Otto Schubart. V. Mitt.—Zoologischer Anzeiger 116:31–35.

Kumar, R., & T. R. Rao. 1999a. Effect of algal food on animal prey consumption rates in the omnivorous copepod, *Mesocyclops thermocyclopoides.*—International Revue of Hydrobiology 84: 419–426.

———. 1999b. Demographic responses of adult *Mesocyclops thermocyclopoides* (Copepoda, Cyclopoida) to different plant and animal diets.—Freshwater Biology 42:487–501.

Marten, G. G. 1984. Impact of the copepod *Mesocyclops leuckarti pilosa* and the green alga *Kirchneriella irregularis* upon larval *Aedes albopictus* (Diptera: Culicidae).—Bulletin of the Society of Vector Ecologists 9:1–5.

———. 1989. A survey of cyclopoid copepods for control of *Aedes albopictus* larvae.—Bulletin of the Society of Vector Ecologists 14:232–236.

———, & G. Thompson. 1997. Copepod production and application for mosquito control.—New Orleans Mosquito Control Board, New Orleans, U.S.A., 42 pp.

———, R. Astaiza, R. Monje, & J. W. Reid. 1989. Natural control of larval *Anopheles albimanus* (Diptera: Culicidae) by the predator *Mesocyclops* (Copepoda: Cyclopoida).—Journal of Medical Entomology 26:624–627.

———, G. Borjas, M. Cush, E. Fernández, & J. W. Reid. 1994a. Control of larval *Aedes aegypti* (Diptera: Culicidae) by cyclopoid copepods in peridomestic breeding containers.—Journal of Medical Entomology 31:36–44.

———, E. S. Bordes, & M. Nguyen. 1994b. Use of cyclopoid copepods for mosquito control.—Hydrobiologia 292/293:491–496.

Omori, M., & T. Ikeda. 1992. Methods in marine zooplankton ecology. Krieger Publishing Co., Florida, 332 pp.

Petkovski, T. K. 1986. Zur Taxonomie des genus *Mesocyclops* G.O. Sars 1914 (Crustacea, Copepoda Cyclopoida) in der Neotropis.—Acta Musei Macedonici Scientiarium Naturalium 18:47–49.

Reid, J. W. 1992. Copepoda (Crustacea) from fresh waters of the Florida Everglades, U.S.A., with a description *Eucyclops conrowae* n. sp.—Transactions of the American Microscopical Society 111:229–254.

Sinh Nam, V., N. Thi Yen, M. Holynska, J. W. Reid, & B. H. Kay. 2000. National progress in dengue vector control in Vietnam: survey for *Mesocyclops* (Copepoda), *Micronecta* (Corixidae), and fish as biological control agents.—American Journal of Tropical Medicine and Hygiene 62: 5–10.

Suárez, M. F. 1992. *Mesocyclops aspericornis* for the control of *Aedes aegypti* in Puerto Rico and Anguilla. Pp. 151–157 *in* S. B. Halstead, & H. Gómez-Dantes, eds., Dengue-a worldwide problem, a common strategy. Proceedings of the International Conference on Dengue and *Aedes aegypti* community-based control. Rockefeller Foundation and Mexican Ministry of Health, Mexico City, 232 pp.

Suárez-Morales, E., & M. A. Gutiérrez-Aguirre. 2001. Morfología y taxonomía de los *Mesocyclops* (Crustacea: Copepoda: Cyclopoida) de México. CONACYT/ECOSUR, México, 207 pp.

———, & J. W. Reid. 1998. An updated list of the free-living freshwater copepods (Crustacea) of Mexico.—Southwestern Naturalist 43(2):256–265.

———, J. W. Reid, T. M. Iliffe, & F. Fiers. 1996. Catálogo de los copépodos (Crustacea) continentales de la Península de Yucatán México. CONABIO/ECOSUR, 298 pp.

Thiébaud, M. 1912. Copépodes de Colombie et des Cordillères de Mendoza.—Mémoires de la Societé Neuchateloise des Sciences Naturelles 5: 160–175.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
116(3):754–802. 2003.

A review of the freshwater crabs of the genus *Hypolobocera* Ortmann, 1897 (Crustacea: Decapoda: Brachyura: Pseudothelphusidae), from Colombia

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Abstract.—A review of the species of *Hypolobocera* from Colombia is presented. A total of 18 species and four subspecies occur in this country. Diagnoses, illustrations, and a key for the identification of species and subspecies based on the morphology of the first male gonopod, are included. The geographical distribution of the genus, species and subspecies is updated based on new material. Two new species, *Hypolobocera murindensis* and *H. velezi,* are described and illustrated. Two more groups of *Hypolobocera* species, groups 7 and 8, are defined to accommodate *H. alata* Campos, and *H. andagoensis* (Pretzmann). One subspecies, *H. bouvieri rotundilobata,* is elevated to specific rank.

The genus *Hypolobocera* Ortmann, 1897, includes 34 species of freshwater crabs that can be found in Venezuela, Colombia, Ecuador, and Perú. This makes *Hypolobocera* the most widely distributed genus of all pseudothelphusid genera. In Colombia, *Hypolobocera* is now represented by 18 species and four subspecies. In reviewing the genus for Ecuador, Rodríguez & Sternberg (1998) listed 12 Ecuadorian species, three of which were new. Rodríguez (1982a) recorded three species for Perú, the southern distributional limit for the family Pseudothelphusidae. The systematics and biogeography of the genus have been reviewed by Rodríguez (1982a, 1994), Rodríguez & Sternberg (1998), and Prahl (1988).

The morphology of the first male gonopod, a basic characteristic for the diagnoses of the species, displays considerable interspecific variability in freshwater crabs. Rodríguez (1982a) divided the genus *Hypolobocera* into six groups based on morphological and biogeographical features. Accordingly, the Colombian *Hypolobocera* can be placed as follows: in group 1, *Hypolobocera beieri* Pretzmann, 1968, *H. martelathani* (Pretzmann, 1965), and *H. noanamensis* Rodríguez, Campos & López, 2002; in group 2, *H. bouvieri* (Rathbun, 1898); in group 3, *H. steindachneri* Pretzmann, 1968; in group 4, *H. cajambrensis* Prahl, 1988, *H. chocoensis* Rodríguez, 1980, *H. dentata* Prahl, 1987, *H. emberarum* Campos & Rodríguez, 1995, *H. lloroensis* Campos, 1989, *H. malaguena,* Prahl, 1988, *H. rotundilobata* Rodríguez, 1994, and *H. velezi,* new species; and in group 5, *H. gorgonensis* Prahl, 1983, and *H. mutisi* Prahl, 1988; group 6, *H. andagoensis* (Pretzmann, 1965), and *H. murindensis,* new species. However, *H. alata* Campos, 1989, and *H. kamsarum* Campos & Rodríguez, 1995 can not be assigned to any of the groups proposed by Rodríguez (1982a) as the features of their gonopods do not match any of Rodriguez's groups. Thus, it is necessary to add two new groups in order to accommodate these latter two species. Group 7 is proposed for *H. alata,* and is characterized by having the lateral lobe of the first male gonopod with a strong triangular process; the apex is oval and bent caudocephalically, the cephalic border is expanded into triangular projection which is folded downwards and has a rounded papilla on the tip. The known distribution of group 7 comprises the San Juan River basin on the Western Cordillera. Group 8 is proposed for *H. kamsarum,* and is distinguished by the lateral lobe of the first male gonopod which is small, transverse and displaced towards the cephalic side; the apex is oval with a rounded expansion distally, and the mesial border is projected proximally, forming a strong triangular mesial lobe. The distribution of group 8 comprises the eastern foothills of the southern Andes of Colombia.

The terminology for the male first gonopod is that of Smalley (1964), and Rodríguez (1982a, 1994). The measurements are reported in the order "cl × cb" (carapace length times carapace breadth). The material was collected by the author except where otherwise indicated, or in some cases by an unknown collector (uk). The material of the Museo de Biología Marina, Universidad del Valle, was reported by Prahl with numbers that apparently corresponded to his collection lot numbers (not museum catalogue numbers), followed by the abbreviation "ADT-CRBMUV" (=Agua Dulce y Terrestres Crustáceos, Biología Marina Universidad del Valle). However, Prahl's material examined that is still extant at the Museo de Biología Marina, Universidad del Valle, Cali now has only museum catalogue numbers. Prahl's collection numbers are included herein in parenthesis only for the material reported as such in his publications. Color nomenclature follows Smithe (1975). Two species, *Hypolobocera buenaventurensis* (Rathbun, 1905), and *H. steindachneri* Pretzmann, 1968, are not illustrated due to the lack of material.

The materials remain deposited in: Colección de Referencia, Museo de Historia Natural, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN); Museo de la Sociedad de Ciencias Naturales La Salle, Caracas (LS); Museo de La Salle, Bogotá (MLS); Museo de Biología Marina, Universidad del Valle, Cali (CRBMUV); Instituto Venezolano de Investigaciones Científicas, Caracas (IVIC); National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM); Natural History Museum, London (BM); Museum of Natural History of Tulane University, New Orleans (TU); Field Museum of Natural History, Chicago (FMNH); and Musée de Strasbourg (SM).

Tribe Hypolobocerini Pretzmann, 1971

Hypolobocera Ortmann, 1897

Diagnosis.—First male gonopod with strong longitudinal caudal ridge. Lateral lobe well developed, sometimes reduced, varying according to species as triangular, rounded or subquadrate, and with or without crenulations over distal margin. Apex outline either rounded, oval, or elongated in distal view. Mesial lobe triangular, semicircular or reduced as strong fold. Third maxilliped with exognath 0.20–0.60 times length of ischium of endognath.

Type species.—*Potamia chilensis* H. Milne Edwards & Lucas, 1844.

Distribution.—Venezuela, Colombia, Ecuador and Perú.

Hypolobocera alata Campos, 1989

Fig. 1A–F

Hypolobocera alata Campos, 1989:145, fig. 2a–g.

Hypolobocera alata.—Rodríguez, 1992: 183.

Material examined.—Colombia. Huila Department, Villavieja, La Batea stream, 400 m alt., 3 Apr 1982, leg. R. Restrepo, ♂ holotype, 13.1 × 20.2 mm, 1 ♀ paratype, 13.4 × 21.4 mm, ICN-MHN-CR 0853.—Risaralda Department, Pueblo Rico, Corregimiento Santa Cecilia, Amurropa stream, 490 m alt., 26 Sep 1991, leg. G.A., 2 ♂, 12.3 × 19.5 mm, 10.1 × 15.2 mm, ICN-MHN-CR 1309; Vereda La Granja, 700 m alt., 22 Oct 1991, 1 ♂, 12.1 × 19.6 mm, ICN-MHN-CR 1306.—Chocó Department,

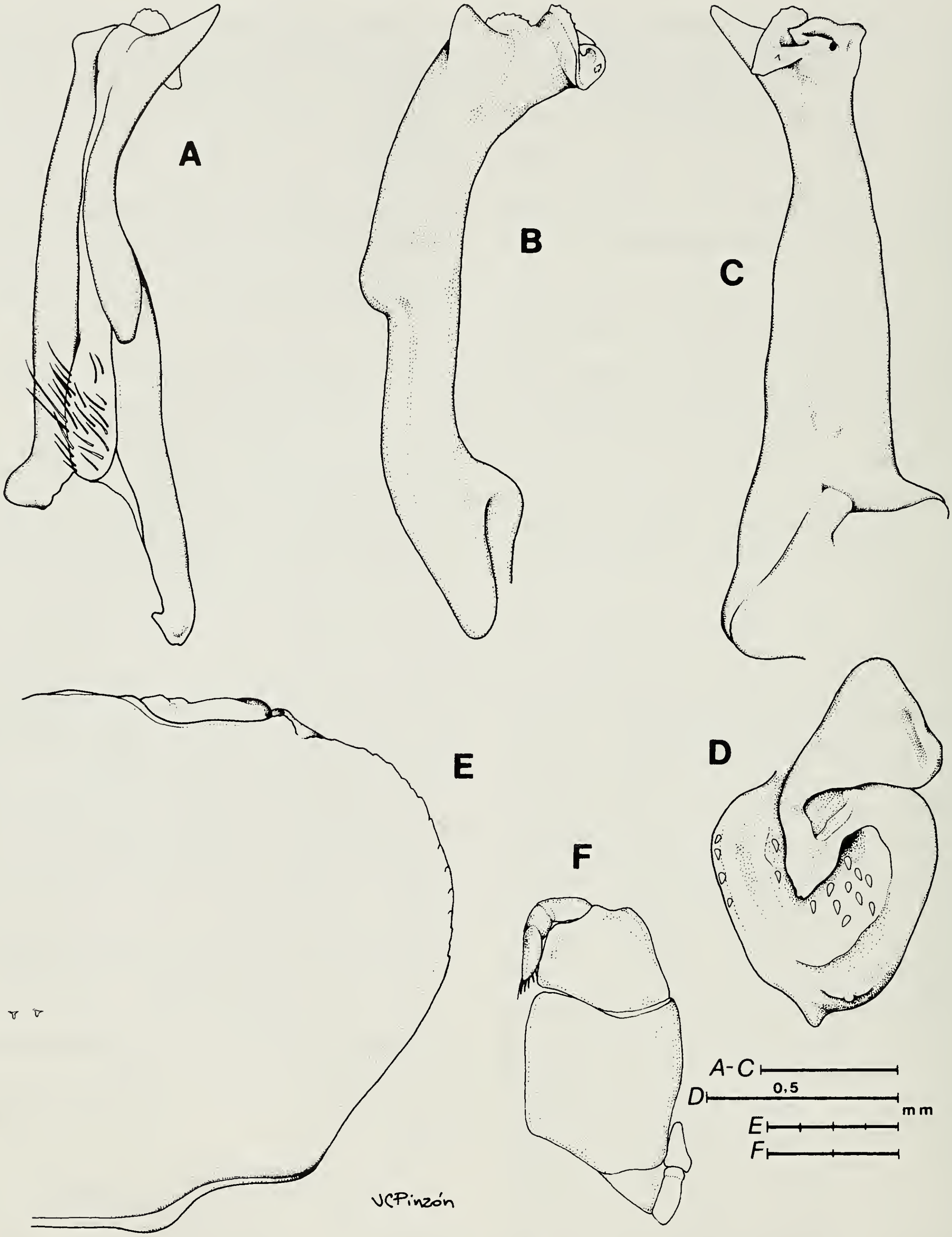

Fig. 1. *Hypolobocera alata* Campos, 1989, male, ICN-MHN-CR 1309: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, apex, distal view; E, right side of carapace, dorsal view; F, left third maxilliped, external view.

Tadó, Corregimiento Guarató, Guadralito stream, 500 m alt., 28 Sep 1991. leg. G. Andrade, 1 ♂, 12.1 × 19.4 mm, ICN-MHN-CR 1308.

Diagnosis.—First male gonopod narrow, strongly bent caudocephalically, distal caudal margin with row of blunt teeth (Fig. 1B). Caudal ridge long, strong, straight; ending beyond lateral lobe. Lateral lobe with strong triangular process (Fig. 1A–C).

Apex bent caudocephalically, apex outline oval in distal view, lateral border raised, with 4 acute spines near caudal border; cephalic border expanded into triangular projection, folded downwards, with rounded papilla on tip; prominent rounded cephalic papilla and small papilla on top. Mesocaudal projection of spermatic channel terminating in slightly bifid papilla. Mesial lobe subtriangular (Fig. 1B–D). Third maxilliped with exognath approximately 0.30 times length of ischium (Fig. 1F).

Remarks.—The type locality of *Hypolobocera alata* is Villavieja, Huila, located on the Magdalena River valley. Subsequently, other specimens were collected in Pueblo Rico, Risaralda, Western Cordillera, upper reaches of the San Juan River, and in Tadó, Chocó, Pacific coastal plain, middle course of the San Juan River. The first male gonopods of these specimens is identical to that of the holotype. Thus, it appears that the type locality may have been misreported, and *Hypolobocera alata* is actually found in the vicinity of Pueblo Rico, Risaralda, and Tadó, Chocó in the San Juan River basin.

Hypolobocera andagoensis
(Pretzmann, 1965)
Fig. 2A–G

Strengeria (*Strengeria*) *andagoensis* Pretzmann, 1965:6.

Hypolobocera (*Hypolobocera*) *andagoensis.*—Preztmann, 1971:17; 1972:51, figs. 170–172.

Hypolobocera andagoensis.—Rodríguez, 1982a:67, fig. 21c, e.—Prahl, 1988: 183.—Rodríguez, 1994:296, fig. 1a–c.

Material examined.—Colombia. Chocó Department. Andagoya, May 1957, leg. M. Latham, 1 ♂ holotype, 19.2 mm × 31.6 mm, USNM 106405.—No data, May 1957, leg. M. Latham, 13 ♂, 16.8 × 27.4 to 11.5 × 19.1 mm, 2 ♀, cl 20.8 × 34.9 mm, 17.5 × 28.8 mm, USNM 106407.—No data, May 1957, leg. M. Latham, 22 ♂, 12.5 × 30.2 to 8.9 × 15.2 mm, 25 ♀, 21.0 × 37.6 to 9.4 × 11.0 mm, USNM 106409.—Andagoya, Condoto and San Juan Rivers, leg. H. G. F. Spurrel, 1 ♀, 19.2 × 32.0 mm, BM 1915.11.1.1.—110 km N of Palestina, Docordó stream, affluent of San Juan River, 4°55′N, 76°55′W, 22 Jan 1971, leg. B. Malkin and P. Bouchard, 1 m, 20.6 × 32.0 mm, 2 ♀, cl 12.6 × 18.9 mm, 11.1 × 16.6 mm, FMNH 3676.

Diagnosis.—Chelae of male lacking tubercles on external base of mobile fingers and fixed fingers (Fig. 2G). First male gonopod with caudal ridge long, strong, slightly sinuous; almost reaching to apex (Fig. 2A). Lateral lobe prominent, subquadrate, narrower distally than proximally, external margin faintly crenulated; caudal surface partially excavated, (Fig. 2A, B). Apex outline oval in distal view, slightly expanded caudally; shallow notch on caudal border, and prominent cephalic papilla. Mesocaudal projection of spermatic channel terminating in acute papilla. Mesial lobe subtriangular (Fig. 2C, D). Third maxilliped with exognath approximately 0.25 times length of ischium (Fig. 2F).

Remarks.—In his original description, Pretzmann (1965) designated as holotype a male specimen from lot USNM 106405 (19.2 mm × 31.6 mm). However, Pretzmann (1972) changed the holotype lot as USNM 106407. Pretzmann designated 14 males and two females from USNM 196405 as paratypes, and incorrectly stated that the two lots were from the same locality. Pretzmann (1972) illustrated the whole holotype specimen (figs. 170, 171), and a detached first male gonopod (figs. 311, 312). As indicated by Rodríguez (1994), this appendage could not have belonged to the holotype (USNM 106405) as it was found still attached.

Hypolobocera beieri Pretzmann, 1968
Fig. 3A–H

Hypolobocera (*Hypolobocera*) *bouvieri beieri* Pretzmann, 1968:9; 1971:17; 1972: 46, figs. 176–181, 308, 309.

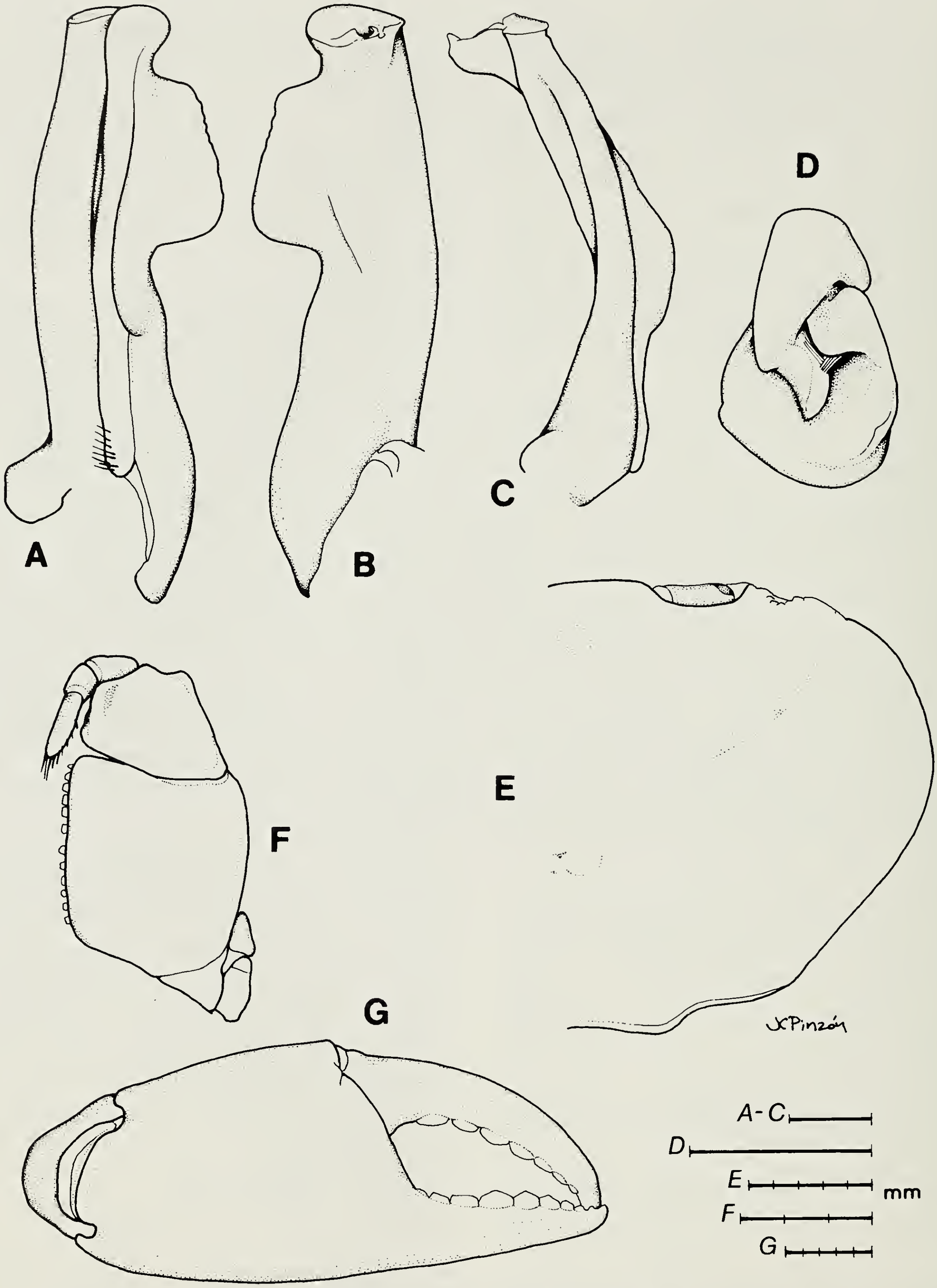

Fig. 2. *Hypolobocera andagoensis* (Pretzmann, 1965), male holotype, USNM 106405: A, left first gonopod, caudal view; B, same, cephalic view; C, same, mesial view; D, same, apex, distal view; E, carapace, dorsal view; F, left third maxilliped, external view; G, right chela, external view.

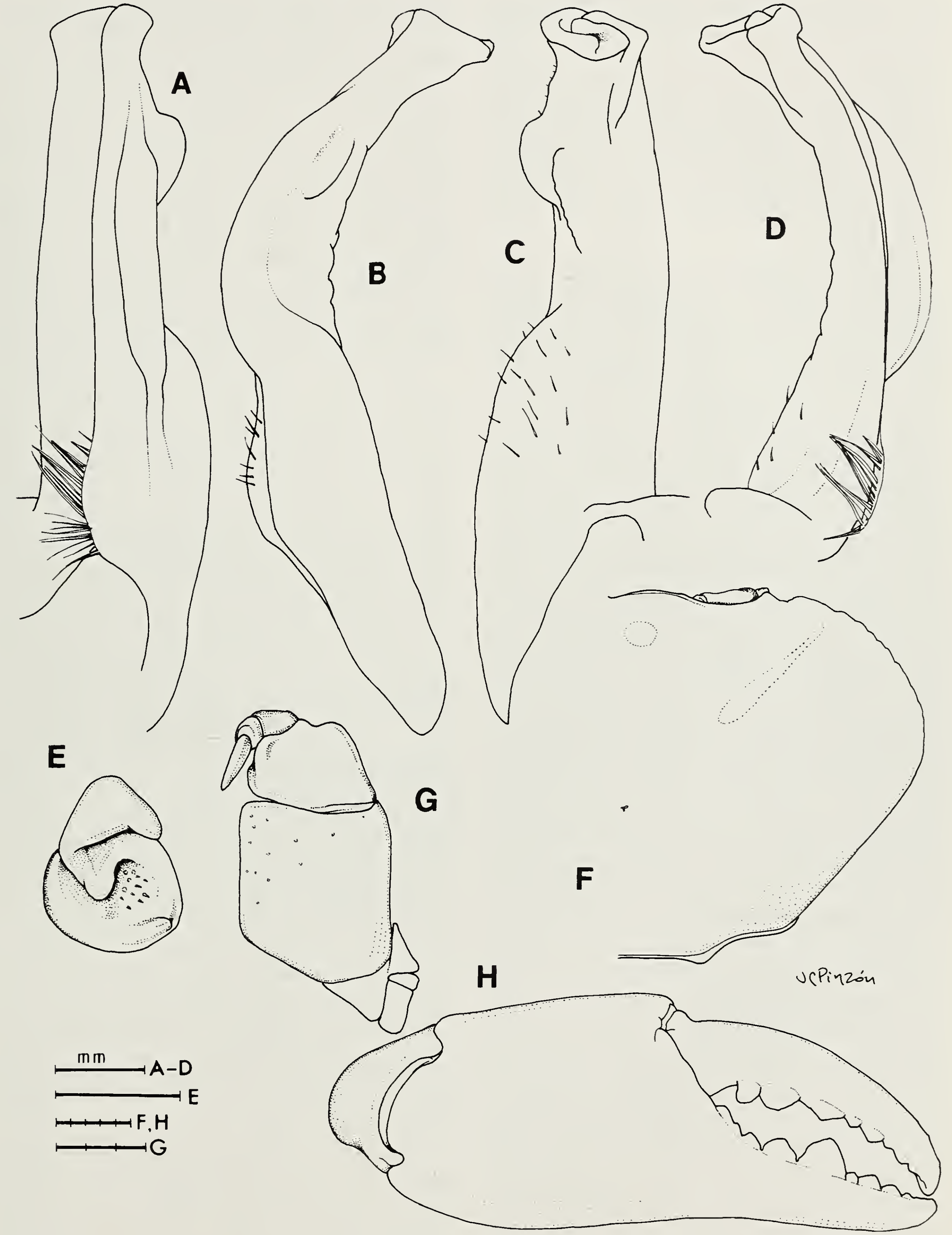

Fig. 3. *Hypolobocera beieri* Pretzmann, 1968, male, ICN-MHN-CR 1749: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, right chela, external view.

Hypolobocera (*Hypolobocera*) *monticola steindachneri*.—Pretzmann, 1972:46 (part.)

Hypolobocera beieri.—Rodríguez, 1982a: 46, figs. 19a, i, 20b, g, 24a–d.—Campos, 1985:275.—Prahl, 1985:43–47, figs. 1–7.—Prahl, 1988:172, fig. 2.—Rodríguez, 1994:297.—Rodríguez et al., 2002:3, 4, fig. 1J–K.

Material examined.—In addition to the material reported by Rodríguez (1982a), Prahl (1985), and Rodríguez et al. (2002), the following has been examined: Colombia, Valle del Cauca Department. Alto Anchicayá, 2 Oct 1982, leg. H. von Prahl, 1 ♂, carapace broken, TU 6383.—Dágua, Vereda El Carmen, Santa Clara Farm 2 Feb 1984, leg. F. Recio, 2 ♂, 27.3 × 45.5 mm, 25.2 × 42.4 mm, 2 ♀, cl 22.3 × 35.8 mm, 19.5 × 30.6 mm, CRBMUV 84059.—Tuluá, Vereda Salónica, 16 Aug 1982, leg. uk, 1 ♂, 17.3 × 27.9 mm, CRBMUV 84002.—La Victoria, San Miguel, 3 km from highway to Tacotá, 4 Feb 1984, leg. uk, 2 ♂, 17.4 × 29.6 mm, 13.9 × 23.8 mm, CRBMUV 84003.—Palmira, Corregimiento La Buitrera, 5 Sep 1986, leg. R. Neira, 5 ♀, 21.8 × 34.2 to 9.4 × 13.0 mm, CRBMUV 82046.—Palmira, Corregimiento La Buitrera, 25 Jun 1982, leg. R. Neira, 1 ♂, 20.8 × 32.9 mm, CRBMUV 82048.—Bugalagrande, Guadualillo, 6 Jan 1986, leg. R. Neira, 2 ♂, 14.8 × 22.9 mm, 11.2 × 16.7 mm, 2 ♀, 16.7 × 25.5 mm, 9.3 × 15.8 mm, CRBMUV 86035.—Old road to Buenaventura, Vereda La Elsa, La Elsa stream, 840 m alt., 25 Aug 1984, leg. H. Restrepo, 1 ♀, 30.7 × 48.6 mm, CRBMUV 84061.—Cali, Corregimiento Felidia, 6 Mar 1988, leg. uk, 3 ♀, 23.6 × 40.8 to 19.2 × 30.0 mm, CRBMUV 88019.—Dágua, Puerta del Diablo near to Tacotá, 3 Feb 1984, leg. H. Arteaga, 1 ♂, 16.9 × 27.7 mm, 1 ♀, 19.2 × 31.4 mm, CRBMUV 84066 (054 ADT-CRBMUV).—Jumbo, Vereda Manga Vieja, San Marcos stream, 4 Feb 1984, leg. uk, 1 ♂, 24.3 × 41.3 mm, 1 ♀, 30.7 × 48.1 mm, CRBMUV 84068.—Jamundí, San Antonio, 1 Apr 1984, leg. uk, 2 ♂, 20.9 × 33.8 mm, 19.8 × 30.5 mm, CRBMUV 84067.—Florida, Corregimiento Betania, 15 Dec 1984, leg. uk, 8 ♂, 21.8 × 34.0 to 11.3 × 16.9 mm, 5 ♀, 21.0 × 32.5 to 10.3 × 15.8 mm, CRBMUV 84076.—La Cumbre, 18 Feb 1984, leg. uk, 1 ♀, 21.7 × 34.0 mm, CRBMUV 84064.—Dágua, La Virgen stream, 8 Feb 1984, leg. F.R., 1 ♂, 16.4 × 25.8, 2 ♀, 22.3 × 34.9 mm, 13.5 × 19.9 mm, CRBMUV 84062.—Versalles, Inspección La Guavía, La Esperanza Farm, 8 Feb 1984, leg. uk, 2 ♂, 19.7 × 31.2 mm, 10.9 × 18.2 mm, CRBMUV 86006.—Ansermanuevo, Seca stream, 26 Feb 1984, leg. F.R., 3 ♂, 22.3 × 32.7 to 18.5 × 29.3 mm, CRBMUV 84080.—Bolivar, Betania, 15 Dec 1984, leg. J. Restrepo, 7 ♂, 21.8 × 34.1 to 11.3 × 16.9 mm, 5 ♀, 21.0 × 32.5 to 10.3 × 15.8 mm, CRBMUV 84076.—Cali, Villa Carmelo, Bellavista Farm, 5 Mar 1983, leg. N. Mesa, 1 ♂, 15.7 × 25.7 mm, 2 ♀, 12.5 × 20.6 mm, 9.6 × 14.9 mm, ICN-MHN-CR 0135.—Calima, Azul River, 1600 m alt., 8 Feb 1984, leg. R.R., 1 ♀, 20.0 × 31.5 mm, ICN-MHN-CR 0548.—Cali, Vereda Peñas Blancas, Pichindé River, 1000 m alt., 29 Sep 1977, 1 ♀, 19.3 × 31.4 mm, ICN-MHN-CR 1264.—Yotoco, 19 km from Buga to Buenaventura, La Cabaña Farm, 1450 m alt., 6 Nov 1998, leg. A. Suárez, 1 ♂, 26.7 × 44.5 mm, ICN-MHN-CR 1749.—Bolivar, Inspección Cerro Azul, 900 m alt., 22 Feb 1994, leg. E. Flórez, 1 ♂, 19.5 × 30.7 mm, ICN-MHN-CR 1881.—Chocó Department, between Cucurrupí and Noanamá, Docordó stream, 5 Jan 1969, leg. B. Malkin, 1 ♂, 23.5 × 35.1 mm, 2 ♀, 45.8 × 69.4 mm, 42.2 × 63.7 mm, FMNH 3689.

Diagnosis.—First male gonopod slender, bent caudocephalically (Fig. 3B). Caudal ridge strong, fusiform, thickened at middle; ending in narrow ridge beyond lateral lobe. Lateral lobe small, slightly rounded, placed far from apex. Cephalic surface with tuberculated ridge parallel to lateral lobe (Fig. 3A–D). Apex outline slightly oval in distal view, with beak-like projection on cephalic border; mesocephalic border transverse. Mesocaudal projection of spermatic channel terminated in rounded papilla. Mesial lobe subtriangular (Fig. 3C, E). Third maxilliped with exognath 0.30–0.40 times length of ischium (Fig. 3G).

Remarks.—Pretzmann (1972) considered the paratypes of this species to be *Hypolobocera* (*Hypolobocera*) *monticola steindachneri* Pretzmann, 1968. Rodríguez (1994), however, disagreed and designated the paratypes again as *Hypolobocera beieri,* based on features of the gonopod and the carapace.

Hypolobocera bouvieri bouvieri
(Rathbun, 1898)
Fig. 4A–H

Pseudothelphusa bouvieri Rathbun, 1898: 518, 533, 537, fig. 9.—Young, 1900: 215.—Rathbun, 1905:289.—Coifmann, 1939:107.

Strengeria (*Strengeria*) *bouvieri* Pretzmann, 1965:7.

Hypolobocera (*Hypolobocera*) *bouvieri* Schmitt, 1969:102.

Hypolobocera (*Hypolobocera*) *bouvieri bouvieri* Pretzmann, 1971:17.—Pretzmann, 1972:45, figs. 194–196, 278–280.

Hypolobocera bouvieri bouvieri.—Rodríguez, 1982a:55, 56, figs. 19, 21, 29.—Campos, 1985:276–277.—Rodríguez et al., 2002:6.

Material examined.—In addition to the material reported by Rodríguez (1982a), and Rodríguez et al. (2002), the following has been examined from six Colombian Departments. (1) Boyacá Department. Soatá, Vereda La Acosta, El Arenal Farm, Soatá-La Uvita Highway, 1500 m alt., 10 Aug 1988, 8 ♂, 30.1 × 49.0 to 17.3 × 27.2 mm, 10 ♀, 38.6 × 65.1 to18.7 × 29.3 mm, ICN-MHN-CR 0887.—Soatá, Vereda Llanogrande, Soatá-Duitama Highway, 2050 m alt., 11 Aug 1988, 3 ♂, 19.6 × 30.8 to 13.9 × 21.9 mm, 3 ♀, 18.2 × 28.6 to 15.3 × 24.3 mm, ICN-MHN-CR 0889.—Puerto Boyacá, Inspección Puerto Romero. Vereda Dosquebradas, 500 m alt., 18 Sep 1996, 9 ♂, 41.1 × 69.1 to 13.0 × 20.5 mm, 9 ♀, 54.1 × 90.4 to 15.1 × 23.6 mm, ICN-MHN-CR 1605, 1613.—Vereda La Fiebre, La Fiebrecita stream, 350 m alt., 20 Sep 1996, 7 m, 23.2 × 35.0 to 12.8 × 18.6 mm, 7 ♀, 50.2 × 81.9 to 21.0 × 33.1 mm, ICN-MHN-CR 1610, 1611.—Stream in Campamento Techint, 320 m alt., 26 Sep 1996, 1 ♀, 31.8 × 57.5 mm, ICN-MHN-CR 1625.—Honda stream, 400 m alt., 30 Sep 1997, leg. E. Flórez, 1 ♂, 32.1 × 50.7 mm, ICN-MHN-CR 1784.—Vereda La Cristalina, La Cristalina stream, 350 m alt., 4 Mar 2000, leg. L. Annichianico, 2 ♀, 22.9 × 35.0 mm, 17.0 × 26.1 mm, ICN-MHN-CR 1841.—Vereda La Fiebre, La Fiebre stream, 380 m alt., 5 Mar 2000, leg. J. Gonzáles, 1 ♂, 18.4 × 28.5 mm, ICN-MHN-CR 1843.—Vereda La Fiebre, El Golfo Farm, 450 m alt., 8 Mar 2000, leg. N. Garzón, 3 ♂, 47.8 × 79.4 to 23.5 × 37.0 mm, 3 ♀, 31.4 × 48.8 to 11.7 × 25.6 mm, ICN-MHN-CR 1847.—Vereda El Oasis, Dosquebradas stream, 520 m alt., 9 Mar 2000, leg. N. Rodríguez, 1 ♀, 61.4 × 101.3 mm, ICN-MHN-CR 1849.—Puerto Boyacá, Vereda El Terminal, El Terminal stream, 320 m alt., 22 Sep 1996, 1 ♂, 23.3 × 34.6 mm, 4 ♀, 40.6 × 64.0 to 19.9 × 29.6 mm, ICN-MHN-CR 1615.—Puerto Boyacá, Vereda La Pizarra, La Pizarra stream, 270 m alt., 25 Sep 1996, 2 ♂, 18.6 × 30.0 mm, 13.0 × 18.5 mm, 4 ♀, 30.7 × 46.2 to 16.7 × 24.4 mm, ICN-MHN-CR 1624.—Otanche, Vereda El Oasis, Honda stream, 625 m alt., 19 Sep 1996, 1 ♂, 27.1 × 43.4 mm, 1 ♀, 62.6 × 102.5 mm, ICN-MHN-CR 1607. (2) Caldas Department. Samaná, Vereda La Miel, Campamento Tasajos, affluent of La Miel River, 550 alt., 18–25 Apr 1994, 2 ♀, cl 41.0 × 64.7 mm, 39.8 × 64.0 mm, 1 juvenile, ICN-MHN-CR 1329, 1345.—Samaná, km 1.3 Samaná-Los Pomos Highway, 1100 m alt., 24 Apr 1994, leg. P. M. Ruiz, 1 ♀, 19.4 × 30.2 mm, ICN-MHN-CR 1352.—Samaná, La Cristalina River, 430 m alt., 25 Apr 1994, leg. P. M. Ruiz, 1 ♀, 26.4 × 41.3 mm, ICN-MHN-CR 1354.—Victo-

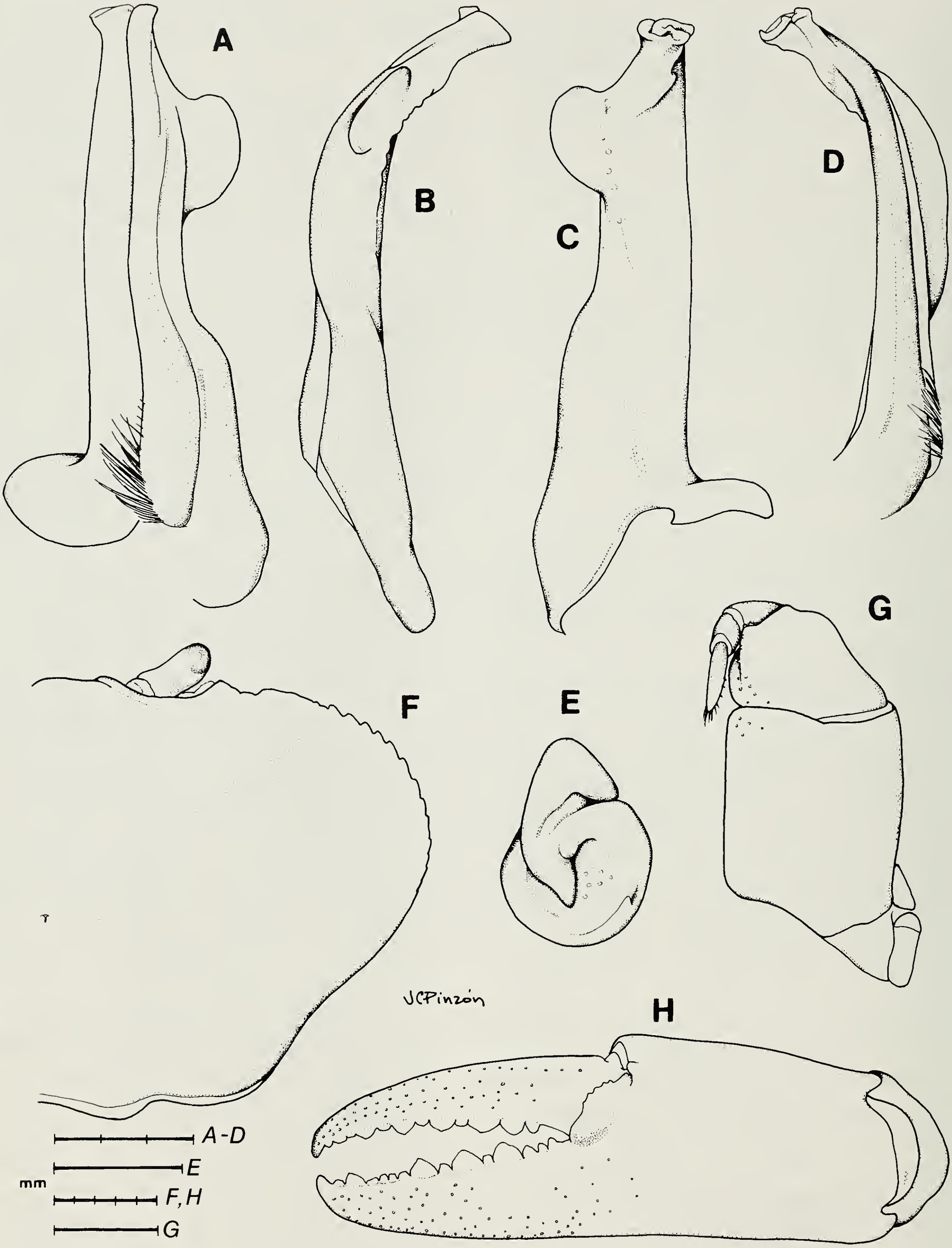

Fig. 4. *Hypolobocera bouvieri bouvieri* (Rathbun, 1898), male, ICN-MHN-CR 1556: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, left chela, external view.

ria, Vereda Hamburgo, Albión stream, 900 m alt., 19–24 Apr 1994, 4 ♂, 30.9 × 46.6 to 13.4 × 21.5 mm, 6 ♀, 49.2 × 82.1 to 15.0 × 22.9 mm, ICN-MHN-CR 1331, 1332, 1343.—Victoria, Vereda Canaán, Victoria-Samaná Highway, 1100 m alt., 19 Apr 1994, 1 ♂, carapace broken, ICN-MHN-CR 1334. (3) Cundinamarca Department. La Mesa, 1991, leg. C. Vieira, 1 ♂, 21.9 × 31.3 mm, CRBMUV 81067.—Sasaima, 14 Mar 1982, 4 ♂, 23.4 × 34.7 to 15.4 × 23.3 mm, 1 ♀, 19.9 × 30.2 mm, CRBMUV 82049, 82050.—Sasaima, El Tranvía stream, 1500 m alt., 26 Feb 1984, 7 Jul 1986, 1 ♂, 41.1 × 61.9 mm, 1 ♀, 32.7 × 50.9 mm, ICN-MHN-CR 0545, 0637.—Sasaima, Vereda Guane, Miramar Farm, 1300–1450 m alt., 21 Apr 1987, 5 ♂, 24.0 × 36.9 to 11.7 × 17.8 mm, 4 ♀, 21.5 × 32.8 to 15.4 × 24.0 mm, ICN-MHN-CR 0719, 0721.—San Antonio de Tequendama, Inspección Santandercito, 22 Sep 1982, 18 Mar 1983, leg. H. von Prahl, 1 ♂, 43.0 × 71.2 mm, 4 ♀, 46.4 × 76.0 mm to 32.8 × 51.0 mm, CRBMUV 82054, 83087.—San Antonio del Tequendama, San Antonio del Tequendama-Araujo Highway, 1450 m alt., 24 Apr 1987, 2 ♂, cl 39.5 × 61.8 mm, 31.5 × 50.4 mm, ICN-MHN-CR 0752.—San Antonio del Tequendama, Vereda San José, Barbosa stream, 1500 m alt., 24 Apr 1987, 1 ♂, 24.1 × 37.6 mm, 1 ♀, 45.0 × 72.3 mm, ICN-MHN-CR 0754.—San Antonio del Tequendama, Vereda Laguna Grande, El Curí stream, 1550 m alt., 6 Apr 1989, 7 ♂, 20.0 × 30.5 to 16.3 × 24.5 mm, 4 ♀, 23.2 × 36.8 to 16.2 × 24.1 mm, ICN-MHN-CR 0947.—Quebradanegra, Vereda Nacederos, 1250 m, 4 Mar 1983, 2 ♂, 45.5 × 77.2 mm, 35.0 × 56.8 mm, ICN-MHN-CR 0129, 0130.—Quebradanegra, Corregimiento La Magdalena, highway to Utica, 1300 m alt., 4–5 Mar, 23 Aug 1983, 3 ♂, 47.1 × 77.4 to 31.1 × 50.5 mm, 5 ♀, 48.2 × 76.8 to 16.3 × 24.6 mm, ICN-MHN-CR 0131, 0132, 0133, 0134, 0513, 0514.—Quebradanegra, Corregimiento La Magdalena, Paraiso Farm, 1180 m alt., 24 Aug 1983, 4 ♂, 31.0 × 49.3 to 13.2 × 20.3 mm, 1 ♀, 17.8 × 26.9 mm, ICN-MHN-CR 0516, 0517, 0519.—Quebradanegra, Vereda Pilares, Honduras stream, 800 m alt., 21 Apr 1987, 1 ♂, 44.5 × 75.5 mm, ICN-MHN-CR 0722.—Guaduas, Vereda El Trigo, San Francisco River, 1300–1650 m alt., 6 Mar, 22 Jun 1983, 5 ♂, 57.6 × 94.7 to 13.9 × 22.5 mm, 2 ♀, 56.4 × 91.0 mm, 53.6 × 86.4 mm, ICN-MHN-CR 0136, 0137, 0138, 0456.—Guaduas, Vereda Versalles, El Chocho stream, 1050 m alt., 20 Apr 1983, 1 ♂, 39.5 × 63.4 mm, 3 ♀, 54.4 × 89.1 to 41.9 × 65.3 mm, ICN-MHN-CR 0143, 0144, 0145, 0146.—Guaduas, Vereda Cucharal, Vallarta Farm, 1300 m alt., 21 Apr 1983, 1 ♂, 51.6 × 86.3 mm, 1 ♀, 44.4 × 73.3 mm, ICN-MHN-CR 0448, 0449.—Guaduas, Corregimiento Guaduero, Varelas stream, 575 m alt., 21 Jun 1983, 2 ♂, 14.3 × 22.2 mm, 18.1 × 27.4 mm, 1 ♀, 19.9 × 31.7 mm, ICN-MHN-CR 0462, 0480.—Guaduas, Vereda El Raizal y Cajón, 1300 m alt., 22 Jun 1983, 2 ♂, cl 55.2 × 91.3 mm, 24.2 × 35.6 mm, 1 ♀, 48.8 × 78.8 mm, ICN-MHN-CR 0467–0469.—Guaduas, Chaguaní stream, 1075 m alt., 24 Jun 1983, 4 ♂, 22.8 × 37.0 to 14.3 × 22.2 mm, 1 ♀, 19.8 × 31.3 mm, ICN-MHN-CR 0474, 0475, 0476.—La Paz, Vereda Carrapal, Carrapal stream, 1050 m alt., 19 Apr 1983, 3 ♂, 33.0 × 54.5 to 26.6 × 43.0 mm, ICN-MHN-CR 0141, 0142.—Caparrapí, Corregimiento El Dindal, El Ajón stream, 560–580 m alt., 21, 22 Jun 1983, 10 ♂, 32.7 × 51.2 to 14.7 × 20.8 mm, ICN-MHN-CR 0459, 0460, 0463–0465.—Caparrapí, Vereda Varelas, Carrapal stream, 550 m alt., 23 Jun 1983, 4 ♂, 39.3 × 64.6 to 21.3 × 32.4 mm, 5 ♀, 29.3 × 46.8 to 15.0 × 22.2 mm, ICN-MHN-CR 0470–0473.—Utica, km 7 highway to La Palma, La Guayabala stream, 775 m alt., 25–26 Aug 1983, 9 ♂, 38.9 × 62.1 to 16.3 × 24.2 mm, 2 ♀, 36.9 × 58.3 mm, 26.7 × 43.0 mm, ICN-MHN-CR 0520–0524.—Guayabal de Síquima, 1400 m alt., 4 Mar 1984, 4 ♂, 17.8 × 27.9 to 10.9 × 16.2 mm, 2 ♀, 14.6 × 23.0 mm, 12.8 × 19.6 mm, ICN-MHN-CR 0546.—Viotá, Vereda Atalá, 1200 m alt., 19 May 1984, leg. J. M. Torres, 1 ♂, 53.8 × 88.0 mm, ICN-MHN-CR 0574.—Tena, Vereda El Rosario, 1500 m alt., 6 Jun 1984, 1 ♂, 39.2 × 62.8 mm, 1 ♀, 48.6 × 81.1 mm, ICN-MHN-CR 0589.—Tena, Vereda El Rosario, Tena-Los Alpes Highway, 1350–1450 m alt., 23–24 Apr 1987, 8 Apr 1989, 5 ♂, 50.3 × 79.8 to 17.7 × 28.1 mm, 10 ♀, 48.7 × 79.0 to 18.0 × 26.8 mm, ICN-MHN-CR 0735–0737, 0748, 0945.—Tena, 2 km highway to San Antonio de Tequendama, 1150 m alt., 24 Apr 1987, 1 ♂, 19.7 × 30.4 mm, 2 ♀, 46.0 × 74.0 mm, 42.9 × 70.1 mm, ICN-MHN-CR 0741, 0742.—Tena, Vereda Guasimal, Las Mercedes Farm, 1100 m alt., 24 Apr 1987, 1 ♀, 27.7 × 43.2 mm, ICN-MHN-CR 0743.—Villeta, Vereda La Masata, Cune stream, 850 m alt., 30 Jan 1985, leg. E. Linares, 4 ♂, 11.7 × 17.9 to 10.3 × 15.2 mm, ICN-MHN-CR 0611.—Villeta, Vereda Cune, La Lorena Farm, 1000 m alt., 22 Apr 1987, 5 ♂, 30.2 × 48.6 to 18.2 × 27.7 mm, 4 ♀, 27.2 × 43.7 to 11.7 × 18.1 mm, ICN-MHN-CR 0723–0725.—San Francisco, San Miguel stream, 1500 m alt., 8 Mar 1987, leg. J. Gaitán, 1 ♂, carapace broken, ICN-MHN-CR 0684.—La Vega, Vereda Tierra Vieja, La Vega-Sasaima Highway, 1250 m alt., 20 Apr 1987, 1 ♂, 21.5 × 35.2 mm, ICN-MHN-CR 0716.—Anolaima, Vereda Pinimá, 1400 m alt., 23 Apr 1987, 4 ♂, 35.0 × 54.5 to 13.8 × 21.7 mm, ICN-MHN-CR 0729.—Cachipay, Vereda La María, El Salitre stream, 1000 m alt., 23 Apr 1987, 1 ♂, 47.9 × 79.8 mm, 1 ♀, 24.6 × 38.6 mm, ICN-MHN-CR 0731.—Cachipay, Cantagallo and El Refugio streams, 1800 m alt., 7 Jan 1996, leg. R. Casallas, 1 ♂, 18.8 × 29.2 mm, ICN-MHN-CR 1658.—La Mesa, Vereda El Rosario, Los Micos stream, 1200 m alt., 23 Apr 1987, 1 ♂, 25.5 × 40.2 mm, 2 ♀, cl 40.1 × 65.1 mm, 34.0 × 55.1 mm, ICN-MHN-CR 0734.—La Mesa, Vereda Zapata, 1200 m alt., 24 Apr 1987, 2 ♀, 25.4 × 41.7 mm, 14.0 × 22.0 mm, ICN-MHN-CR 0739.—La Mesa, Tres Esquinas, 1200 m alt., 24 May 1987, leg. R. Jaramillo, 1 ♀, 38.4 × 60.0 mm, ICN-MHN-CR 0759.—La Mesa, Vereda Florían, Payacala stream, 1200 m alt., 22 May 1989, leg. C. Galán, 2 ♂, cl 52.3 × 87.3 mm, 48.9 × 82.5 mm, ICN-MHN-CR 0960.—Mesitas del Colegio, Vereda Coiba, 990 m alt., 29 Sep 1990, leg. G. Acosta, 4 ♂, 29.5 × 47.8 to 15.5 × 23.5 mm, 2 ♀, 22.1 × 34.9 mm, 18.1 × 27.2 mm, ICN-MHN-CR 1202.—Fusagasugá, Vereda La Pampa, Fusa-Chinauta Highway, 2000 m alt., 8 Jan 1993, leg. M. Ramírez, 1 ♀, 47.4 × 77.5 mm, ICN-MHN-CR 1293.—Silvania, Vereda Panamá Alta, San Antonio de los Bogas Farm, El Hato stream, 1830 m alt., 8 Aug 1995, leg. R. Restrepo, 1 ♀, 43.0 × 73.0 mm, ICN-MHN-CR 1458.—Yacopí, Inspección Aposentos, El Hático stream, 850 m alt., 26 Oct 1995, leg. G. Galvis, 1 ♀, 19.0 × 30.4 mm, ICN-MHN-CR 1512.—Yacopí, Inspección Guadualito, Vereda La Laguna, 900–1050 m alt., 28–29 Oct 1995, 2 ♂, 41.7 × 67.0 mm, 30.2 × 47.0 mm, 1 ♀, 34.2 × 55.7 mm, ICN-MHN-CR 1519–1521.—Yacopí, Inspección Guadualito, Vereda Lamal, Agua Blanca stream, 700 m alt., 31 Oct–4 Nov 1995, 2 ♂, 56.2 × 90.1 mm, 11.6 × 17.4 mm, 4 ♀, 54.5 × 86.2 to 11.3 × 17.1 mm, ICN-MHN-CR 1524, 532, 1535.—Yacopí, Inspección Guadualito, Vereda Gramales, Barbascales, Salitrona stream, 740 m alt., 2 Nov 1995, 1 ♂, 17.0 × 26.0 mm, ICN-MHN-CR 1528.—Yacopí, Inspección Guadualito, Vereda Lamal, Albercas, 900 m alt., 3 Nov 1995, 1 ♀, 55.0 × 89.3 mm, ICN-MHN-CR 1529.—Yacopí, Vereda La Oscura, La Oscura stream, 350 m alt., 24 Sep 1996, 6 ♂, 40.5 × 64.8 to 12.6 × 15.6 mm, 8 ♀, 24.4 × 37.2 to 10.6 × 15.6 mm, ICN-MHN-CR 1621. (4) Norte de Santander Department. Pamplonita, stream near to town, 1600 m alt., 26 Mar 1987, 2 ♂, 20.0 × 30.2 mm, 20.6 × 31.0 mm, 1 ♀, 29.8 × 46.2 mm, ICN-MHN-CR 0691.—Pamplonita, Vereda San José de Cunutá, 1100–1250 m alt., 26 Mar 1987, 2 ♂, 39.5 × 63.2 mm, 32.8 × 51.3 mm, ICN-MHN-CR 0692, 0693.—Chinácota, Vereda El Urengue, 1075 m alt., 26 Mar 1987, 1 ♂, 35.2 × 57.3

mm, ICN-MHN-CR 0694.—Chinácota, Vereda Sonival, Chinácota-Toledo Highway, 1600 m alt., 27 Mar 1987, 1 ♀, 42.0 × 67.7 mm, ICN-MHN-CR 0699.—Chinácota, Vereda El Asilo, Cácua stream, Chinácota-Ragonvalia Highway, 1600 m alt., 9 Oct 1988, 1 ♀, 34.6 × 55.2 mm, ICN-MHN-CR 0928.—Bucarasica, Vereda Santa Rita, Sardinata-Ocaña Highway, 400 m alt., 29 Mar 1987, 3 ♂, 21.6 × 35.2 to 14.2 × 22.5 mm, 1 ♀, 16.5 × 25.5 mm, ICN-MHN-CR 0703.—Bucarasica, Vereda Fortunas, Sardinata-Ocaña Highway, 500 m alt., 29 Mar 1987, 10 ♂, 19.4 × 31.4 to 12.5 × 20.1 mm, 3 ♀, 26.9 × 44.4 to 16.7 × 26.0 mm, ICN-MHN-CR 0704.—Bochalema, Corregimiento La Donjuana, Vereda Cachirí, Durania-Lamus Highway, 1050 m alt., 30 Mar 1987, 1 ♂, 22.5 × 36.1 mm, 1 ♀, 18.0 × 27.7 mm, ICN-MHN-CR 0705.—Bochalema, Corregimiento La Donjuana, Vereda Cachirí, 1125 m alt., 30 Mar 1987, 5 ♀, 26.8 × 41.8 to 11.2 × 17.6 mm, ICN-MHN-CR 0706.—Durania, Vereda La Palma, Lavapatas stream, 900 m alt., 31 Mar 1987, 6 ♂, 34.6 × 55.6 to 16.0 × 24.5 mm, 1 ♀, 33.8 × 55.9 mm, ICN-MHN-CR 0708.—Cucutilla, Vereda Cuesta Rica, Limoncito stream, 1700 m alt., 8 Oct 1988, 1 ♀, 25.9 × 38.6 mm, ICN-MHN-CR 0926.—Cucutilla, Vereda Aguada Bajo, Pamplona-Cucutilla Highway, 1450 m alt., 8 Oct 1988, 1 ♀, 35.1 × 56.5 mm, ICN-MHN-CR 0927. (5) Santander Department. Piedecuesta, Vereda El Fical, San Miguel stream, 950 m alt., 1 Apr 1987, 3 ♂, 33.8 × 55.2 to 20.1 × 35.7 mm, 13 ♀, 37.3 × 61.0 to 20.1 × 33.3 mm, ICN-MHN-CR 0710.—Aratoca, Vereda Monterredondo, San Miguel stream, 1650 m alt., 1 Apr 1987, 1 ♂, 19.6 × 30.0 mm, 1 ♀, 18.8 × 45.4 mm, and 15 juveniles, ICN-MHN-CR 0711.—Simacota, Vereda Náuno, Socorro-Simacota Highway, 1050 m alt., 22 Sep 1988, 3 ♂, 19.1 × 28.8 to 16.4 × 24.9 mm, 2 ♀, 18.7 × 28.9 mm, 15.6 × 23.7 mm, and 2 juveniles, ICN-MHN-CR 0906.—Simacota, Vereda Pedregales, San Miguel stream, Sogamoso-Simacota Highway, 950 m alt., 22 Sep 1988, 2 ♂, 39.3 × 62.7 mm, 14.7 × 22.1 mm, ICN-MHN-CR 0907.—Chima, Vereda Tierra Amarilla, El Guamal stream, Simacota-Chima Highway, 1050 m alt., 22 Sep 1988, 1 ♂, 26.3 × 41.4 mm, ICN-MHN-CR 0908.—Suáita, Vereda La Aguadita, La Aguadita stream, 1600 m alt., 5 Jan 1994, leg. A. Rodríguez, 3 ♂, 16.7 × 29.5 to 12.2 × 19.3 mm, ICN-MHN-CR 1452. (6) Tolima Department. 8 km South of Ibagué, Combeima River, 12 Jun 1977, leg. H. Díaz, 1 ♂, 52.0 × 84.0 mm, 6 ♀, 54.3 × 88.4 to 45.2 × 71.5 mm, IVIC.—Icononzo, Las Lajas stream, 1070 m alt., 28 Mar 1978, leg. C. Escallón, 3 ♂, 37.1 × 60.6 to 35.3 × 57.2 mm, ICN-MHN-CR 0499, 0500, 0501.—Icononzo, Vereda Chaparro, La Juanita Farm, 1200 m alt., 16 Nov 1986, 1 ♂, 25.5 × 40.7 mm, ICN-MHN-CR 0681.

Diagnosis.—Chelae of male with small rounded or oblong tubercle on external base of mobile fingers, and prominent, rounded tubercle on external base of fixed fingers (Fig. 4H). First male gonopod with caudal ridge long, slightly sinuous; ending in narrow ridge beyond lateral lobe (Fig. 4A). Lateral lobe semicircular, with or without crenulations over distal margin. Cephalic surface with transverse crest on distal half, and tuberculated ridge parallel to lateral lobe (Fig. 4A–D). Apex outline oval, borders raised; prominent cephalic papilla and auxiliary rounded papilla near spermatic channel. Mesocaudal projection of spermatic channel terminating in blunt papilla. Mesial lobe subtriangular (Fig. 4D, E). Third maxilliped with exognath 0.20–0.30 times length of ischium (Fig. 4G).

Remarks.—This subspecies is widely distributed in the slopes of the Central and Eastern Cordilleras where waters drain to the Magdalena River. In males, the main feature that distinguishes this subspecies from the others are the chelae, which feature a prominent, rounded tubercle on the external base of the fixed fingers (Fig. 4H).

Hypolobocera bouvieri angulata (Rathbun, 1915)
Fig. 5A–H

Pseudothelphusa angulata Rathbun, 1915: 98.—Coifmann, 1939:106.—Rodríguez, 1966:129, fig. 9.—Rodríguez, 1967:10.

Strengeria (*Strengeria*) *angulata* Pretzmann, 1965:7.

Hypolobocera (*Hypolobocera*) *bouvieri angulata* Pretzmann, 1971:17, pl. 17.—Pretzmann, 1972:45, figs. 156–158, 208–210.

Hypolobocera bouvieri angulata.—Rodríguez, 1982a:56–57.—Rodríguez, 1994: 299.—Campos, 1985:275–276, Rodríguez et al., 2002:6.

Material examined.—In addition to the material reported by Rodríguez (1982a), and Rodríguez et al. (2002), the following has been examined: Colombia, Magdalena Department. Santa Marta, Minca, 880 m alt., M holotype, 40.0 × 65.0 mm, USNM 98398.—Sierra Nevada de Santa Marta, 10 Aug 1987, leg. uk, 1 ♂, 30.4 × 47.9 mm, CRBMUV 87014.—Santa Marta, Parque Nacional, Natural Tayrona, Los Cedros. 2–6 Jul 1983, leg. G. Galvis. 4 ♂, 43.3 × 61.4 to 16.1 × 25.8 mm, 6 ♀, 42.6 × cb 59.0 to 16.8 × 24.6 mm, ICN-MHN-CR 0528–0530.—Santa Marta, Minca, 850 m alt., 23 May 1989, leg. R. Sánchez, 1 ♀, 34.6 × 55.6 mm, ICN-MHN-CR 0961.—Santa Marta, Vereda Alto Guachaca, stream affluent of Guachaca River, 700 m alt., 30 Sep 1992, leg. A. Ferrer, 1 ♀, 54.6 × 87.4 mm, ICN-MHN-CR 1296.—Cesar, Serranía de Perijá, La Jagua de Ibirico, Corregimiento La Victoria de San Isidro. Vereda Alto de las Flores, stream near Escuela Nueva de las Flores, 1200 m alt., 8 Mar 1996, 2 ♂, 47.5 × 79.2 mm, 21.9 × 33.3 mm, 1 ♀, 13.4 × 19.9 mm, ICN-MHN-CR 1551, 1556.—Vereda Nueva Granada, El Indio stream, 590 m alt., 9 Mar 1996, 4 ♂, 57.3 × 95.5 to 15.8 × 23.9 mm, 2 ♀, 48.0 × 78.1 mm, 20.0 × 31.4 mm, ICN-MHN-CR 1554, 1555, 1573.—Vereda El Zumbador, El Zumbador stream, 400 m alt., 10 Mar 1996, 2 ♂, 19.8 × 30.7 mm, 20.6 × 31.5 mm, 6 ♀, 38.2 × 59.5 to 13.0 × 20.3 mm, ICN-MHN-CR 1557.—Vereda Alto de las Flores, Tucuy River, 915 m alt., 11 Mar 1996, 2 ♂, 29.9 × 34.6 mm, 21.0 × 32.0 mm, 1 ♀, 21.8 × 35.2 mm, ICN-MHN-CR 1558.—Vereda El Zumbador, Zumbador River, 1000 m alt., 14–17 Mar 1996, 8 ♂, 48.3 × 73.9 to 15.0 × 23.0 mm, 16 ♀, 54.2 × 89.2 to 8.3 × 13.8 mm, 2 juveniles, ICN-MHN-CR 1563, 1564, 1566, 1567.—Vereda Nueva Granada, Buenavista Farm, Zumbador River, 500 m alt., 20 Mar 1996, leg. O. V. Castaño, 1 ♂, 24.1 × 36.7 mm, 1 ♀, 42.4 × 69.9 mm, ICN-MHN-CR 1572.—

Venezuela. Estado Zulia, Serranía de Perijá, Socuy River, Cueva Los Laureles, 1300 m, alt., 20 Dec 1990, leg. A. L. Viloria and T. R. Barros, 1 ♂, 39.8 × 62.1 mm, IVIC.—Estado Zulia, Serranía de Perijá, Socuy River, Los Encantos, 850 m, alt., 20 Dec 1995, leg. F. Herrera, 1 ♂, 29.5 × 47.7 mm, IVIC.

Diagnosis.—Chelae of male with small tubercle on external base of mobile fingers, and swelling on external base of fixed fingers (Fig. 5H). First male gonopod with caudal ridge long, either sinuous or straight; ending in narrow ridge beyond lateral lobe (Fig. 5A, B). Lateral lobe usually subtriangular with small crenulations on distal margin. Cephalic surface with transverse crest on distal half and tuberculated ridge parallel to lateral lobe (Fig. 5A–D). Apex outline oval in distal view; prominent cephalic papilla, and auxiliary rounded papilla near spermatic channel. Mesocaudal projection of spermatic channel terminating in slightly acute papilla. Mesial lobe subtriangular (Fig. 5D, E). Third maxilliped with exognath 0.20–0.32 times length of ischium (Fig. 4G).

Remarks.—This subspecies is broadly distributed in an area that reaches from the Sierra Nevada de Santa Marta to both slopes of the Sierra de Perijá and the Cordillera de Mérida in Venezuela. The distribution includes two disjunct areas that cover two different basins: the Cesar, and the

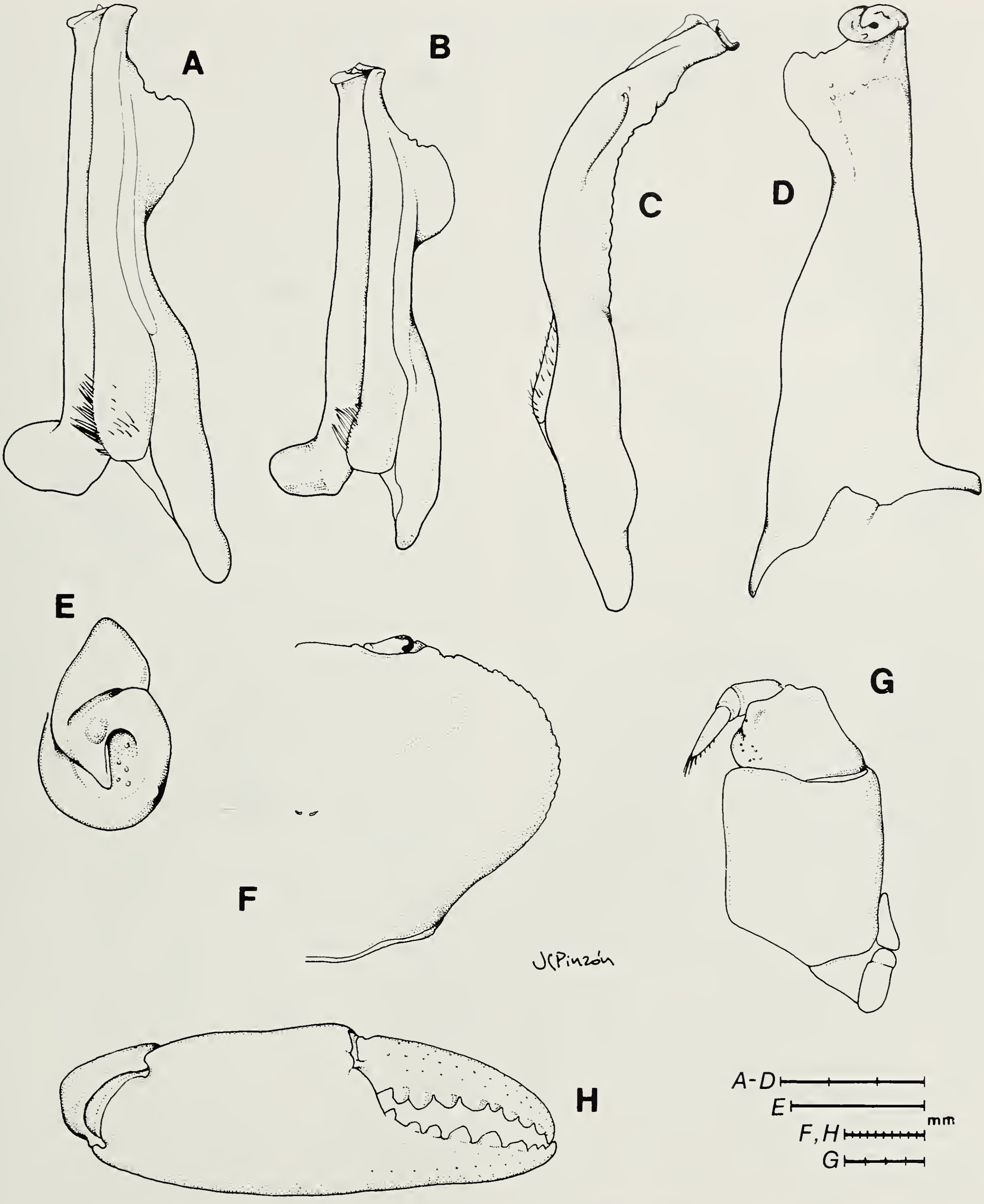

Fig. 5. *Hypolobocera bouvieri angulata* (Rathbun, 1915), male, Colombia, Santa Marta, ICN-MHN-CR 0528: A, left first gonopod, caudal view; C, same, lateral view; D, same cephalic view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, right chela, external view. Male, Venezuela, Estado Zulia, Serranía de Perijá, Socuy River, IVIC: B, left first gonopod, caudal view.

Catatumbo Rivers. This type of distribution, possibly due to temperature differences, is considered a relict distribution. There are slight differences in the first male gonopods of the specimens found in the Sierra Nevada de Santa Marta in Colombia and in the Sierra de Perijá in Venezuela. The most significant difference is the shape of the lateral lobe, which is slightly semicircular (Fig. 5B). This difference is most likely caused by different environmental conditions.

Hypolobocera bouvieri monticola
(Zimmer, 1912)
Fig. 6A–H

Pseudothelphusa monticola Zimmer, 1912: 3, figs. 6–10, pl. 1.—Coifmann, 1939: 108.

Strengeria (*Strengeria*) *monticola* Pretzmann, 1965:7.

Hypolobocera (*Hypolobocera*) *monticola monticola* Pretzmann. 1971:17.—Pretzmann, 1972:46, figs. 197–199, 206, 207.

Hypolobocera bouvieri monticola.—Rodríguez, 1982a:56, figs. 19, 21, 30.

Material examined.—Colombia. (1) Antioquia Department. 28 Jun 1966, leg. uk, 1 ♂, 22.7 × 37.1 mm, CRBMUV 66001.—Los Lagos, leg. uk, 1 ♂, carapace broken, CRBMUV 67001.—Caucasia, Rojo River, 5 Jan 1969, leg. M. Serna, 1 ♂, 23.8 × 38.7 mm, 1 ♀, 14.5 × 26.1 mm, CRBMUV 69002.—San Luis, Vereda Manizales, 1600 m alt., 12 Nov 1981, leg. P. Pinto, 1 ♀, 49.5 × 85.9 mm, ICN-MHN-CR 0128.—Santa Fé de Antioquia, Vereda Chaparral, highway to Guasabra, 1600 m alt., 6 Jan 1988, leg. M. T. Murillo, 2 ♂, 24.3 × 39.7 mm, 15.6 × 24.4 mm, 2 ♀, 20.1 × 36.0 mm, 15.0 × 23.0 mm, CN-MHN-CR 0849.—Urrao, Valle de Pérdidas, 1700 m alt., 1 Sep 1994, leg. P. Duque, 2 ♂, cl 21.0 × 32.7 mm, 14.0 × 21.4 mm, 2 ♀, cl 19.5 × 29.8 mm, 13.6 × 20.7 mm, ICN-MHN-CR 1384.—Urrao, Valle de Pérdidas, 1750 m alt., 14 Mar 1994, leg. A. L. Salazar, 1 ♂, 23.5 × 37.0 mm, ICN-MHN-CR 1385.—Fredonia, Vereda La Cristalina, 1800 m alt., 8 Jul 2000, leg. L. E. Velásquez, 1 ♂, 28.0 × 44.2 mm, 1 ♀, 36.9 × 61.3 mm, ICN-MHN-CR 1864. (2) Quindio Department. Quimbaya, Inspección La Española, 27 May 1987, leg. uk, 1 ♂, 21.9 × 31.3 mm, CRBMUV 87013. (3) Risaralda Department. Pueblo Rico, 3 km from Pueblo Rico to Santa Cecilia, 1430 m alt., 18 Aug 1987, 2 ♂, 13.0 × 19.1 mm, 10.6 × 15.6 mm, 1 ♀, 13.3 × 20.4 mm, ICN-MHN-CR 0780.—8 km from Pueblo Rico to Villa Claret, Tolda Seca stream, 1550 m alt., 21 Aug 1987, 2 ♂, 17.8 × 27.0 mm, 16.3 × 24.1 mm, 2 ♀, one with carapace broken, 12.7 × 18.6 mm, 2 juveniles, ICN-MHN-CR 0781.—Vereda Zabarraga Piunda, Piunda stream, 730 m alt., 21 Aug 1987, 1 ♀, 28.5 × 45.9 mm, ICN-MHN-CR 0786.—Vereda Ciató, Cristalina stream, 1500 m alt., 20–23 Sep 1991, 7 ♂, 21.7 × 33.1 to 9.5 × 13.2 mm, 3 ♀, 15.8 × 23.2 to 9.1 × 13.7 mm, ICN-MHN-CR 1239, 1240, 1245—Stream affluent to Negro River, 1600 m alt., 21 Sep 1991, 1 ♂, 12.7 × 18.7 mm, 1 ♀, 14.3 × 21.5 mm, ICN-MHN-CR 1242.—Vereda Los Pueblos, 1500 m alt., 22 Sep 1991, 5 ♂, 25.1 × 39.8 to 12.0 × 17.9 mm, 1 ♀, 9.8 × 14.0 mm, ICN-MHN-CR 1243.—Vereda Palo Blanco, Moravia Farm, 1300 m alt., 23 Sep 1991, 8 ♂, 21.4 × 32.1 to 11.3 × 15.9 mm, 3 ♀, 14.6 × 22.7 to 11.8 × 17.5 mm, ICN-MHN-CR 1247, 1249.—Vereda Ciatocito, 1550 m alt., 24 Sep 1991, 1 ♂, 14.6 × 22.1 mm, 3 ♀, 11.2 × 17.4 to 11.0 × 17.1 mm, ICN-MHN-CR 1251.—Vereda San José, La Palestina Farm, Pueblo Rico-Villa Claret Highway, 1500–1600 m alt., 25, 26 Sep 1991, 14 ♂, 23.0 × 34.7 to 11.2 × 17.0 mm, 7 ♀, 29.5 × 47.3 to 12.2 × 18.9 mm, ICN-MHN-CR 1253, 1254.—Vereda La Selva, La Pava stream, way to Repetidora, 1350 m alt., 27 Sep 1991, 1 ♂, 16.3 × 24.2 mm, 2 juveniles, ICN-MHN-CR 1256.—Vereda Caja de Oro, 1600 m alt., 27 Sep 1991, leg. A. Loaiza, 1 ♂, 15.0 × 22.7 mm, 1 ♀, 13.5 × 20.3 mm, 1 juvenile, ICN-MHN-CR 1258.—Negro River, 1600 m alt., 28 Sep 1991, 1 ♂, 17.4 × 27.0 mm, 5 ♀,

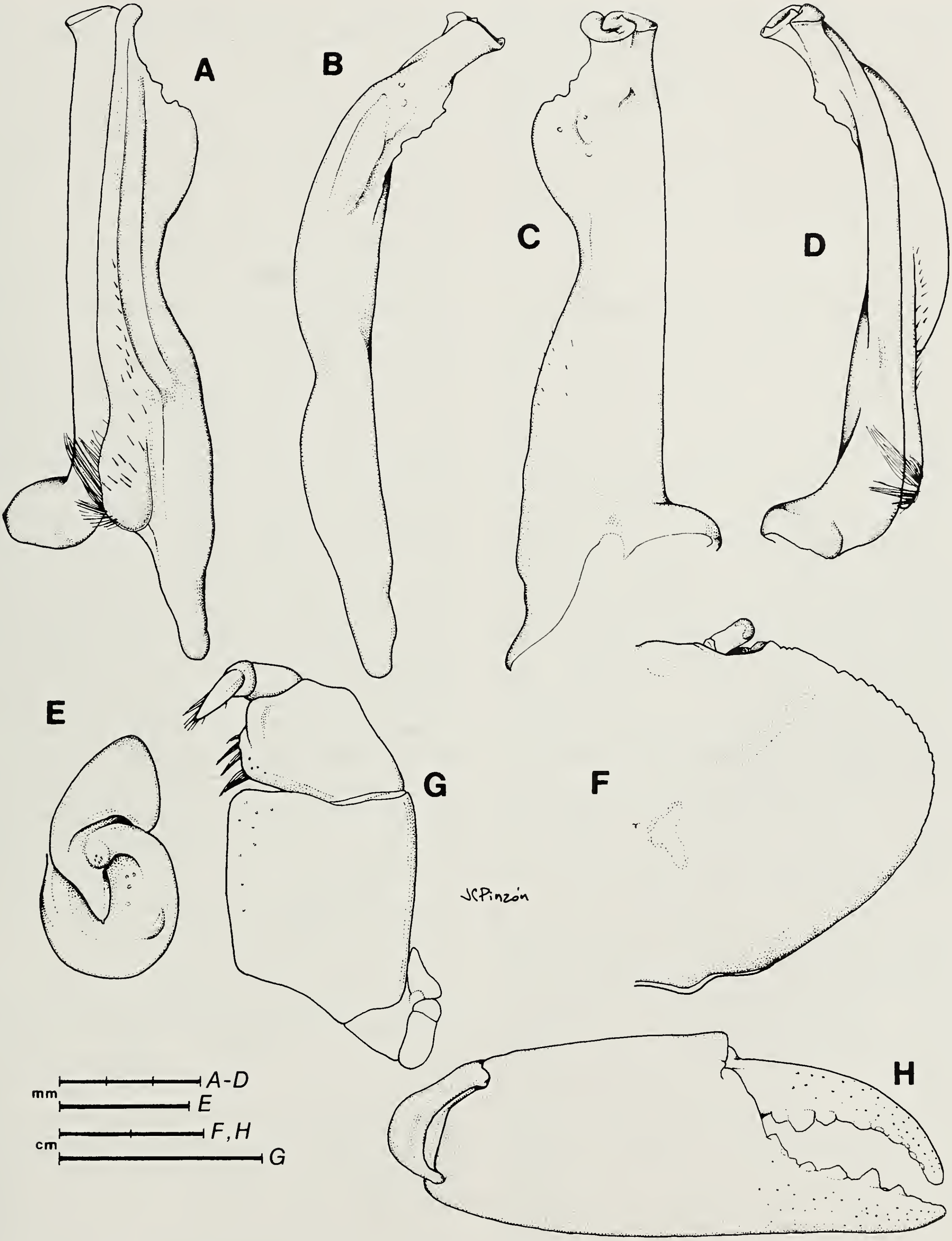

Fig. 6. *Hypolobocera bouvieri monticola* (Zimmer, 1912), male, ICN-MHN-CR 0086: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, right chela, external view.

28.9 × 46.0 to 16.2 × 25.3 mm, ICN-MHN-CR 1260.—La Florida, Vereda La Suiza, stream by "Camino Ecológico", 1850 m alt., 12 Jun 1989, leg. M. Morales, 1 ♂, 24.0 × 39.0 mm, ICN-MHN-CR 0966.—Mistrató. Corregimiento San Antonio del Chamí. Vereda La Florida, San Antonio del Chamí-Geguadas Highway, 1100 m alt., 30 Mar 1992, 13 ♂, 25.7 × 39.0 to 11.8 × 17.5 mm, 9 ♀, 20.8 × 32.2 to 13.0 × 19.8 mm, ICN-MHN-CR 1268.—Vereda La Palestina, San Antonio del Chamí-Mistrató Highway, 1150 m alt., 30 Mar 1992, 3 ♂, 20.0 × 31.8 to 11.0 × 15.9 mm, 4 ♀, 15.1 × 22.7 to 14.4 × 21.9 mm, ICN-MHN-CR 1269.—Vereda Arcacay, 900 m alt., 1 Apr 1992, 3 ♂, 14.0 × 21.8 to 10.9 × 16.1 mm, 2 ♀, 17.2 × 26.5 mm, 13.5 × 20.2 mm, ICN-MHN-CR 1270.—Vereda Empalado, 1800 m alt., 1 Apr 1992, 1 ♀, cl 34.8 mm, cb 55.2 mm (ICN-MHN-CR 1271).—Vereda Mampay, Sutú stream, 1750 m alt., 3 Apr 1992, 7 ♂, 19.5 × 29.2 to 12.5 × 18.6 mm, 3 ♀, 17.7 × 26.3 to 11.5 × 17.2 mm, ICN-MHN-CR 1272.—Vereda La Florida, 1350 m alt., 4 Apr 1992, 10 ♂, 24.5 × 37.4 to 12.6 × 19.5 mm, 13 ♀, 31.0 × 47.0 to 12.0 × 18.0 mm, ICN-MHN-CR 1273.—San Antonio stream, 800 m alt., 4 Apr 1992, 1 ♂, 33.5 × 51.6 mm, 1 ♀, 30.3 × 47.6 mm, ICN-MHN-CR 1274.—Vereda La Gabriela, Sutú stream, 1700 m alt., 6 Apr 1992, 1 ♂, 15.8 × 23.5 mm, 1 ♀, carapace broken, ICN-MHN-CR 1275.—Vereda Puerto de Oro, Carbones stream, 1080 m alt., 22 May 1992, leg. R. Sánchez, 1 ♀, 19.8 × 31.6 mm, ICN-MHN-CR 1778. (4) Tolima Department, Chaparral. Vereda El Linday, La Miel stream, 900 m alt., 26 Jul 1981, 6 ♂, 37.7 × 59.7 to 21.5 × 33.9 mm, 8 ♀, 38.0 × 60.4 to 12.1 × 18.6 mm, ICN-MHN-CR 0069, 0070, 0071, 0072, 0073, 0074, 0075, 0076.—Vereda El Linday, Agua Dulce stream, 850–900 m alt., 22 May 1984, 15 Jul 1995, 4 ♂, 45.7 × 73.6 to 23.4 × 36.7 mm, 2 ♀, 40.2 × 64.1 mm, 31.8 × 51.9 mm, ICN-MHN-CR 0570, 1457.—Tuluní stream, 920 m alt., 24 Aug 1982, leg. D. H. Campos, 1 ♂, 51.4 × 86.0 mm, ICN-MHN-CR 0086.—Corregimiento El Limón, Lake in Camacho Angarita Farm, 900 m alt., 20 Mar 1983, 1 ♂, 45.1 × 75.6 mm, ICN-MHN-CR 0139.—Corregimiento El Limón, Vereda Betania, 900 m alt., 15 Jul 1983,11 Jan 1988, 11 ♂, 38.7 × 59.5 to 13.8 × 20.7 mm, 9 ♀, 59.5 × 100.9 to 16.8 × 26.9 mm, ICN-MHN-CR 0506, 0507, 0509, 0845.—Corregimiento El Limón, Vereda Buenosaires, Miraflores Farm, 920 m alt., 17 Jul 1983, 30 Mar 1994, 6 ♂, 27.8 × 43.0 to 10.3 × 15.5 mm, 5 ♀, 26.3 × 40.7 to 21.0 × 32.5 mm, ICN-MHN-CR 0510, 0511, 0512, 1311.—Vereda Maito, Santa Ana stream, 950 m alt., 7 Jan 1985, 1 ♂, 25.8 × 41.0 mm, ICN-MHN-CR 0606.—Vereda Potrerito de Aguayo, 900 m alt., 15 May 1988, 20 Jul 1989, leg. D. Campos, 2 ♂, 47.4 × 79.4 mm, 38.1 × 61.0 mm, ICN-MHN-CR 0872, 0976.—Corregimiento El Limón, Vereda Betania, La Angostura, 1200–1300 m alt., 16–21 Oct 1993, 4 ♂, 45.0 × 73.7 to 20.3 × 31.6 mm, 4 ♀, 34.2 × 52.9 to 13.9 × 20.8 mm, ICN-MHN-CR 1298, 1302, 1305.—Corregimiento El Limón, Vereda Chicalá, 1100 m alt., 17 Oct 1993, 1 ♂, 21.8 × 33.8 mm, 2 ♀, 24.0 × 37.1 mm, + another with carapace broken, ICN-MHN-CR 1300.—Corregimiento El Limón, Vereda Providencia, 1000 m alt., 19, 20 Oct 1993, 9 ♂, 24.7 × 38.2 to 13.7 × 20.5 mm, 7 ♀, 29.3 × 46.7 mm to 15.5 × 22.5 mm, ICN-MHN-CR 1303, 1304.—Rioblanco, Blanca stream, 900 m alt., 22 May 1984, 1 ♀, 36.9 × 59.0 mm, ICN-MHN-CR 0568.—Purificación, Vereda San Antonio, El Consuelo stream, 300 m alt., 22 Aug 1997, leg. A. Fajardo, 1 ♀, 51.8 × 84.9 mm, ICN-MHN-CR 1667. (5) Valle del Cauca Department. Bolivar, Vereda Santa Marta, Aguas Lindas stream, 26 Feb 1983, leg. uk, 2 ♂, cl 20.3 × 31.1 mm, 14.7 × 21.6 mm, 2 ♀, cl 19.2 × 29.5 mm, 16.5 × 25.2 mm, CRBMUV 83082.—Bolivar, El Manzano Farm, 25 Jan 1984, leg. J. Restrepo, 1 ♂, 30.1 × 47.8 mm, CRBMUV 84083.—Sevilla, Inspección Morro Azul, La Miranda Farm, 28 Mar 1985, leg. F. Recio, 2 ♂, 20.2 × 31.0 mm, 14.6 × 21.7 mm, 2 ♀, 19.0 × 29.3 mm, 16.1 × 25.0 mm, CRBMUV 85134.

Diagnosis.—Chelae of male with small, rounded or irregularly shaped tubercle on external base of mobile fingers, and swelling on external base of fixed fingers (Fig. 6H). First male gonopod with caudal ridge long, straight; ending in narrow ridge beyond lateral lobe (Fig. 6A). Lateral lobe small, subtriangular, usually with crenulations on distal margin. Cephalic surface with transverse crest on distal half and tuberculated ridge parallel to lateral lobe (Fig. 6A–D). Apex outline oval, borders raised; prominent cephalic papilla and auxiliary rounded papilla near spermatic channel. Mesocaudal projection of spermatic channel terminated in blunt papilla, with distal spinule. Mesial lobe subtriangular (Fig. 6C–E). Third maxilliped with exognath 0.20–0.30 times length of ischium (Fig. 6G).

Remarks.—This subspecies has a trans-basin distribution covering the Central and Western Cordilleras in the mid-Magdalena and Cauca River basins. Females of this subspecies produced a large number of eggs, and thus have a great potential to colonize new habitats.

Hypolobocera bouvieri stenolobata
Rodríguez, 1980
Fig. 7A–H

Hypolobocera bouvieri stenolobata Rodríguez, 1980:891.—Rodríguez, 1982a: 58.—Rodríguez, 1994:299.

Material examined.—Colombia, Huila Department, Pitalito. Oritoguaza stream, 1200 m alt., 28 Aug 1986, 1 ♂, 33.4 × 52.9 mm, 1 ♀, 44.2 × 71.4 mm, ICN-MHN-CR 0656, 0657.—Vereda La Palma, stream near coffee plantation, 1200 m alt., 29 Aug 1986, 2 ♀, 43.1 × 69.4 mm, 38.3 × 60.7 mm, ICN-MHN-CR 0658, 0659.—Vereda Calamó, Yamboró Farm, 1175 m alt., 29 Aug 1986, 4 ♂, 34.9 × 55.3 to 15.0 × 22.8 mm, 1 ♀, 24.8 × 38.6 mm, ICN-MHN-CR 0661.—Gigante, Vereda Bajo Corozal, Catalina stream, 1200 m alt., 30 Aug 1986, 5 ♂, cl 27.9 × 45.5 to 10.5 × 15.8 mm, 1 ♀, 28.2 × 45.6 mm, ICN-MHN-CR 0662, 0663.—Rivera, 1000 m alt., 15 Jan 1988, 1 ♀, 43.1 × 69.4 mm, ICN-MHN-CR 0846.

Diagnosis.—Chelae of male with irregular shape tubercle on external base of mobile fingers, and swelling on external base of fixed fingers (Fig. 7H). First male gonopod with caudal ridge long, straight, recurved proximally; ending in narrow ridge beyond lateral lobe (Fig. 7A). Lateral lobe small, semicircular with crenulations on distal margin. Cephalic surface with transverse crest on distal half and tuberculated ridge parallel to lateral lobe (Fig. 7A–D). Apex outline oval in distal view; prominent cephalic papilla and auxiliary rounded papilla near spermatic channel. Mesocaudal projection of spermatic channel terminated in blunt papilla. Mesial lobe subtriangular (Fig. 7C–E). Third maxilliped with exognath 0.26–0.30 times length of ischium (Fig. 7G).

Remarks.—This subspecies is distributed in the Eastern Cordillera, in the upper reaches of the Magdalena River, which drains into the Caribbean Sea.

Hypolobocera buenaventurensis
(Rathbun, 1905)

Pseudothelphusa buenaventurensis Rathbun, 1905:307, fig. 98.—Coifmann, 1939:107.—Pretzmann, 1965:10.

Hypolobocera (*Hypolobocera*) *buenaventurensis* Pretzmann, 1971:17.—Pretzmann, 1972:48–49.

Hypolobocera buenaventurensis Rathbun, 1905).—Rodríguez, 1982a:190.

?*Hypolobocera buenaventurensis.*—Prahl 1985:44.—Prahl 1987:61.—Prahl, 1988: 171–172.

Material.—Colombia. Valle del Cauca Department, Buenaventura, 2 ♀, syntypes, 22.1 × 35.7 mm, 21.7 × 33.7 mm, MPB 3075.—Bajo Anchicayá, Anchicayá River, 16 Oct 1983, leg. uk, 1 ♂, 25.0 × 36.0 mm, 043 ADT-CRBMUV.

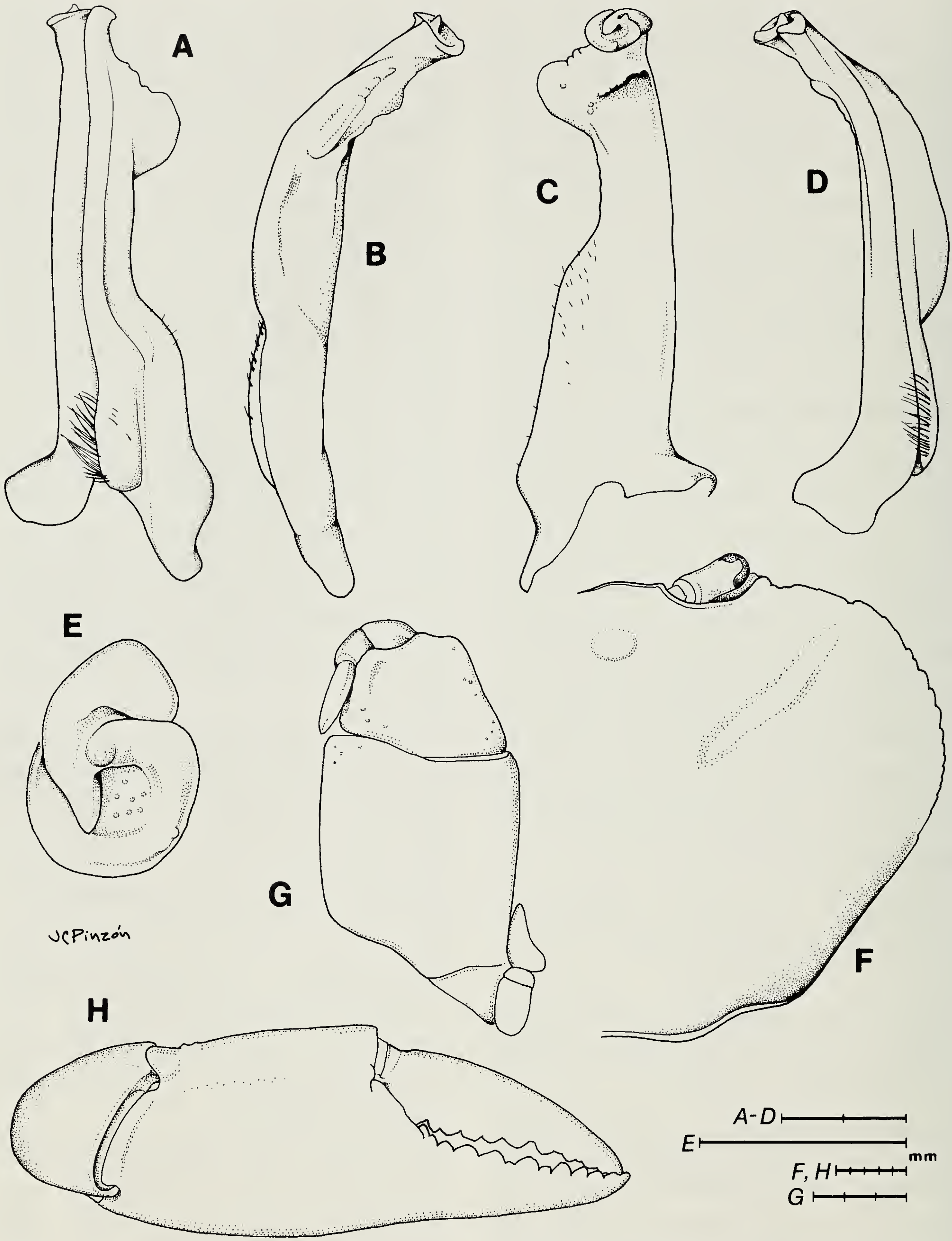

Fig. 7. *Hypolobocera bouvieri stenolobata* Rodríguez, 1980, male, ICN-MHN-CR 0656: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, right chela, external view.

Remarks.—This species was described from only two female syntypes from Buenaventura. Rodríguez (1982a), however, established that *Hypolobocera buenaventurensis* resembles *H. beieri,* based on the carapace, third maxilliped shape, length of exognath, and shape of branchial efferent channel. Prahl (1987) reported a male (25.0 × 36.0 mm), and described the carapace and first male gonopod. Prahl's male specimen could not be found at CRBMUV, so its identity cannot be confirmed.

Hypolobocera cajambrensis Prahl, 1988
Fig. 8A–H

Hypolobocera cajambrensis Prahl, 1988: 177, figs. 7, 8.

Hypolobocera cajambrensis.—Rodríguez, 1992:183.

Material examined.—Colombia. Valle del Cauca Department. Cajambre River, 700 m alt., 25 Aug 1983, leg. R. Ríos, 1 ♂ holotype, 15.0 × 24.0 mm, 041-0 ADT-CRBMUV.—Same data, 1 ♂ paratype, USNM 210727.—Cajambre River, 9 Aug 1983, 1 ♂ juvenile, 9.3 × 15.2 mm, leg. uk, 3 ♀, 13.5 × 22.3 to 10.5 × 17.3 mm, CRBMUV 83084.—Cajambre River, 25 Aug 1983, leg. uk, 1 ♀, 15.6 × 25.4 mm, CRBMUV 83085.—Buenaventura, Pogodó stream, affluent of Cajambre River, 50 m alt., 29 Apr 1999, leg. E. Flórez, 1 ♂, 13.6 × 23.7 mm, ICN-MHN-CR 1876.

Cauca Department, Timbiquí, Saija River, 100 m alt., 2°50′N, 77°30′W, 3 Nov 1971, leg. B. Malkin and A. Granja, 1 ♂, 24.9 × 47.6 mm, FMNH 3675.

Diagnosis.—Carapace with front extremely wide, approximately half of carapace width (Fig. 8F). Chelae of male with irregularly shaped tubercle on external base of mobile fingers, and swelling on external base of fixed fingers (Fig. 8H). First male gonopod with caudal ridge long, fusiform; ending in narrow ridge beyond lateral lobe (Fig. 8A). Lateral lobe triangular, and auxiliary lobe parallel to lateral lobe on lateral side (Fig. 8A–C). Apex outline slightly oval in distal view; caudolateral border transverse and expanded. Mesocaudal projection of spermatic channel terminating in rounded papilla. Mesial lobe projected on cephalic surface as a wide, semicircular lobe (Fig. 8B–D). Third maxilliped with exognath approximately 0.30 times length of ischium (Fig. 8G).

Remarks.—This species can be easily distinguished from others within the genus by the presence on the first male gonopod of an auxiliary lobe parallel to the lateral lobe.

Hypolobocera chocoensis Rodríguez, 1980
Fig. 9A–I

Hypolobocera Hypolobocera dubia.—Pretzmann, 1972:48, figs. 224–226, 230–232, 236, 237.

Hypolobocera chocoensis Rodríguez, 1980: 891.—Rodríguez, 1982a:59, figs. 19, 21, 31.—Prahl, 1988:177, fig. 9.—Rodríguez, 1994:300.

Material examined.—Colombia, Chocó Department. Guntas, Tamaná River, leg. uk, ♂ holotype, 18.8 × 31.5 mm, BM 1910.3.4.3–4.—Same data, 1 ♀ paratype, 18.2 × 26.9 mm, BM 1910.3.4.3–4.—Condoto, leg. H. G. F. Spurrel, 2 ♂, 20.4 × 32.4 mm, 19.9 × 32.2 mm, BM 1913.10.28.1–3.—Mountains of upper San Juan River, Chocó jungle, nearest village Playa de Oro, 28 Mar 1962, leg. M. Latham, 10 ♂, 22.8 × 36.7 to 23.8 × 39.7 mm, USNM 240102.—Condoto. 23 Jul 1985, leg. uk, 2 ♂, 21.0 × 28.0 mm, 18.5 × 27.0 mm, 045-0, 045-1 ADT-CRBMUV.—Lloró, Granja Codechocó, left margin of Atrato River, 50 m alt., 23 Mar 1988, leg. O. Reyes, 1 ♂, 16.0 × 27.1 mm, ICN-MHN-CR 0851.—Pizarro, Bajo Baudó, Torreidó stream, 20 m alt., leg. R. Sánchez. 30 Aug 1990, 2 ♂, cl 19.2 × 31.7 mm, 16.5 × 27.9 mm, 1 ♀, 23.2 × 40.0 mm, ICN-MHN-CR 1201.

Diagnosis.—Chelae of male lacking tubercles on external base of mobile and fixed fingers (Fig. 9I). First male gonopod with caudal ridge strong, long, straight; ending

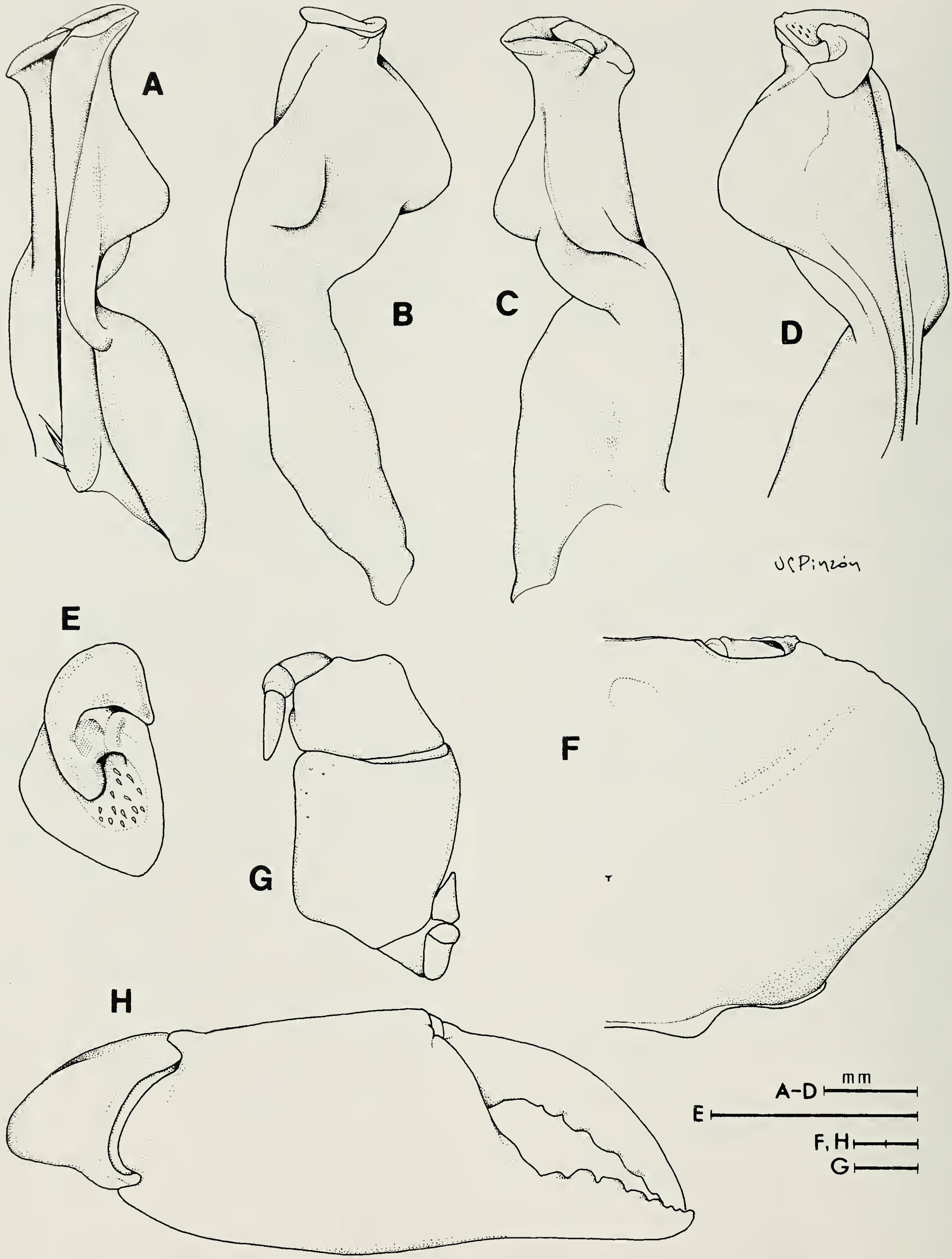

Fig. 8. *Hypolobocera cajambrensis* Prahl, 1988, male, ICN-MHN-CR 1876: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, carapace, dorsal view; G, left third maxilliped, external view; H, right chela, external view.

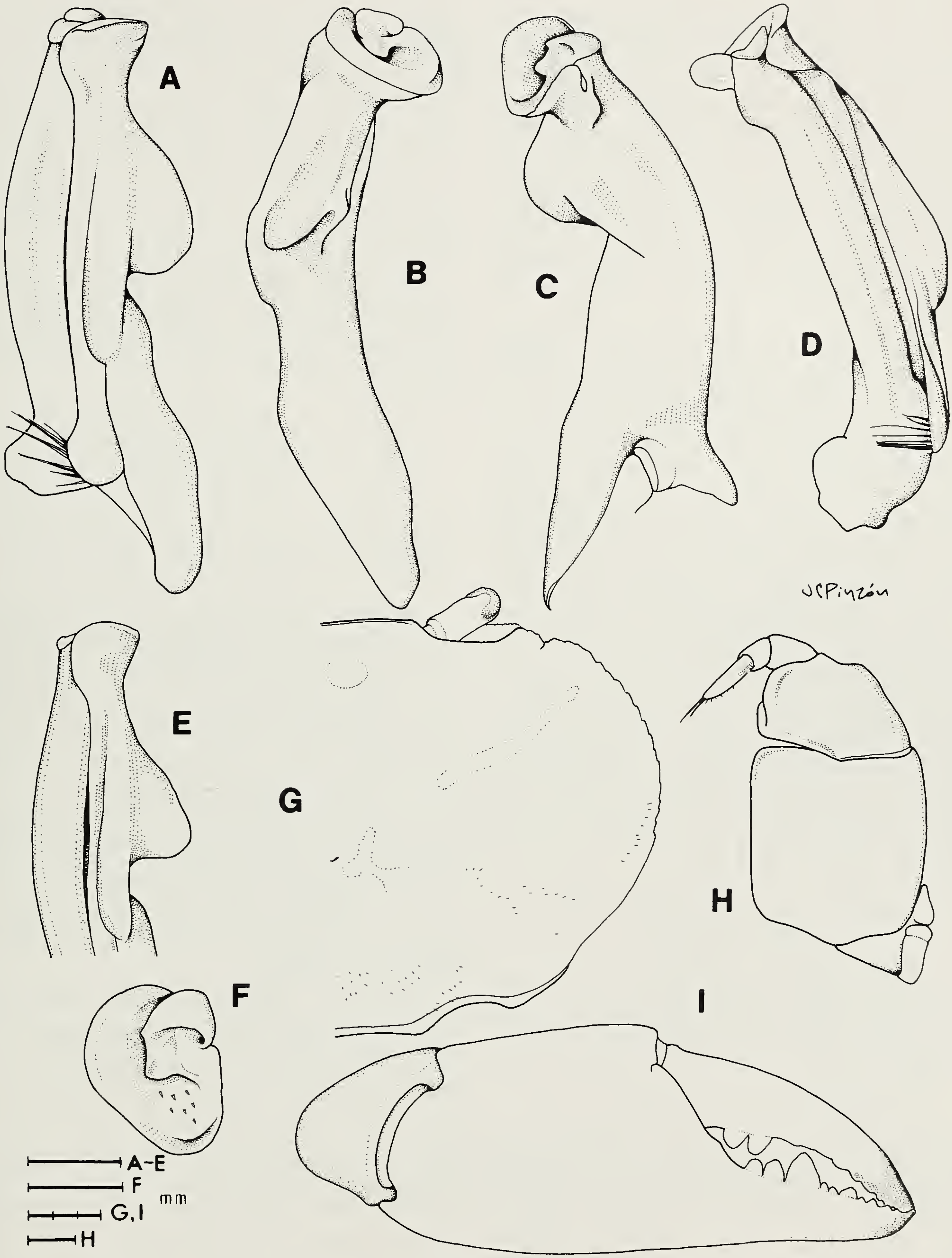

Fig. 9. *Hypolobocera chocoensis* Rodríguez, 1980, male, ICN-MHN-CR 1201: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; F, same, apex, distal view; G, right side of carapace, dorsal view; H, left third maxilliped, external view; I, right chela, external view. Male, ICN-MHN-CR 0851: E, left first gonopod, caudal view.

in narrow ridge beyond lateral lobe (Fig. 9A, C). Lateral lobe triangular, with proximal margin either rounded, or straight (Fig. 9A, C, E). Apex outline slightly rounded in distal view, expanded mesocaudally into rounded projection. Mesocaudal projection of spermatic channel terminating in semiacute papilla. Mesial lobe semicircular (Fig. 9B, F). Third maxilliped with exognath 0.20–0.25 times length of ischium (Fig. 9H).

Remarks.—This species is most similar to *Hypolobocera lloroensis* Campos, 1989. The two can be differentiated by features of the carapace and first male gonopod. The anterolateral border of the carapace in *H. lloroensis* (Fig. 14F) has a deep depression behind the external orbital angle, followed by another deep depression at the level of the cervical groove. In contrast, *H. chocoensis* has the anterolateral border of the carapace with a deep depression behind the external orbital angle, but the border is not continuous with the margin of the depression (Fig. 9G). The caudal edge of the apex of the first male gonopod is transverse in caudal view in *Hypolobocera lloroensis* (Fig. 15A), whereas it is rounded and expanded in *H. chocoensis.*

Hypolobocera dentata Prahl, 1987
Fig. 10A–G

Hypolobocera dentata 1987:93–95, fig. 1A–E.—Prahl, 1988:180, fig. 12.

Hypolobocera dentata.—Rodríguez, 1992: 183.

Material examined.—Colombia, Valle del Cauca Department. Bolivar, El Manzano, near Betania, 1600 m alt., 28 Jan 1984, leg. E. Velasco, ♂ holotype, 15.6 × 24.0 mm, 071 ADT-CRBMUV.—Same data, 1 ♀ paratype, 17.0 × 25.7 mm, 072 ADT-CRBMUV.

Diagnosis.—First male gonopod with caudal ridge long, sinuous, recurved proximally; ending in narrow ridge beyond lateral lobe (Fig. 10A). Lateral lobe subtriangular, with tubercles on distal external margin, and on cephalic surface (Fig. 10A–D). Apex outline oval in distal view, expanded caudocephalically into rounded projection; laterocephalic border toothed. Mesocaudal projection of spermatic channel terminated in rounded papilla. Mesial lobe slightly semicircular (Fig. 10E). Third maxilliped with exognath approximately 0.40 times length of ischium (Fig. 10G).

Remarks.—This species differs from the others in the genus in having a toothed laterocephalic border in the apex of the first male gonopod.

Hypolobocera emberarum Campos & Rodríguez, 1995
Fig. 11A–H

Hypolobocera emberarum Campos & Rodríguez, 1995:652, Figs. 3, 4.

Material examined.—Colombia. Chocó Department. El Carmen de Atrato, Vereda El Veinte, 2500 m alt., 30 May 1994, leg. I. D. Vélez, ♂ holotype, 14.2 × 23.8 mm, ICN-MHN-CR 1358.—Same data, 2 ♂ paratypes, 13.1 × 22.0 mm, 13.0 × 21.8 mm, 3 ♀ paratypes, 13.4 × 22.6 to 12.7 × 21.4 mm, ICN-MHN-CR 1359.—Antioquia Department. Urrao, Valle de Pérdidas, 1800 m alt., 3 Sep 1994, leg. P. Duque, 3 ♂, 14.1 × 23.8 to 10.9 × 18.3 mm, 3 ♀, 14.0 × 23.5 to 12.7 × 21.4 mm 9 juveniles, ICN-MHN-CR 1383.

Diagnosis.—Carapace lateral sides conspicuously pubescent in larger specimens (Fig. 11F). Chelae of male lacking tubercles on external base of mobile and fixed fingers (Fig. 11H). First male gonopod with caudal ridge long, fusiform; ending in narrow ridge beyond lateral lobe (Fig. 11A, B). Lateral lobe prominent, subtriangular, hatchet shaped, wide proximally, extending near apex of gonopod and forming deep notch distally; caudal face excavated, covered partially with spinules (Fig. 11A–C). Apex outline oblong in distal view, caudocephalic expanded into elongated projection. Mesocaudal projection of spermatic channel terminated in rounded papilla. Me-

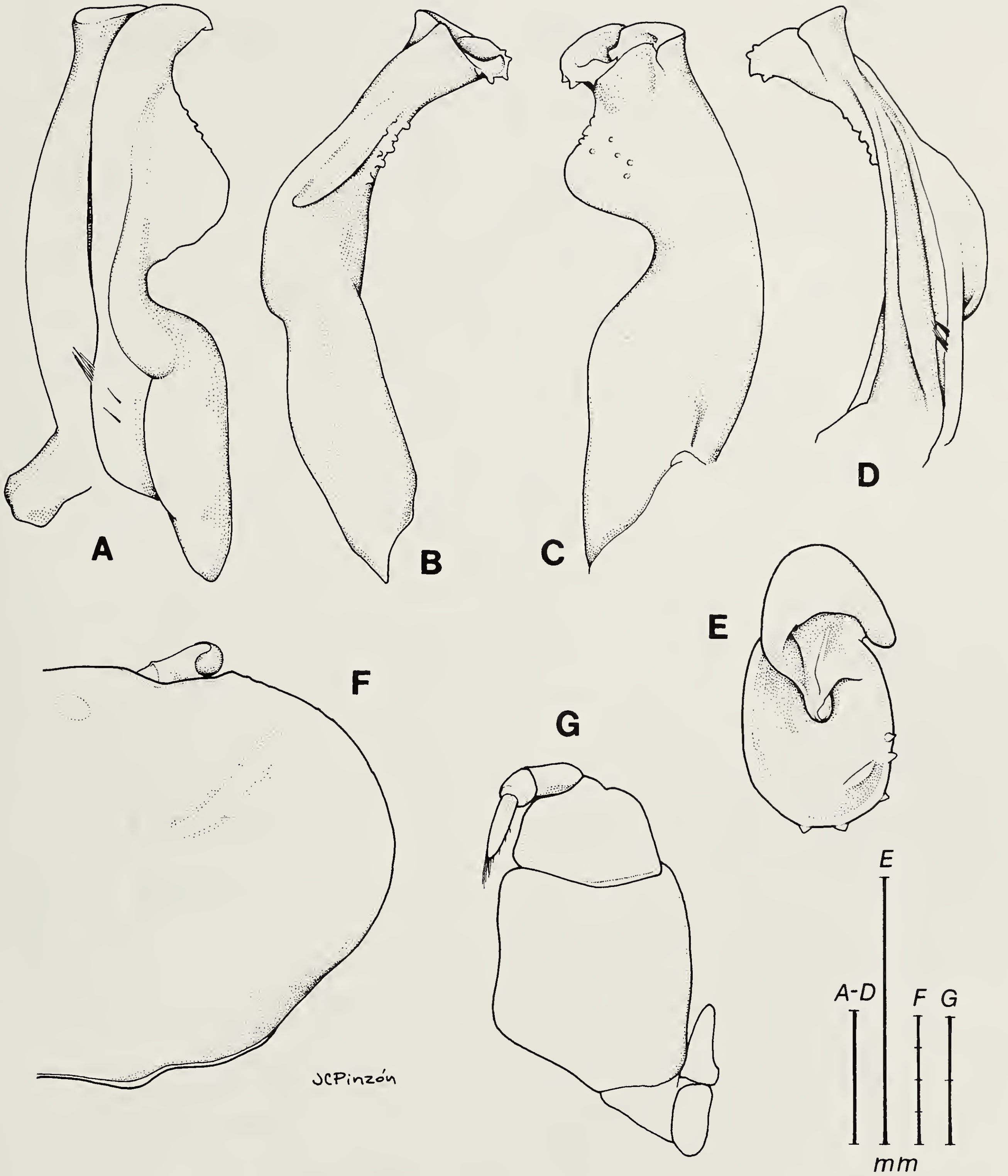

Fig. 10. *Hypolobocera dentata* Prahl, 1987, male, CRBMUV 84077: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view.

sial lobe subtriangular (Fig. 11E). Third maxilliped with exognath approximately 0.20 times length of ischium (Fig. 11G).

Remarks.—The shape of the lateral lobe of the first male gonopod of this species resembles that of *Hypolobocera chocoensis* Rodríguez, 1980 (Fig. 9A). However, the lateral lobe of *H. chocoensis* does not extend near the apex, and lacks a distal notch as seen in *H. emberarum.*

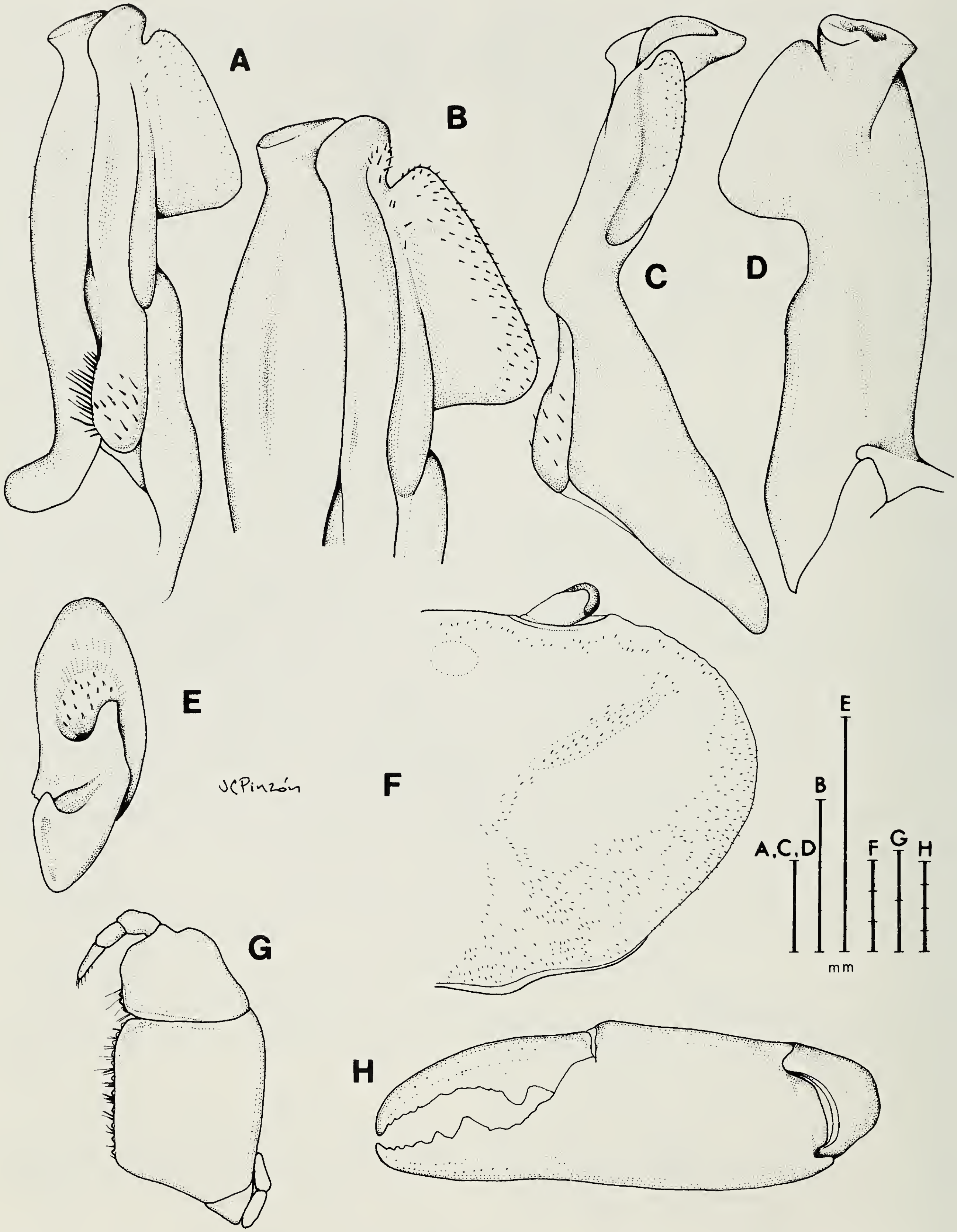

Fig. 11. *Hypolobocera emberarum* Campos & Rodríguez, 1995, male holotype, ICN-MHN-CR 1358: A, left first gonopod, caudal view; B, same, lateral lobe, caudal view; C, same, lateral view; D, same, cephalic view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, left chela, external view.

Hypolobocera gorgonensis Prahl, 1983
Fig. 12A–H

Hypolobocera gorgonensis Prahl, 1983: 106, fig. 1.—Prahl, 1988:181, fig. 13.
Hypolobocera gorgonensis.—Rodríguez, 1992:183.—Rodríguez et al., 2002:7.

Material examined.—Colombia, Cauca Department, Gorgona Island. Marranera stream, 22 May 1979, leg. uk, ♂ holotype, 49.3 × 73.4 mm, 013 ADT-CRBMUV.—El Yucal, La Esperanza, leg. uk, 1 ♀, 53.2 × 80.0 mm, 012 ADT-CRBMUV.— 20 May 1979, leg. uk, 3 ♀, 50.3 × 82.1 to 31.7 × 49.5 mm, CRBMUV 79055.—El Azufral, 12 Nov 1982, leg. uk, 1 ♀, 55.6 × 89.2 mm, CRBMUV 82055 (027 ADT-CRBMUV).— 3 Nov 1989, leg. H. von Prahl, 1 ♂, 44.0 × 72.5 mm, CRBMUV 89023.—26 Aug 1984, leg. uk, 1 ♀, 8.3 × 13.1 mm, CRBMUV 84072.—26 Aug 1984, leg. uk, 1 ♀, carapace broken, CRBMUV 84073.—22 Aug 1980, leg. H. von Prahl, 1 ♂, 50.6 × 83.3 mm, TU 6303.—Pacific, 1 Feb 1962, leg. F. Medem, 2 ♂, 50.2 × 81.2 mm, 43.2 × 69.9 mm, 1 ♀, cl 47.2 mm, cb 76.4 mm, FMNH 3687.—29 Apr 1985, leg. J. M. Rengifo, 3 ♂, 47.9 × 79.1 to 43.9 × 71.2 mm, ICN-MHN-CR 0612.

Diagnosis.—Chelae of male with small tubercle on external base of mobile fingers, and swelling on external base of fixed fingers (Fig. 12H). First male gonopod with caudal ridge strong, straight; ending in narrow ridge distally. Mesial margin with rows of conspicuous setae (Fig. 12A). Lateral lobe triangular, increasing in width distally; distal external margin rounded (Fig. 12A, C). Apex outline elongated along mesolateral axis in distal view; caudocephalic border rounded. Mesocaudal projection of spermatic channel terminating in rounded papilla. Mesial lobe elongated and subtriangular (Fig. 12E). Third maxilliped with exognath approximately 0.35 times length of ischium (Fig. 12G).

Remarks.—This species is considered endemic to Gorgona, an island with a surface of 2400 ha.

Hypolobocera kamsarum Campos & Rodríguez, 1995
Fig. 13A–H

Hypolobocera kamsarum Campos & Rodríguez, 1995:649, Figs. 1, 2.

Material examined.—Colombia. Putumayo Department, Mocoa, Vereda Alto Campucana, 1350 m alt., 2 Jun 1994, leg. O. V. Castaño, ♂ holotype, 14.0 × 23.7 mm, ICN-MHN-CR 1349.—Same data, 1 ♂ paratype, 13.4 × 21.8 mm, 1 ♀ paratype, 14.6 × 24.8 mm, 2 juveniles, ICN-MHN-CR 1350.

Diagnosis.—Chelae of male lacking tubercles on external base of mobile and fixed fingers (Fig. 13H). First male gonopod with caudal ridge long, concave; almost reaching apex (Fig. 13A). Lateral lobe small, transverse, displaced towards cephalic side, evenly rounded in lateral view, placed far from apex (Fig. 13A–D). Apex outline oval in distal view, with rounded expansion directed distally. Mesocaudal projection of spermatic channel terminating in rounded papilla. Mesial border projected proximally, forming strong triangular mesial lobe (Fig. 13C, E). Third maxilliped with exognath relatively long, approximately 0.60 times length of ischium (Fig. 13G).

Remarks.—This species differs from the others in the genus in having the mesial border projected proximally, forming a strong triangular mesial lobe (Fig. 13C, E).

Hypolobocera lloroensis Campos, 1989
Fig. 14A–G

Hypolobocera lloroensis Campos, 1989: 143, fig. 1.
Hypolobocera lloroensis.—Rodríguez, 1992:183.—Rodríguez et al., 2002:7.
Hypolobocera chocoensis.—Prahl, 1988: 177, 179.

Material examined.—Colombia, Chocó Department. Lloró, Vereda Peñalosa, Gran-

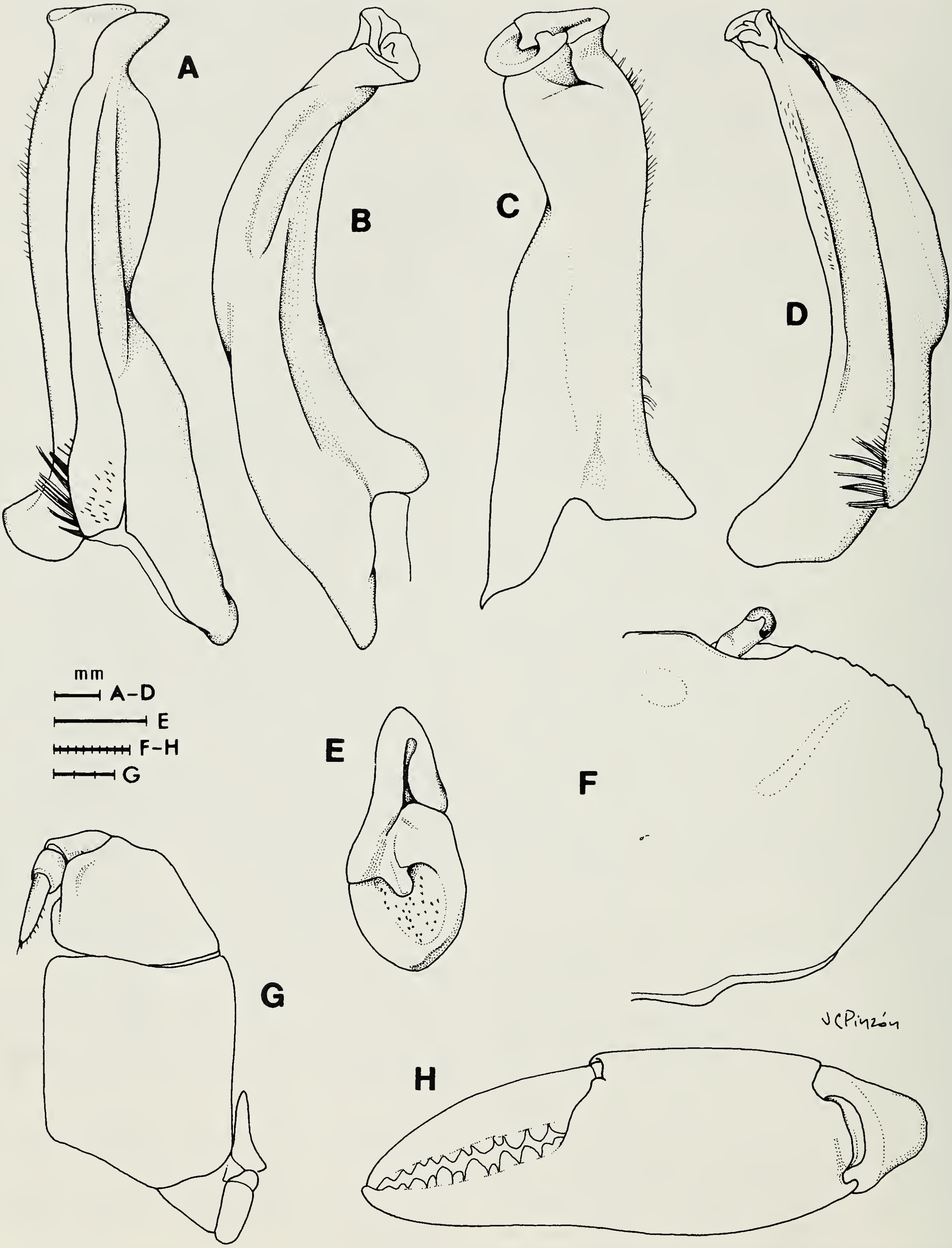

Fig. 12. *Hypolobocera gorgonensis* Prahl 1983, male, ICN-MHN-CR 0612: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, left chela, external view.

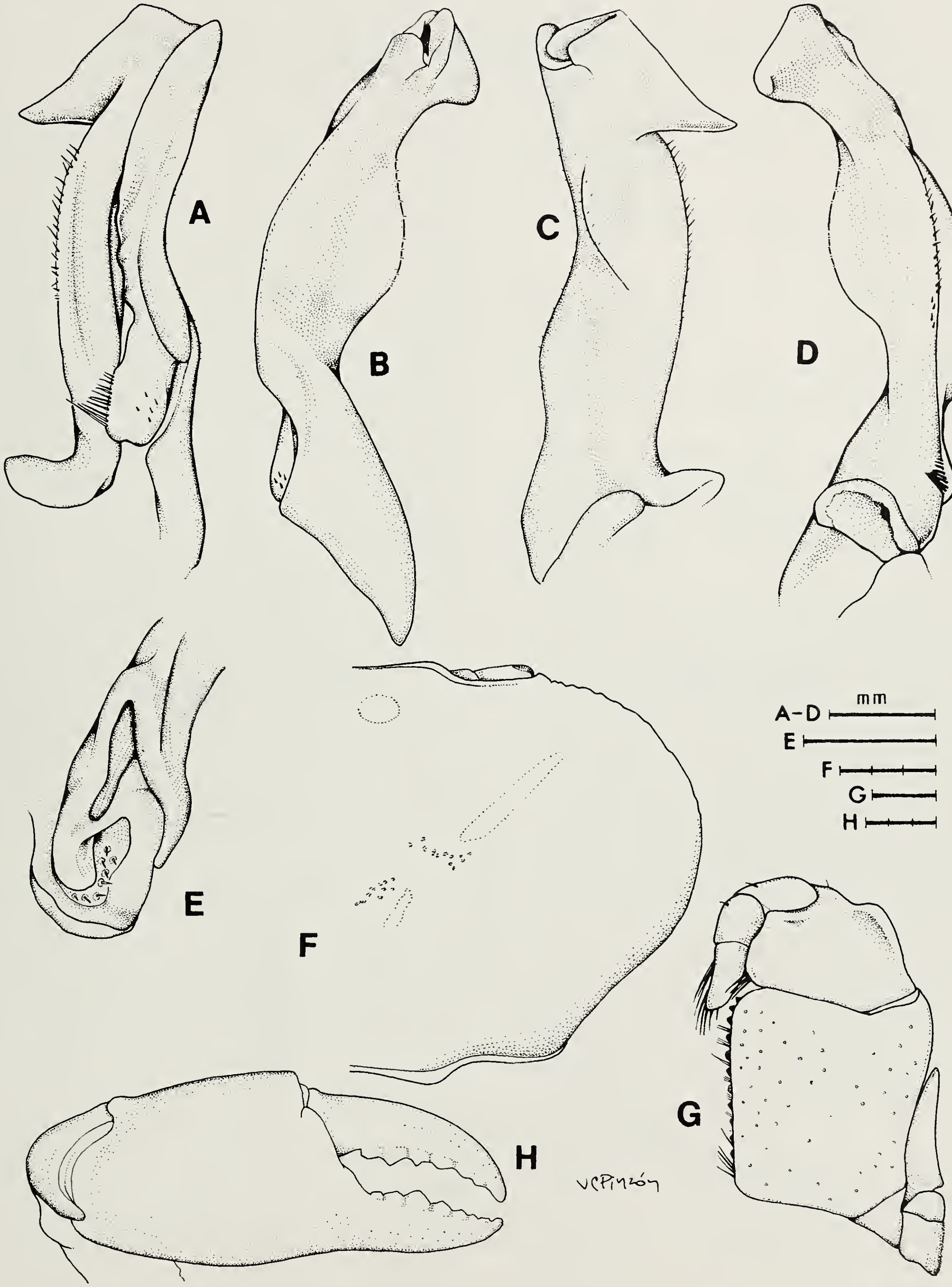

Fig. 13. *Hypolobocera kamsarum* Campos & Rodríguez, 1995, male holotype, ICN-MHN-CR 1349: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, right chela, external view.

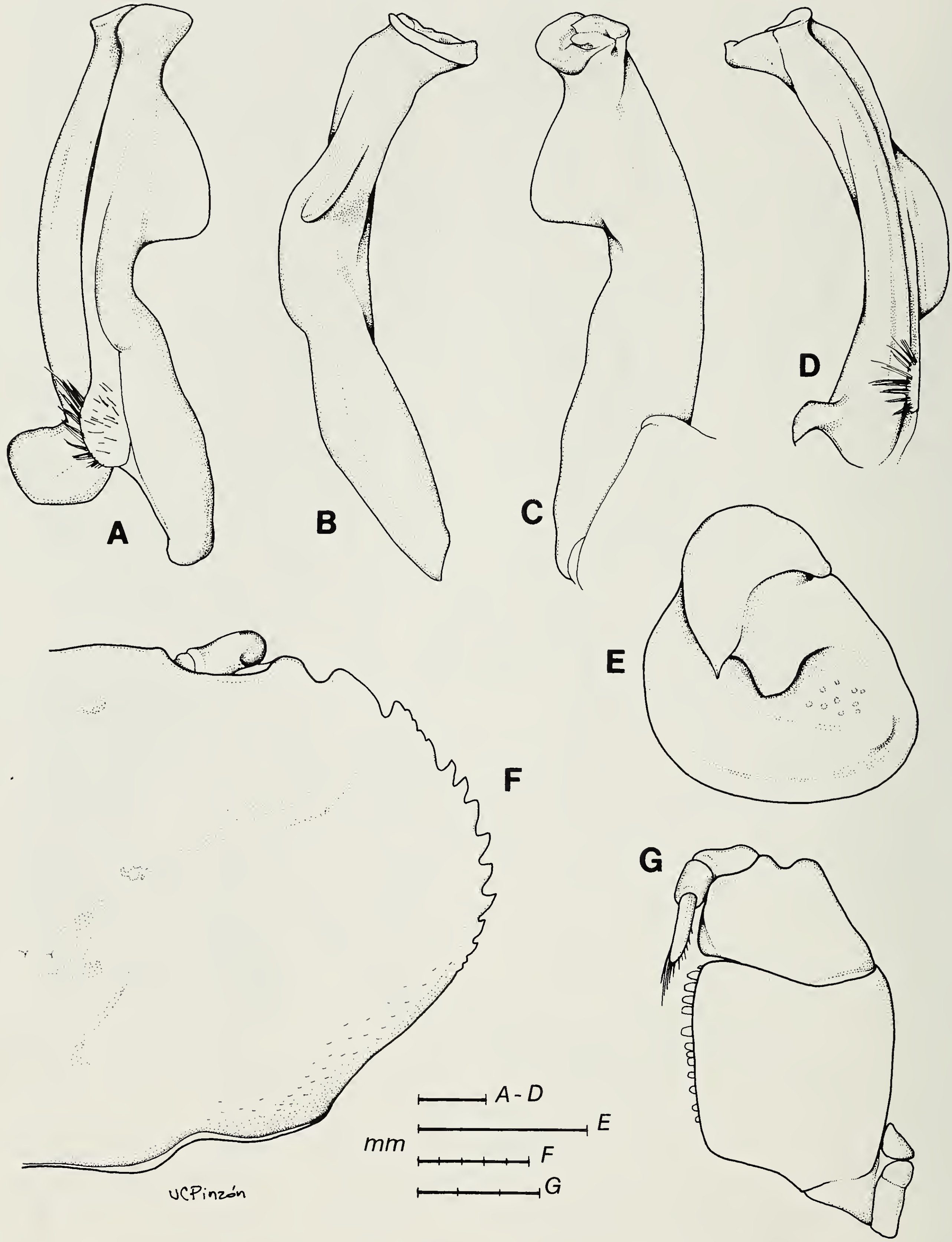

Fig. 14. *Hypolobocera lloroensis* Campos 1989, male, ICN-MHN-CR 1386: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view.

ja Experimental CEMA, Universidad de Chocó, La Lana, 50 m alt., 22 Mar 1988, leg. M. C. Ardila, M holotype, 17.8 × 30.3 mm, 1 ♂ paratype, 11.0 × 17.5 mm, ICN-MHN-CR 0850.—Condoto, 23 Jul 1985, leg. H. von Prahl, 1 ♂, 18.1 × 28.0 mm, 1 ♀, 14.7 × 23.1 mm, CRBMUV 85132 (045-0, 045-1 ADT-CRBMUV).—Condoto, Inspección Santa Rita de Iro, Iro River, 14 Jun 1987, leg. H. Almendiger, 1 ♂, 23.6 × 40.6 mm, CRBMUV 87016.—Istmina, San Juan River, 8 Aug 1969, leg. Dale Little, 1 ♂, cl 24.4 × 40.0 mm, 2 ♀, 26.3 × 43.9 mm, 13.8 × 21.8 mm, TU 6193.—Tutunendó, km 29 Quibdó-Carmen de Atrato Highway, 170 m alt., 25 Aug 1987, leg. R. Sánchez, 1 ♂, 11.7 × 19.2 mm, 1 ♀, 11.2 × 17.9 mm, 1 juvenile, ICN-MHN-CR 0783.—Tadó, km 20.6 Santa Cecilia-Quibdó, 100 m alt., 10 Abr 1991, leg. G. Susatama, 4 ♀, 17.5 × 31.3 to 14.0 × 24.0 mm, 1 juvenile, ICN-MHN-CR 1262.—Tutunendó, La Barbuda stream, 100 m alt., 17 Oct 1987; leg. C. Román, 2 ♀, 21.9 × 37.2 mm, 20.4 × 34.5 mm, ICN-MHN-CR 1263.—Antioquia Department, Urrao, Andabú stream, 1800 m alt., 23 Sep 1994, leg. I. D. Vélez, 5 ♂, 23.5 × 40.3 to 16.5 × 21.9 mm, 6 ♀, 25.1 × 42.1 to 17.4 × 29.0 mm, ICN-MHN-CR 1386.

Diagnosis.—Anterolateral margin of carapace with deep depression behind external orbital angle, followed by another deep depression at cervical groove level. First male gonopod with caudal ridge long, straight, recurved proximally; ending in narrow ridge distally (Fig. 14A). Lateral lobe subtriangular, wide proximally, narrow distally (Fig. 14A, C). Apex outline oval in distal view, mesocephalic border transversely expanded; prominent cephalic papilla. Mesocaudal projection of spermatic channel terminating in semiacute papilla. Mesial lobe semicircular, with acute spine directed laterally (Fig. 14C, E). Third maxilliped with exognath approximately 0.20 times length of ischium (Fig. 14G).

Remarks.—Prahl's (1988) report of two males of *Hypolobocera chocoensis* from Condoto, Chocó (045-0, 045-1 ADT-CRBMUV), actually are of *H. lloroensis.* Contrary to Prahl's report, the lot does not contain two males, but one male (18.1 × 28.0) and one female (14.7 × 23.1 mm).

Hypolobocera malaguena Prahl, 1988
Fig. 15A–G

Hypolobocera malagueña Prahl, 1988:180, fig. 10, 11.

Hypolobocera malagueña.—Rodríguez, 1992:183.—Rodríguez, 1994:300.

Material.—Colombia. Valle del Cauca Department, Málaga Bay, La Alegría stream, 23 Dec 1985, leg. N. Ospina, ♂ holotype, 24.6 × 40.7 mm, 0750 ADT-CRBMUV.

Diagnosis.—Anterolateral margin of carapace with depression fringed with approximately 8 papillae, behind external orbital angle, followed by shallow depression at level of cervical groove (Fig. 15F). First male gonopod with caudal ridge long, sinuous; almost reaching apex (Fig. 15A). Lateral lobe subtriangular with distal border rounded. Lateral lobe oblique in relation to axis of appendage (Fig. 15B). Apex outline oval in distal view, mesocephalic border transversely expanded; prominent cephalic papilla. Mesocaudal projection of spermatic channel terminating in blunt papilla. Mesial lobe semicircular, with acute spine directed laterally (Fig. 15E). Third maxilliped with exognath approximately 0.25 times length of ischium (Fig. 15G).

Remarks.—The specific name *malagueña* was given by (Prahl 1988) to this species. However, the Code does not allow the use of the "ñ" in a latinized scientific name and requires correction to *H. malaguena.* This species closely resembles *H. lloroensis* in the shape of the first male gonopod (Fig. 14A), but the lateral lobe is oblique in relation to the axis of the appendage in *H. malaguena* (Fig. 15B), while it is parallel in *H. lloroensis* (Fig. 14B).

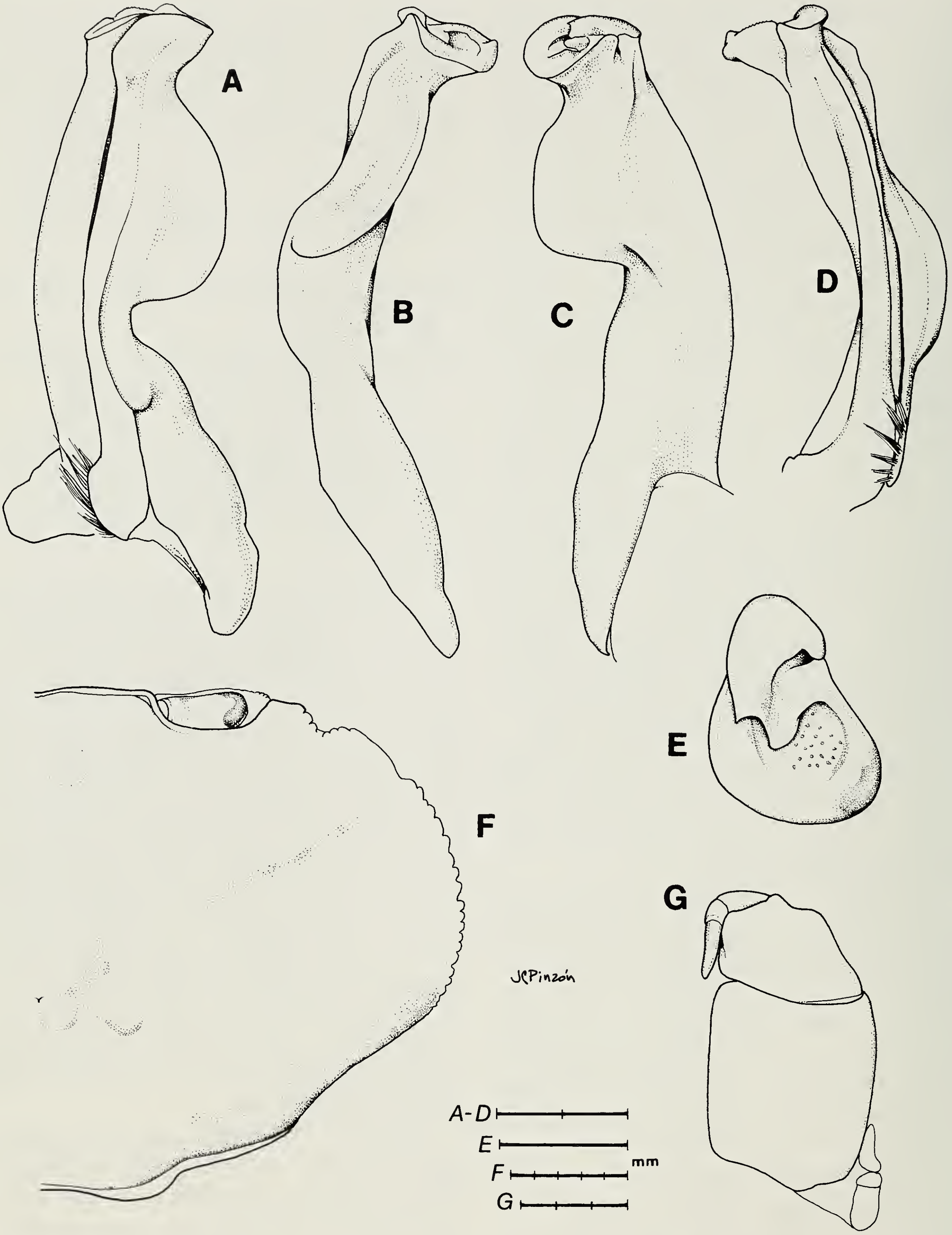

Fig. 15. *Hypolobocera malaguena* Prahl 1988, male, CRBMUV 85133: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view.

Hypolobocera martelathani (Pretzmann, 1965)
Fig. 16A–I

Strengeria Strengeria martelathani Pretzmann, 1965:6.

Hypolobocera (*Hypolobocera*) *martelathami*.—Pretzmann, 1971:17.—Pretzmann, 1972:50, figs. 159–161, 242–244.

Hypolobocera matelathami.—Rodríguez, 1982a:52.—Campos & Rodríguez, 1984: 538, fig. 4c, f.—Rodríguez, 1994:300, fig. 1D–F.

Hypolobocera merenbergiensis Prahl & Giraldo, 1985:2, fig. 1.

Hypolobocera merenbergiensis.—Rodríguez, 1992:183.—Rodríguez et al., 2002:7.

Material examined.—Colombia, Huila Department. San Agustín, De Quintero stream, near Yalconia Hotel, 1500 m alt., 27 Aug 1986, 10 ♂, 16.2 × 27.1 to 11.6 × 13.9 mm, 12 ♀, 16.6 × 28.1 to 11.7 × 18.5 mm, ICN-MHN-CR 0653.—San José de Isnos, Vereda Primavera, 1600 m alt., 27 Aug 1986, 5 ♂, 18.8 × 32.2 to 13.2 × 20.0 mm, 10 ♀, 17.5 × 29.0 to 11.0 × 17.1 mm, ICN-MHN-CR 654.—San Agustín, Inspección Obando, 1400 m alt., 28 Aug 1986, 5 ♂, 14.1 × 23.3 to 12.3 × 19.8 mm, 6 ♀, 16.0 × 25.5 to 11.2 × 17.2 mm, ICN-MHN-CR 0655.—Acevedo, Inspección San Adolfo, Vereda Changuayaco, 1300 m alt., 29 Aug 1986, 13 ♂, 14.8 × 24.8 to 12.4 × 19.7 mm, 10 ♀, 15.8 × 27.2 to 10.7 × 17.7 mm, ICN-MHN-CR 0660.—La Plata, Merenberg stream, 2300 m alt., 9 Apr 1982, leg. H. von Prahl and J. Giraldo, M holotype, 13.1 × 20.1 mm, No. 42 (lote 006 ADT) MBMUV.—Same data, 1 ♂ paratype, No. 43 (lote 006 ADT) MBMUV.—Same data, 1 ♀ paratype, 14.2 × 22.5 mm, ICN-MHN-CR 0541.—Same data, 3 ♀, 14.0 × 23.4 to 11.5 × 18.2 mm, CRBMUV 82051.—Same data, 2 ♂, cl 12.3 × 18.8 mm, 10.5 × 16.5 mm, TU 6369.—Cauca, Inza, Vereda Tierras Blancas, 2200 m alt., 25 Mar 1982, leg. R. Restrepo, 4 ♂, 14.1 × 22.9 to 12.9 × 20.2 mm, 3 ♀, 18.1 × 29.0 to 14.1 × 22.4 mm, ICN-MHN-CR 0087.

Diagnosis.—Chelae of male lacking tubercles on external base of mobile and fixed fingers (Fig. 16I). First male gonopod with caudal fusiform; ending in narrow ridge distally (Fig. 16A). Lateral lobe large, reaching middle of gonopod, wide distally, narrow proximally; covered with minute spinules and scattered short setae in caudal view (Fig. 16A, B, D, E); slightly semicircular in cephalic view (Fig. 16C). Apex outline oblong in distal view, with caudocephalic border slightly rounded. Mesocaudal projection of spermatic channel terminating in wide papilla. Mesial lobe elongated and subtriangular (Fig. 16D, F). Third maxilliped with exognath approximately 0.50 times length of ischium (Fig. 16H).

Remarks.—The morphology of the first male gonopods of *Hypolobocera martelathani* and *H. merenbergiensis* Prahl & Giraldo, 1985 are identical, and both species are found in the Central Cordillera, in the upper reaches of the Magdalena River. Thus, *H. merenbergiensis* is considered a junior synonym of *H. martelathani*. The original spelling of the species name is *martelathani* (Pretzmann, 1965), although Pretzmann (1971, 1972) later used the spelling *martelathami*.

Hypolobocera meineli Prahl, 1988
Fig. 17A–I

Hypolobocera meineli Prahl, 1988:173, figs. 3, 4.

Hypolobocera meineli.—Rodríguez, 1992: 183.

Material examined.—Colombia. Valle del Cauca Department, Naya River, 15 Feb 1984, leg. R. Rios, 2 ♂, 043-00 ADT-CRBMUV. Nariño Department, Ricaurte, 3 km to Pasto, Apr 1982, leg. L. Gómez, 1 ♂, 27.5 × 44.6 mm, CRBMUV 82058.—Ricaurte, 22 May 1984, leg. L. Gómez, 1 ♂ paratype, 043-1 ADT-CRBMUV. Cauca Department, Naya River, Feb 1984, leg. uk, 2 ♂, 39.8 × 63.3 mm, 38.6 × 63.1 mm,

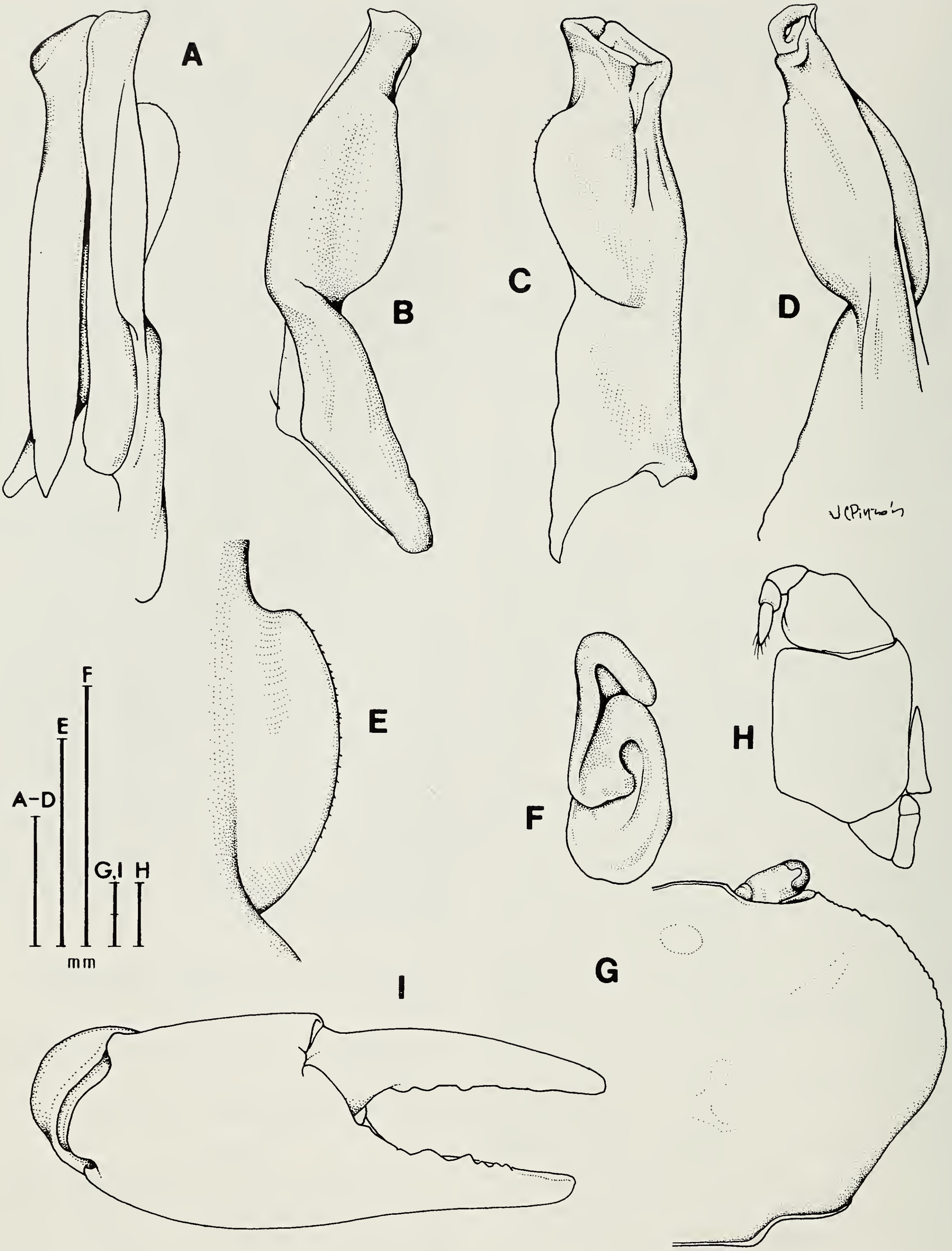

Fig. 16. *Hypolobocera martelathani* (Pretzmann, 1965), male holotype, No. Cat. 82051, CRBMUV: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, lateral lobe, caudolateral view; F, same, apex, distal view; G, right side of carapace, dorsal view; H, left third maxilliped, external view; I, right chela, external view.

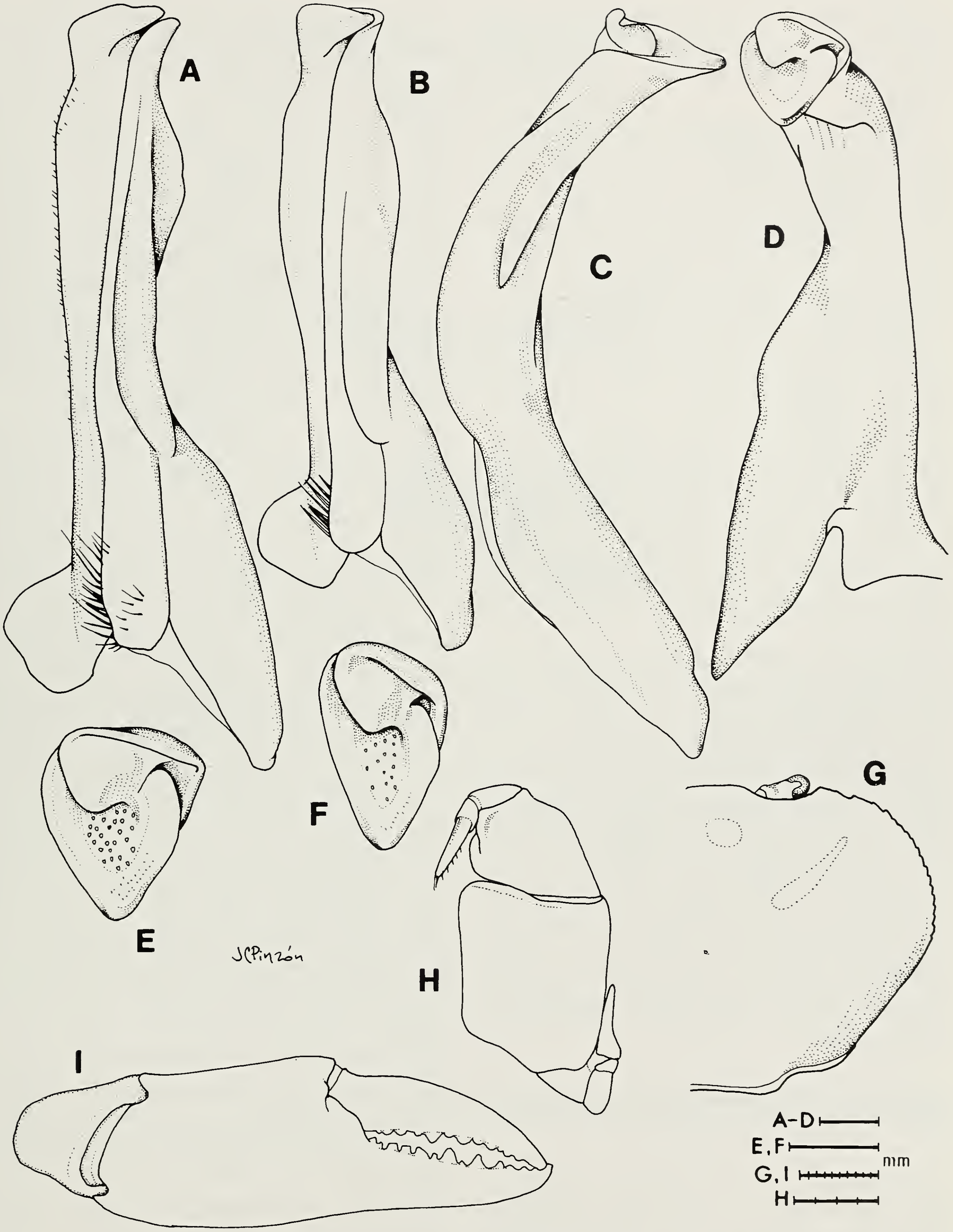

Fig. 17. *Hypolobocera meineli* Prahl 1988, male, CRBMUV 84075: A, left first gonopod, caudal view; C, same, lateral view; D, same, cephalic view; E, same, apex, distal view; G, right side of carapace, dorsal view; H, left third maxilliped, external view; I, right chela, external view. Male, ICN-MHN-CR 1866: B, left first gonopod, caudal view; F, apex, distal view.

CRBMUV 84075.—Guapi, Guapi River, El Naranjo, 50 m alt., 20 Sep 2000, leg. E. Guerra, 1 ♂, 29.8 × 46.9 mm, ICN-MHN-CR 1866.

Diagnosis.—Chelae of male lacking tubercles on external base of mobile and fixed fingers (Fig. 17I). First male gonopod with caudal ridge long, either fusiform thickened at proximal half or prominent and wide; ending in narrow ridge beyond lateral lobe. Mesial margin with or without rows of conspicuous setae (Fig. 17A, B). Lateral lobe small, slightly rounded, with or without slightly middle notch (Fig. 17A, B). Apex outline oval in distal view; expanded into a triangular projection cephalically. Mesocaudal projection of spermatic channel terminating in wide papilla. Mesial lobe reduced as strong fold along margin (Fig. 17E, F). Third maxilliped with exognath approximately 0.40 times length of ischium (Fig. 17H).

Remarks.—Prahl (1988) designated as holotype a male (043-00 ADT-CRBMUV) from Naya River, and as paratype a male (043-1 ADT-CRBMUV) from Ricaurte, without indicating their sizes. He only provided the measurements of the largest male (43.2 × 60.3 mm). In a recent examination of Prahl's material at the CRBMUV the labels with the catalogue numbers corresponding to the type material could not be found. Only two males from Naya River (CRBMUV 84075) were located, but with sizes that do not match those indicated by Prahl (1988).

Hypolobocera murindensis, new species
Figs. 18A–D, 19A–F

Holotype.—Colombia, Antioquia Department, Murindó, 25 m alt., 23 Sep 1994, leg. I. D. Vélez, ♂, 11.9 × 21.4 mm, ICN-MHN-CR 1388.

Paratypes.—Same locality data as holotype: 2 ♂, 11.8 × 21.3 mm, 10.5 × 18.8 mm, 1 ♀, 9.5 × 16.5 mm, 5 juveniles, ICN-MHN-CR 1389.

Diagnosis.—Chelae of male lacking tubercles on external base of mobile and fixed fingers (Fig. 18A). First male gonopod with caudal ridge long, fusiform; almost reaching apex (Fig. 19A, E). Lateral lobe prominent, subquadrate, external margin smooth (Fig. 19A, C, E). Apex outline oval in distal view; caudolateral expanded into rounded projection; cephalic border with row of spinules; prominent cephalic papilla. Mesocaudal projection of spermatic channel terminating in semiacute papilla. Mesial lobe slightly semicircular (Fig. 19C–F). Third maxilliped with exognath approximately 0.20 times length of ischium (Fig. 18C).

Description.—Carapace (Fig. 18A, B) with cervical groove straight, shallow, ending some distance from lateral margin. Anterolateral margin with shallow depression behind external orbital angle. Lateral margin with approximately 10 irregular tubercles. Postfrontal lobes small, rounded; delimited anteriorly by 2 depressions. Median groove shallow. Surface of carapace in front of postfrontal lobes regularly inclined anteriorly. Front low, upper border well demarcated with row of coalescent papillae; lower margin visible in dorsal view, sinuous in frontal view. Dorsal surface of carapace smooth, covered by small papillae, regions distinctly demarcated (Fig. 18A, B). Third maxilliped with rounded angle on distal half of external margin of merus; exognath approximately 0.20 times length of ischium (Fig. 18B, C). Orifice of efferent branchial channel irregularly ovate (Fig. 18D). First pereiopods heterochelous (Fig. 18A), right chela larger than left. Merus with 3 longitudinal crests as follows: upper crest with rows of tubercles, internal lower crest with rows of teeth, and external lower crest with row of tubercles. Carpus with 3 tubercles on internal crest, and blunt distal spine. Palms of both chelae smooth, and moderately swollen, fingers of larger chela slightly gaping when closed, finger tips crossing and surface of palms and fingers with rows of minute dark tubercles, (Fig. 18A). Walking legs (pereiopods 2–5) (Fig.

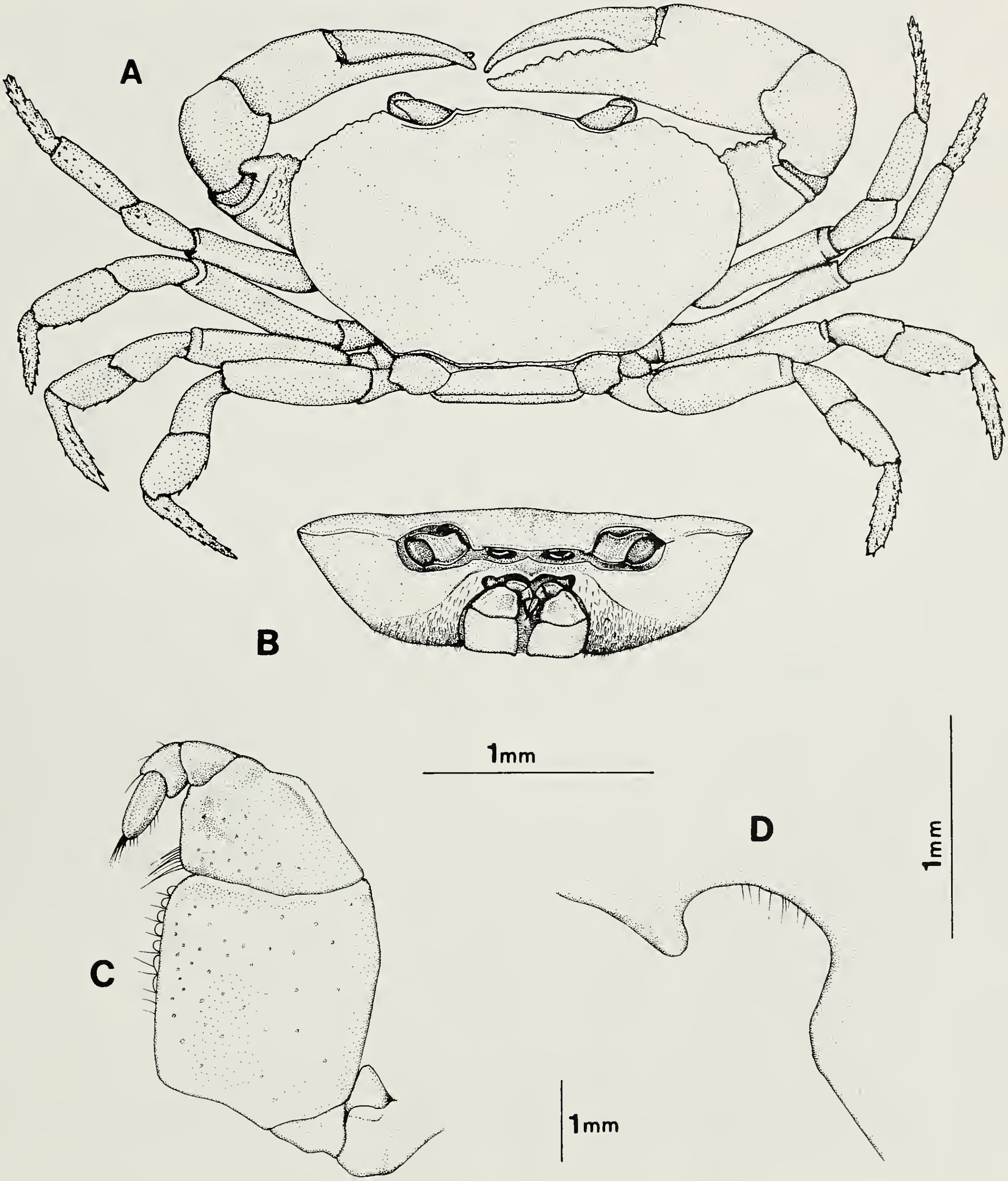

Fig. 18. *Hypolobocera murindensis,* new species, male holotype, ICN-MHN-CR 1388: A, carapace and pereiopods, dorsal view; B, carapace, frontal view; C, left third maxilliped, external view; D, opening of left efferent branchial channel, external view.

18A) with dactyli elongated, 5 longitudinal rows, and 4 to 6 spines on each row.

First male gonopod with caudal ridge long, fusiform; almost reaching apex (Fig. 19A, E). Lateral lobe prominent, subquadrate, external margin smooth (Fig. 19A, C, E). Apex outline oval in distal view, caudolateral expanded into rounded projection; cephalic border with row of spinules; prominent cephalic papilla. Mesocaudal projection of spermatic channel terminating in semiacute papilla. Mesial lobe slightly semicircular and projected on the caudal surface (Fig. 19A, C–F).

Color.—In alcohol, dorsal surface of the carapace light brown (near 136, Raw Si-

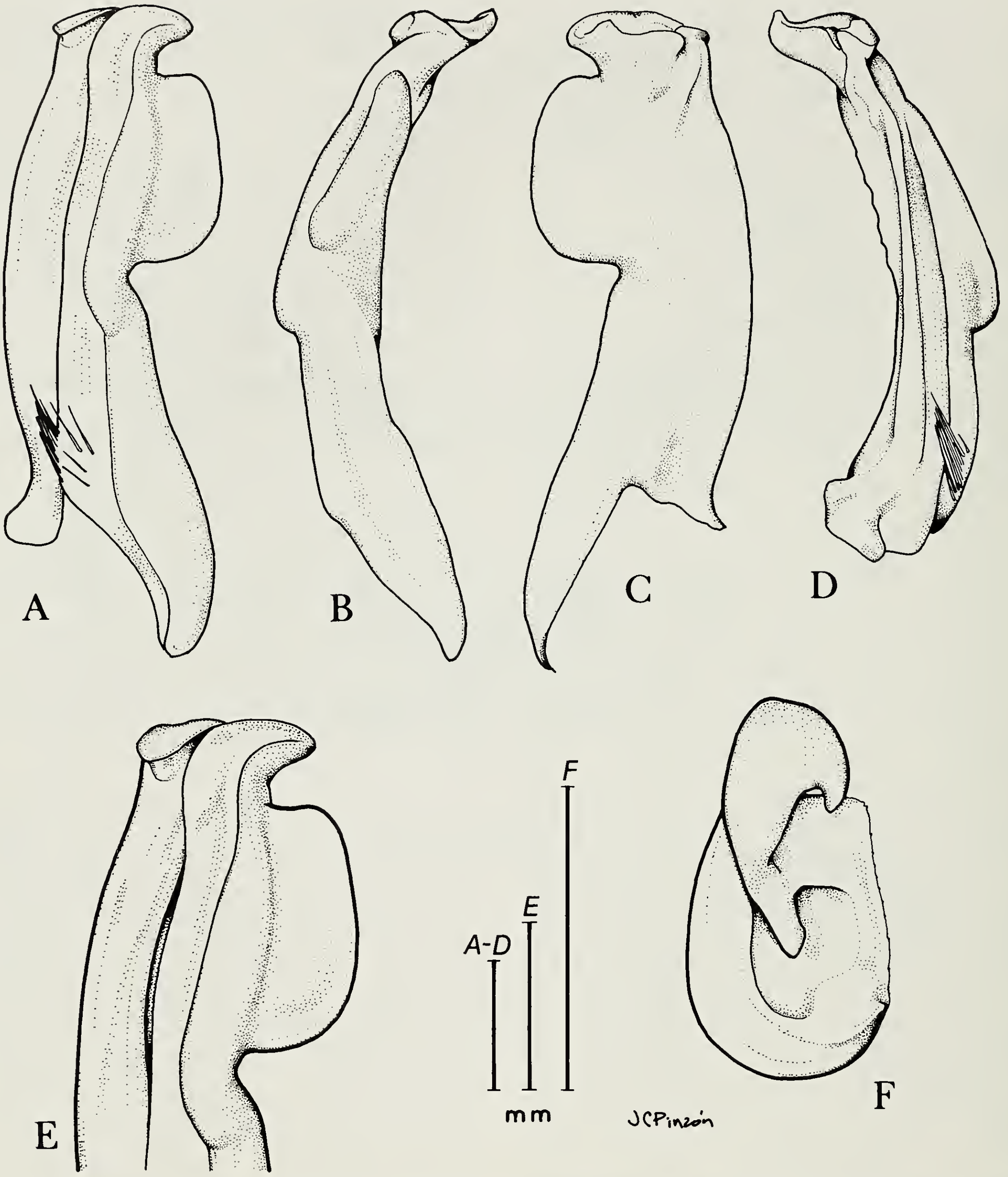

Fig. 19. *Hypolobocera murindensis,* new species, male holotype, ICN-MHN-CR 1388: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, lateral lobe, caudal view; F, same, apex, distal view.

enna) with dark brown (near Raw Umber, 223) speck on postfrontal portion of carapace. Walking legs and chelae brown (near True Cinnamon, 139) dorsally, and light brown (near Sayal Brown, 223C) ventrally. Ventral surface of the carapace brown (Verona Brown, 223B).

Etymology.—The specific name refers to Murindó, where the specimens were collected.

Remarks.—This species belongs to group 6, and is most similar to *Hypolobocera andagoensis.* The two can be distinguished by differences in the third maxilliped, and in the first male gonopod. In the new species the merus of the third maxilliped has a rounded angle, whereas in *H. andagoensis* it is sharp (Fig. 2F). The lateral lobe of the gonopod in *H. murindensis* is thick, and subquadrate, with the external margin rounded, slightly convex in lateral view, and with a narrow constriction below the lateral lobe. In contrast, *H. andagoensis* has the lateral lobe thin, narrower distally than proximally, with a faintly crenulated external margin, and a wide constriction below the lateral lobe (Fig. 2A, B). The mesial lobe is projected as a rounded lobe on the caudal surface, slightly semicircular in distal view in *H. murindensis,* whereas, in *H. andagoensis* it is subtriangular, and not projected on the caudal surface (Fig. 2D).

Hypolobocera mutisi Prahl, 1988
Fig. 20A–G

Hypolobocera mutisi Prahl, 1988:175, figs. 5, 6.

Hypolobocera mutisi.—Rodríguez, 1992: 183.

Material examined.—Colombia, Valle del Cauca Department. Cajambre River, 500 m alt., 16 Jul 1983, leg. R. Rios, M holotype, 042-0 ADT-CRBMUV.—Same data, 1 ♂ paratype (USNM 210728).—El Piñuelal, Cajambre River, 16 Aug 1983, leg. R.R., 1 ♂, 23.3 × 38.6 mm, CRBMUV 83086.

Diagnosis.—Chelae of male with small tubercle on external base of mobile fingers, and swelling on external base of fixed fingers (Fig. 20G). First male gonopod with caudal ridge long, straight; ending in narrow ridge beyond lateral lobe (Fig. 20A). Lateral lobe outline irregular, slightly trapezoidal; projected into narrow expansion distally (Fig. 20A, C). Apex outline elongated in distal view, caudolaterally expanded into rounded projection; prominent, acute cephalic papilla. Mesocaudal projection of spermatic channel terminating in rounded papilla. Mesial lobe elongated, subtriangular (Fig. 20C, D). Third maxilliped with exognath approximately 0.30 times length of ischium (Fig. 20F).

Remarks.—An exhaustive search of the CRBMUV collections failed to produce the holotype of this species. Only the male specimen from El Piñuelal, Cajambre River (CRBMUV 83086) was found, and is illustrated herein.

Hypolobocera noanamensis Rodríguez, Campos & López, 2002
Fig. 21A–H

Hypolobocera noanamensis Rodríguez, Campos & López, 2002:4–6, fig. 1A–H.

Material examined.—Colombia, Chocó Department, Noanamá, San Juan River, 50 m alt., 4°42′N, 26°56′W, 8 Aug 1969, leg. Dale Little, ♂ holotype, 50.9 × 80.3 mm, TU 6191.—Same data, 1 ♀ paratype, 53.9 × 80.3 mm, TU 5337.

Diagnosis.—Chelae of male without tubercle on external base of mobile fingers, with a swelling on external base of fixed fingers (Fig. 21H). First male gonopod with caudal ridge strong, fusiform; ending in narrow ridge beyond lateral lobe (Fig. 21A). Lateral lobe small, subtriangular, distal angle rounded, placed transversely in relation to axis of appendage; cephalic surface with tuberculated crest (Fig. 21A–C). Apex outline oval in distal view, mesocephalic border rounded expanded; flat papilla on caudolateral border. Mesocaudal projection of spermatic channel terminating in rounded papilla with spiny ridge on cephalic side. Mesial lobe subtriangular (Fig. 21E). Third maxilliped with exognath 0.30 times length of ischium (Fig. 21G).

Remarks.—This species closely resembles *Hypolobocera beieri* in the shape of the lateral lobe, and the outline of the apex of the first male gonopod. The species can be differenciated from each other by the spiny ridge on the cephalic side of the mesocaudal projection in *H. noanamensis,* which is lacking in *H. beieri.*

Hypolobocera rotundilobata Rodríguez, 1994
Fig. 22A–H

Hypolobocera bouvieri rotundilobata Rodríguez, 1994:297, fig. 2.

Hypolobocera bouvieri rotundilobata.—Rodríguez et al., 2002:6.

Material examined.—Colombia. Chocó Department, Mountains of upper San Juan

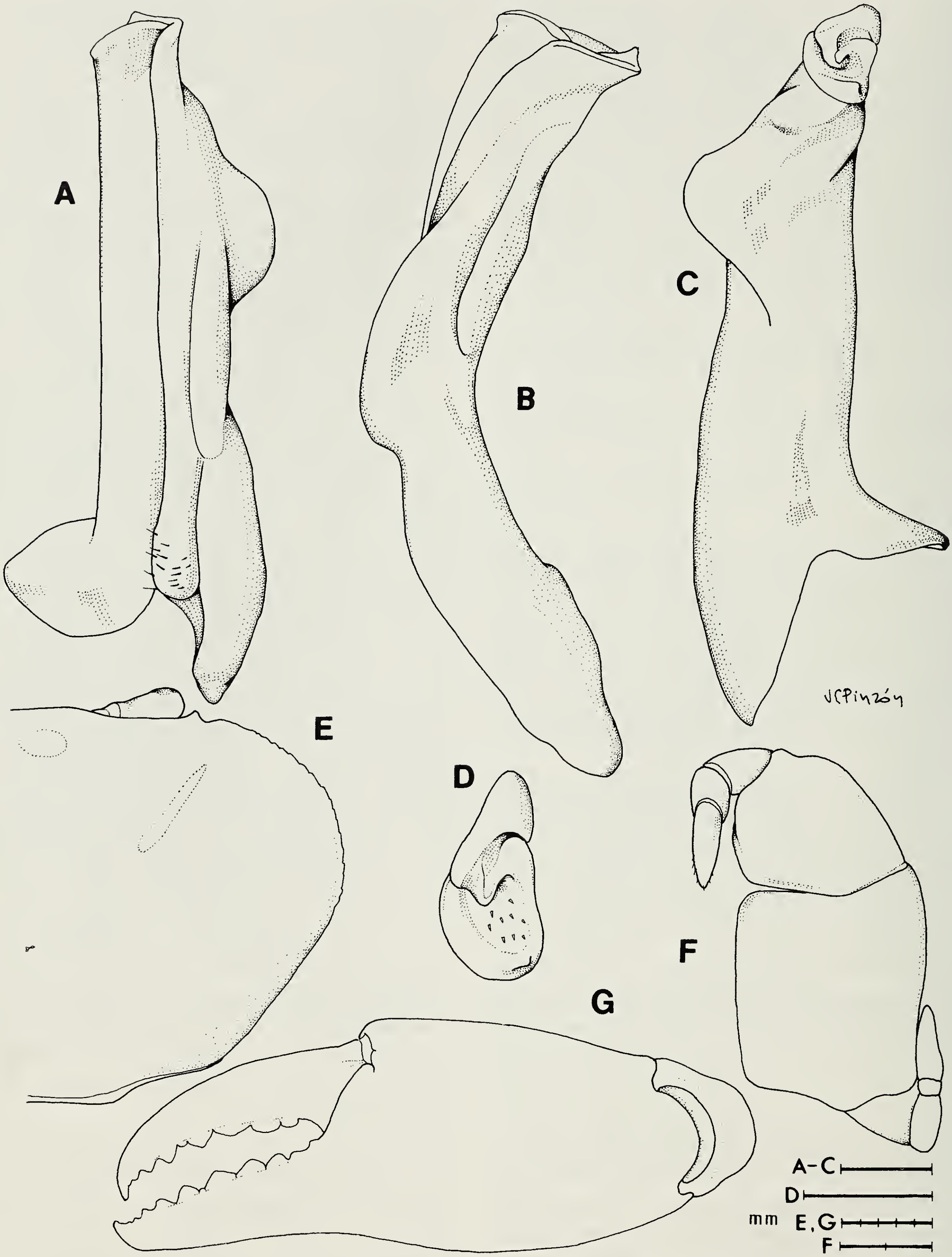

Fig. 20. *Hypolobocera mutisi* Prahl 1988, male, CRBMUV 83086: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, apex, distal view; E, right side of carapace, dorsal view; F, left third maxilliped, external view; G, left chela, external view.

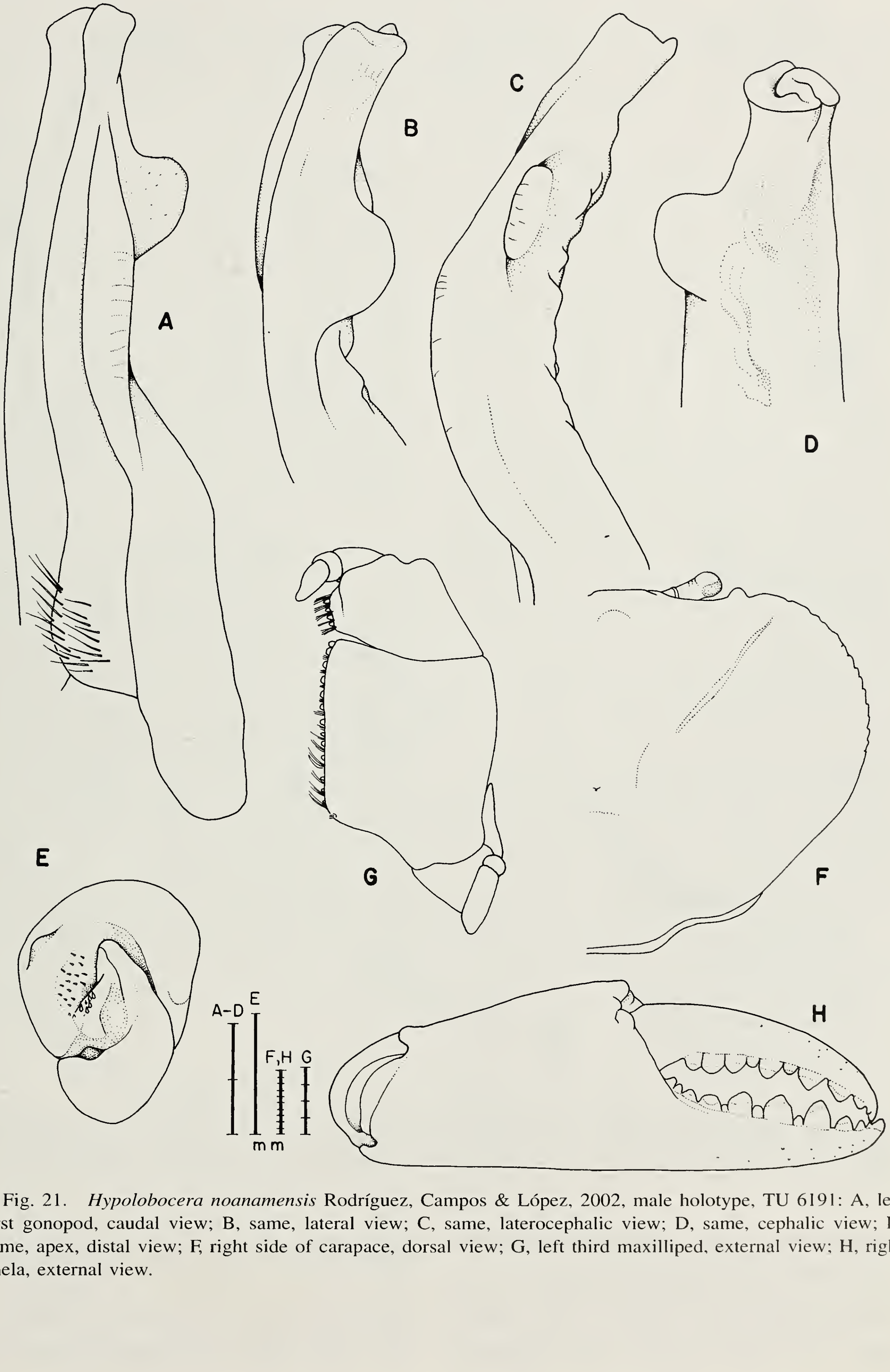

Fig. 21. *Hypolobocera noanamensis* Rodríguez, Campos & López, 2002, male holotype, TU 6191: A, left first gonopod, caudal view; B, same, lateral view; C, same, laterocephalic view; D, same, cephalic view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, right chela, external view.

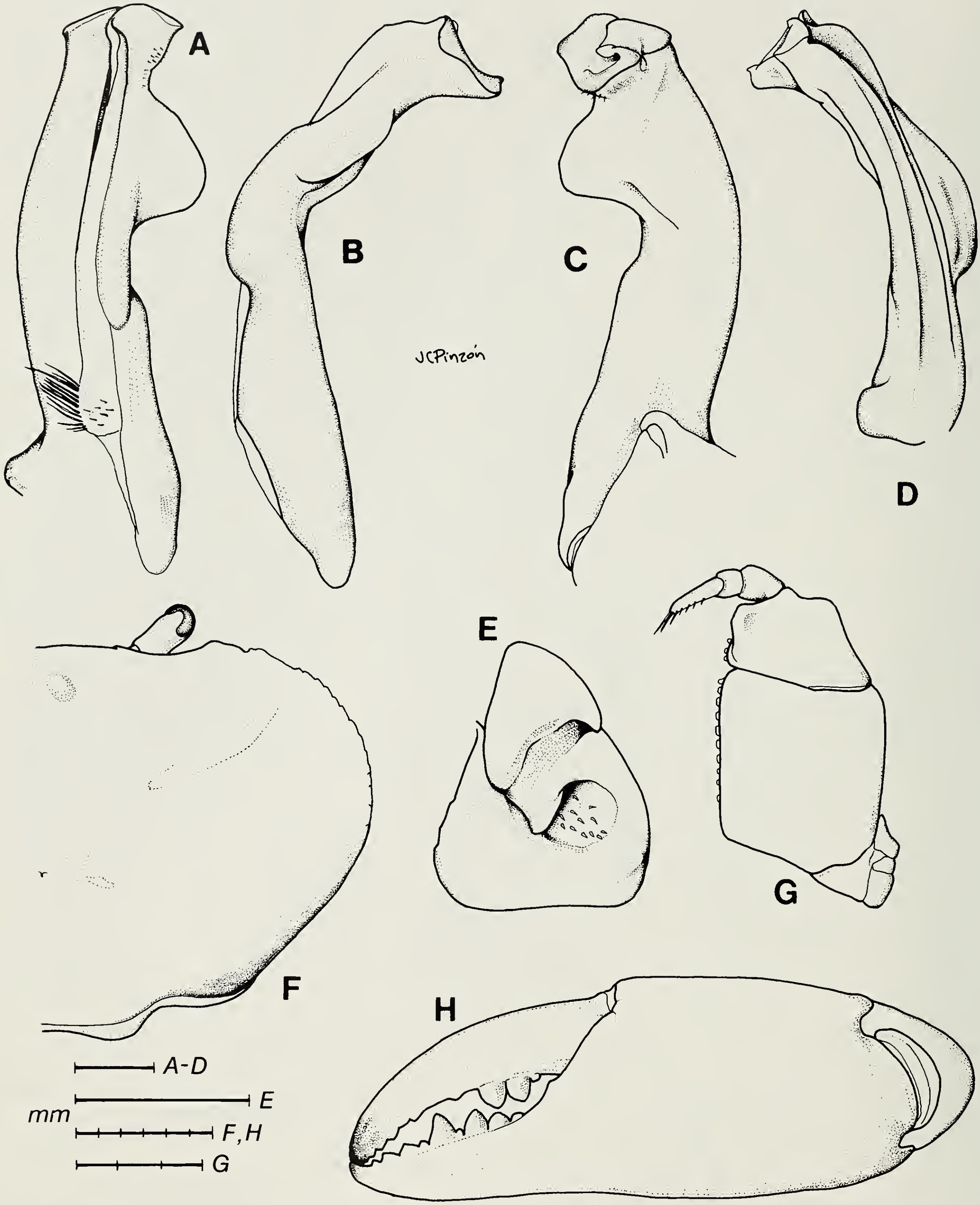

Fig. 22. *Hypolobocera rotundilobata* Rodríguez, 1994, male holotype, USNM 240104: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, left chela, external view.

River, nearest village Playa de Oro, 28 Mar 1962, leg. M. Latham, ♂ holotype, 46.2 × 68.4 mm, USNM 240103.—Same data, 5 ♂ paratypes, 15.4 × 26.3 to 12.1 × 22.6 mm, 1 ♀, 18.0 × 31.6 mm, USNM 240104.—Borderline between Chocó and Valle del Cauca Departments, Paso de Galápagos, 15 May 1985, leg. M. Alberico, 2 ♂, 13.3 × 23.3 mm, 12.4 × 21.1 mm, 6 ♀, 13.1 × 22.6 to 10.2 × 17.2 mm, CRBMUV

85147.—Chocó Department, San José del Palmar, Ingará River, 2000 m alt., 22 Oct 2000, leg. E. Guerra, 1 ♂, 13.1 × 22.8 mm, 1 ♀, 13.3 × 22.9 mm, ICN-MHN-CR 1867, 1868.

Diagnosis.—Chelae of male lacking tubercles on external base of mobile and fixed fingers (Fig. 22H). First male gonopod with caudal ridge long, straight; ending in narrow ridge distally (Fig. 22A). Lateral lobe slightly semicircular (Fig. 22A, C). Apex outline subtriangular in distal view; lateral border straight; rounded cephalic papilla. Mesocaudal projection of spermatic channel terminating in semiacute papilla. Mesial lobe subtriangular and projected mesially (Fig. 22A, C, E). Third maxilliped with exognath 0.30–0.40 times length of ischium (Fig. 22G).

Remarks.—Rodríguez (1994) described this taxon as *Hypolobocera bouvieri rotundilobata.* The subspecies of *H. bouvieri* are characterized by the male chelae, featuring a small, rounded or irregularly shaped tubercle on the external base on each of the the mobile fingers, and a swelling or prominent tubercle on external base on each of the fixed fingers. The apex outline of the first male gonopod is oval, with prominent cephalic papilla, and an auxiliary rounded papilla near the spermatic channel. However, in *H. rotundilobata* the male chelae lack tubercles on the external base of the mobile and fixed fingers. The apex outline is subtriangular, and without an auxiliary papilla. In view of this, *H. b. rotundilobata* is elevated to specific rank.

Hypolobocera steindachneri Pretzmann, 1968

Hypolobocera (*Hypolobocera*) *monticola steindachneri* Pretzmann, 1968:9.—Pretzmann, 1971:17.—Pretzmann, 1972: 46, figs. 204, 205, 227–229.

Hypolobocera steindachneri.—Rodríguez, 1982a:58.

Material examined.—Colombia, Valle del Cauca Department. 1897, leg. Steindachneri, ♂ holotype, cl 27.7 mm, 1 ♂ paratype, cl 20.6 mm (Museum Wien Nr. 3779).—Bitaco, 1957, leg. M. Latham, 2 ♂, cl 18.0, 15.3 mm, 2 ♀, cl 21.0, 15.6 mm, USNM.

Remarks.—I have been unable to examine any material of this species. Pretzmann (1968:9) in his original description of *Hypolobocera* (*Hypolobocera*) *monticola steindachneri* described as features "the first male gonopod is slender; the lateral lobe is smaller, the external margin is folded back strongly, and it is placed far from apex. The exognath of third maxilliped is 0.12 the length of ischium". Pretzmann (1972) described again, including illustrations, the morphological features of *H.* (*H.*) *m. steindachneri,* partially contradicting his previous description (Pretzmann, 1968). He stated that "the lateral lobe is placed not far from apex" and that "the exognath of third maxilliped is shorter, only 0.17 the length of ischium".

Hypolobocera velezi, new species
Fig. 23A–H

Holotype.—Colombia. Chocó Department, Carmen de Atrato, Vereda El Veinte, 2400 m alt., 25 May 1994, leg. I. D. Vélez, 1 ♂, 16.1 × 29.2 mm, ICN-MHN-CR 1387.

Paratypes.—Same locality data as holotype: 1 ♀, 16.6 × 28.2 mm, 1 ovigerous ♀, 15.3 × 27.4 mm, ICN-MHN-CR 1889.

Non-paratypes.—Colombia. Risaralda Department, Pueblo Rico, Corregimiento Santa Cecilia, Vereda La Granja, 600 m alt., 23 Oct 1991, 1 ♂, 15.5 × 25.4 mm, 1 ♀, 16.5 × 27.1 mm, ICN-MHN-CR 1307.—Chocó Department, Carmen de Atrato, km 53 Carmen de Atrato-Quibdó Highway, 420 m alt., 27 Aug 1987, leg. R. Sánchez, 2 ♀, 13.0 × 21.3 mm, 11.9 × 19.6 mm, ICN-MHN-CR 0784.

Diagnosis.—Chelae of male lacking tubercles on external base of mobile and fixed fingers (Fig. 23H). First male gonopod with caudal ridge strong, straight, narrow distally; ending some distance from apex (Fig.

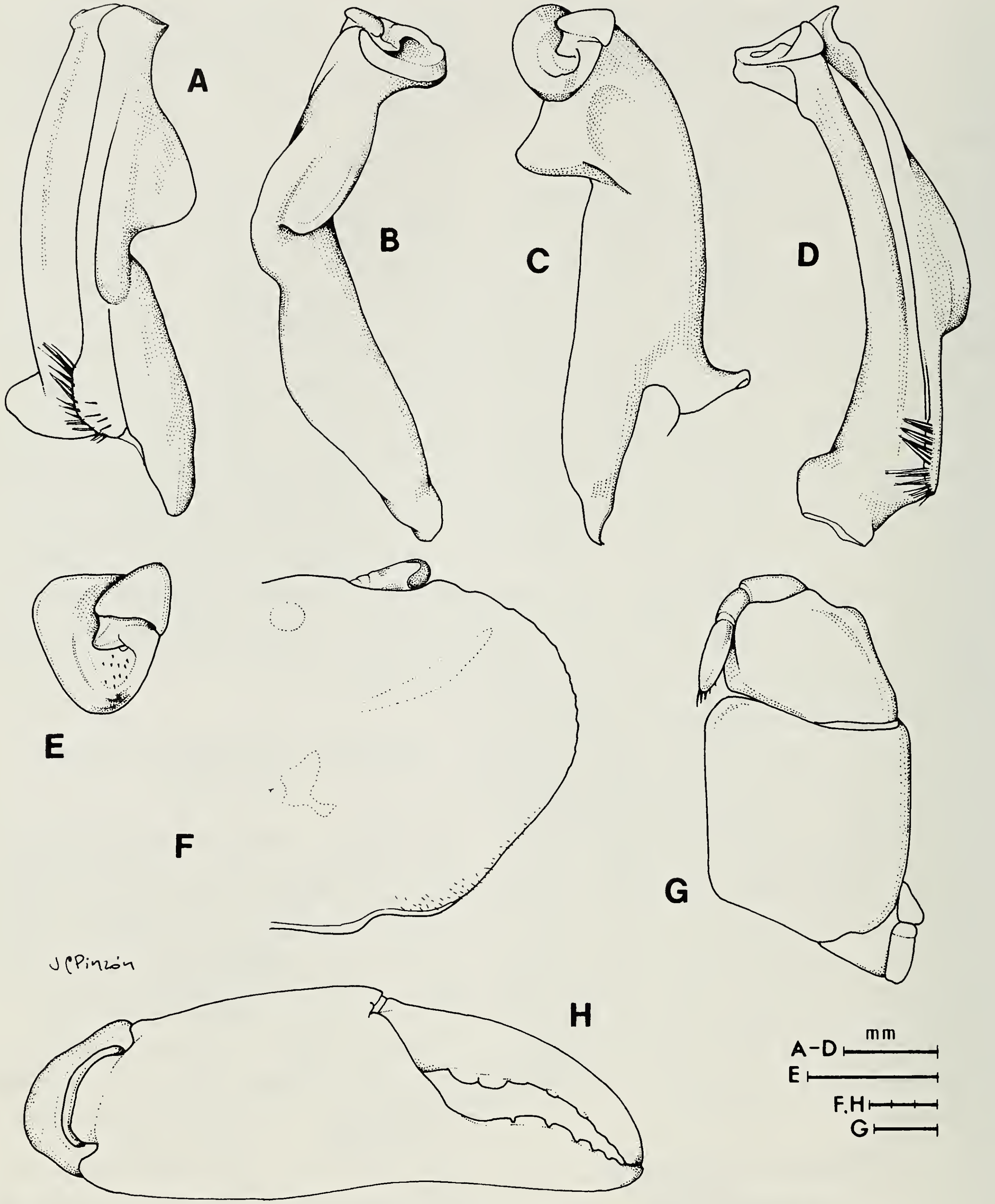

Fig. 23. *Hypolobocera velezi,* new species, male holotype, ICN-MHN-CR 1387: A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same, mesial view; E, same, apex, distal view; F, right side of carapace, dorsal view; G, left third maxilliped, external view; H, right chela, external view.

23A). Lateral lobe subtriangular; proximal external margin angled and curved upward (Fig. 23A, C). Apex outline slightly rounded in distal view, mesocaudally expanded into rounded projection; rounded papilla near cephalic border. Mesocaudal projection of spermatic channel terminating in semiacute papilla. Mesial lobe subtriangular

(Fig. 23C, E). Third maxilliped with exognath approximately 0.20 times length of ischium (Fig. 23G).

Description.—Carapace (Fig. 23F) with cervical groove deep, straight, recurved posteriorly, ending some distance from lateral margin. Anterolateral margin with shallow depression behind external orbital angle, anterolateral border not continuous with margin of depression, but runing dorsally to it, forming rounded lobe. Lateral margin with approximately 12 blunt teeth. Postfrontal lobes oval, low; delimited anteriorly by 2 transverse depressions. Median groove wide, shallow. Surface of carapace in front of postfrontal lobes regularly inclined anteriorly. Front lacking distinct upper border, regularly curving downward; slightly bilobed in dorsal view; lower margin slightly sinuous in frontal view. Dorsal surface of carapace smooth, covered by small papillae, regions distinctly demarcated (Fig. 23F). Third maxilliped with sharp angle on distal half of external margin of merus; exognath approximately 0.20 times length of ischium (Fig. 23G). Orifice of efferent branchial channel slightly ovate. First pereiopods heterochelous, right chela larger than left. Merus with 3 longitudinal crests as follows: upper crest with rows of tubercles, internal lower crest with rows of teeth, and external lower crest with row of tubercles. Carpus with 3 tubercles on internal crest, and blunt spine distally. Palm of male chelae swollen, fingers gaping when closed. Walking legs (pereiopods 2–5) with 5 longitudinal rows, and 4 to 6 spines on each row.

First male gonopod with caudal ridge strong, straight, narrow distally; ending at some distance from apex (Fig. 23A). Lateral lobe subtriangular; proximal external margin angled and curved upward (Fig. 23A, C). Apex outline slightly rounded in distal view, mesocaudally expanded into rounded projection; rounded papilla near cephalic border. Mesocaudal projection of spermatic channel terminated in semiacute papilla. Mesial lobe subtriangular (Fig. 23C, E).

Color.—In alcohol, dorsal surface of the carapace brown (near 37, Antique Brown) with light brown (near Cinnamon, 39) speck on posterior portion of carapace. Walking legs and chelae brown (near 37, Antique Brown) dorsally, and light brown (near Sayal Brown, 223C) ventrally. Ventral surface of the carapace light brown (near Cinnamon, 39).

Etymology.—The species is named in honor of Colombian scientist Dr. Ivan Darío Vélez, professor of the Universidad de Antioquia, who promotes research in Paragonimosis and other tropical diseases, and who collected the specimens.

Remarks.—This species belongs to group 4, and is most similar to *Hypolobocera lloroensis.* The two can be differentiated by feature of the first male gonopod. The proximal external margin of the lateral lobe in *H. velezi* is angled, and curved upward (Fig. 23A, C), whereas that margin is rounded, and not caudally curved in *H. lloroensis* (Fig. 14A).

Key to Species and Subspecies of *Hypolobocera* from Colombia

1. Outline of apex of gonopod in distal view oval, rounded or subtriangular 2
– Outline of apex of gonopod in distal view elongated 16
2. Lateral lobe rounded or subtriangular 9
– Lateral lobe regularly rounded 3
3. Lateral lobe with strong triangular process .... *H. alata*
– Lateral lobe without strong triangular process 4
4. Latero-cephalic border of apex toothed .... *H. dentata*
– Latero-cephalic border of apex not toothed 5
5. Lateral lobe displaced towards cephalic side (Fig. 13B–D) .... *H. kamsarum*
– Lateral lobe not displaced towards cephalic side 6
6. Mesial lobe well developed, subtriangular or semicircular 7

– Mesial lobe reduced as strong fold along margin .... *H. meineli*
7. Lateral border of apex straight in distal view (Fig. 22E) .... *H. rotundilobata*
– Lateral border of apex rounded in distal view (Figs. 3E, 4E, 6E) 8
8. With auxiliary papilla near spermatic channel 19
– Without auxiliary papilla near spermatic channel 9
9. Mesocaudal projection with spiny ridge on cephalic side .... *H. noanamensis*
– Mesocaudal projection without spiny ridge on cephalic side .... *H. beieri*
10. Lateral lobe rounded or subtriangular 11
– Lateral lobe subquadrate 13
11. Proximo-external margin of lateral lobe rounded 12
– Proximo-external margin of lateral lobe angled and curved upwards .... *H. velezi*
12. An auxiliary lobe parallel to lateral lobe on lateral side .... *H. cajambrensis*
– No auxiliary lobe on lateral side 13
13. External margin of lateral lobe faintly crenulated .... *H. andagoensis*
– External margin of lateral lobe not crenulated .... *H. murindensis*
14. Distal border of lateral lobe rounded (Fig. 15A, C) .... *H. malaguena*
– Distal border of lateral lobe not rounded (Fig. 9A, E) 15
15. Mesocephalic border of apex transverse expanded (Fig. 14E) ...... *H. lloroensis*
– Mesocephalic border of apex not transverse expanded (Fig. 9F) *H. chocoensis*
16. Distal end of lateral lobe with a deep notch .... *H. emberarum*
– Distal end of lateral lobe lacking notch 17
17. Outline of lateral lobe irregular *H. mutisi*
– Outline of lateral lobe regularly recurved 18
18. Apex in distal view with bifid papilla near spermatic channel .. *H. gorgonensis*
– Apex in distal view with slightly rounded papilla near spermatic channel .... *H. martelathani*
19. Lateral lobe subtriangular 20
– Lateral lobe semicircular 21
20. Mesocaudal projection of spermatic channel with distal spinule .... *H. bouvieri monticola*
– Mesocaudal projection of spermatic channel without distal spinule .... *H. bouvieri angulata*
21. Chelae of male with prominent tubercle on external base of fixed fingers .... *H. bouvieri bouvieri*
– Chelae of male without prominent tubercle on external base of fixed fingers .... *H. bouvieri stenolobata*

Summary of Distributions

This review of the genus *Hypolobocera* from Colombia has made possible the study of the geographic distribution of this genus. However, some species are known from single or few localities, and additional sampling is needed.

The distribution of *Hypolobocera* species comprises a vast portion of the Colombian territory (Fig. 24), and includes most of Colombia's major basins: the Magdalena, Cauca, and Atrato Rivers basins, which drain to the Caribbean; the San Juan, Anchicayá, Dagua, Cajambre, Naya, and Guapi Rivers basins, which drain to the Pacific; and the Caquetá River basin, which drains to the Amazon River.

Seven species and two subspecies have trans-basin distribution: *Hypolobocera buenaventurensis, H. cajambrensis, H. chocoensis, H. lloroensis, H. meineli, H. velezi, H. beieri, H. bouvieri angulata,* and *H. b. monticola.* The distribution of the latter subspecies is particularly interesting, because it encompasses rivers that flow into the Atlantic and the Pacific Oceans.

Hypolobocera bouvieri bouvieri, H. b. stenolobata, and *H. martelathani* are found exclusively in the Magdalena River basin, while *H. alata, H. andagoensis,* and *H. rotundilobata* have only been found in the San Juan River basin; *H. emberarum* occurs only in the Atrato River basin.

Hypolobocera bouvieri bouvieri has an extensive distribution on the slopes of the Central and Eastern Cordilleras, in systems that drain to the Magdalena River. Another subspecies with a broad trans-basin distribution is *H. b. monticola.* The known distribution of this subspecies includes the

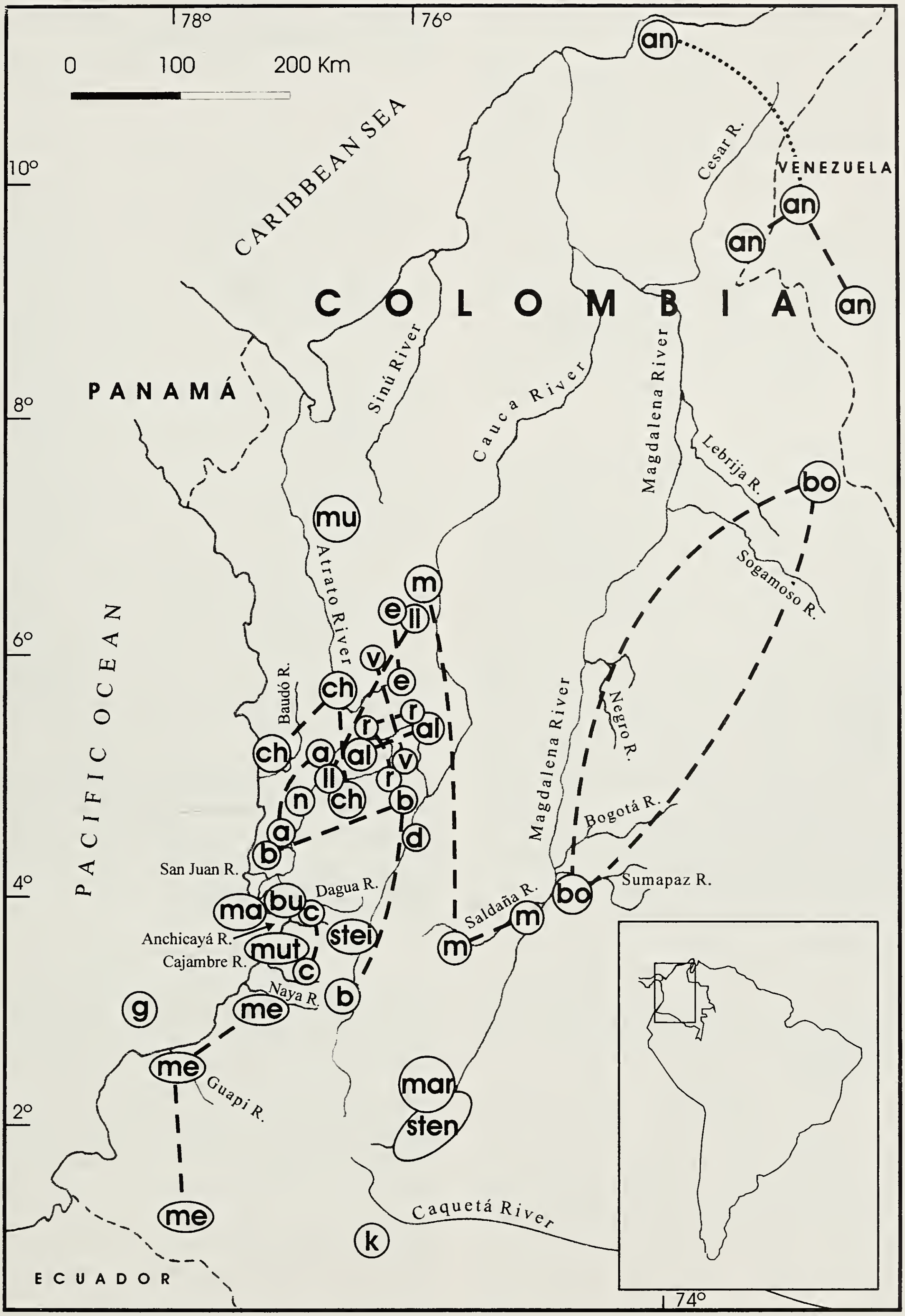

Fig. 24. Geographical distribution of *Hypolobocera* in Colombia. a, *H. andagoensis*; al, *H. alata*; b, *H. beieri*; an, *H. bouvieri angulata*; bo, *H. bouvieri bouvieri*; m, *H. bouvieri monticola*; sten, *H. bouvieri stenolobata*; bu, *H. buenaventurensis*; c, *H. cajambrensis*; ch, *H. chocoensis*; d, *H. dentata*; e, *H. emberarum*; g, *H. gorgonensis*; k, *H. kamsarum*; ll, *H. lloroensis*; ma, *H. malaguena*; mar, *H. martelathani*; me, *H. meineli*; mu, *H. murindensis*; mut, *H. mutisi*; n, *H. noanamensis*; r, *H. rotundilobata*; stei, *H. steindachneri*; v, *H. velezi*. The bold, dashed lines indicate continuous distribution ranges, and the dotted line a disjunct distribution.

Central and Western Cordilleras in the middle course of the Magdalena and Cauca River basins. This subspecies has a great potential to colonize new habitats due, in part, to the ability of females to hatch large number of eggs. The distribution of *H. b. angulata* includes the Sierra Nevada de Santa Marta to both slopes of the Sierra de Perijá, and also the Cordillera de Mérida in Venezuela. This disjunct distribution, covering the Cesar and Catatumbo River basins, is considered a relict distribution modified by temperature changes (G. Rodríguez, pers. comm.).

Hypolobocera lloroensis and *H. chocoensis* are known from the headwaters of the Atrato River, which flows northwards into the Gulf of Urabá to the Caribbean Sea. In addition, records are here included from the basin of the San Juan River which drains into the Pacific Sea, for *H. chocoensis* (upper San Juan River, Chocó, USNM 240102; Condoto, 045-0, 045-1 ADT-CRBMUV); and *H. lloroensis* (Condoto, CRBMUV 85132; CRBMUV 87016; Istmina, TU 6193; Tadó, ICN-MHN-CR 1262). This trans-basin distribution can be attributed to the intermittent communication between both basins which can occur during flooding seasons in areas below 100 m of altitude.

Hypolobocera dentata, H. kamsarum, H. malaguena, H. mutisi, H. murindensis, and *H. noanamensis* are species known from single localities.

The vertical distribution of the species (Table 1) ranges from 20 to 2500 m. *Hypolobocera lloroensis* extends from 50 to 2400 m along the San Juan River and headwater of the Atrato River. *Hypolobocera andagoensis, H. buenaventurensis, H. cajambrensis, H. chocoensis, H. gorgonensis, H. malaguena, H. meineli, H. murindensis, H. mutisi,* and *H. noanamensis,* have been found along the coastal plain of the Pacific, between 20 and 700 m. The other species from the Pacific drainage are *H. beieri,* between 500 and 1600 m; *H. rotundilobata,* between 70 and 2000 m. The inland species, which range between 270 and 2500 m are: *H. dentata, H. emberarum, H. martelathani, H. steindachneri, H. velezi,* and the subspecies *H. b. bouvieri, H. b. monticola,* and *H. b. stenolobata.*

Table 1.—Altitudes (in meters above sea level) reported for Colombian *Hypolobocera.*

Hypolobocera alata	490–700
H. andagoensis	20–50
H. beieri	500–1600
H. bouvieri angulata	400–1300
H. bouvieri bouvieri	270–2050
H. bouvieri monticola	300–1850
H. bouvieri stenolobata	1175–1200
H. buenaventurensis	20–200
H. cajambrensis	50–700
H. chocoensis	20–500
H. dentata	1600
H. emberarum	1800–2500
H. gorgonensis	20–300
H. kamsarum	1350
H. lloroensis	50–2400
H. malaguena	0–50
H. martelathani	1300–2300
H. meineli	50–100
H. murindensis	25
H. mutisi	500
H. noanamensis	50
H. rotundilobata	70–2000
H. steindachneri	1500
H. velezi	420–2400

Acknowledgments

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Literature Cited

Campos, M. R. 1985. Decápodos de agua dulce del Suborden Brachyura reportados para Colombia. Caldasia 14(67):265–284.

———. 1989. Nuevas especies de cangrejos de agua dulce del género *Hypolobocera* (Crustacea: Decapoda: Pseudothelphusidae) para Colombia.—Trianea 3:143–147.

———, & G. Rodríguez. 1984. New species of freshwater crabs (Crustacea: Decapoda: Pseudothelphusidae) from Colombia.—Proceedings of the Biological Society of Washington 97:538–543.

———, & ———. 1995. Two new species of freshwater crabs of the genus *Hypolobocera* from Colombia (Crustacea: Decapoda: Pseudothelphusidae).—Proceedings of the Biological Society of Washington 108:649–655.

Coifmann, I. 1939. Potamonidi della Guiana Inglese raccolti dal Prof. Nello Beccari.—Archivio Zologico Italiano 27:93–116.

Milne Edwards, H., & H. Lucas. 1842–1844. Crustacés. In A. d'Orbigny, Voyage dans l'Amérique méridionale dans le cours des annés 1826–1833 6:1–39, Atlas 9: pl. 1–17.

Ortmann, A. 1897. Carcinologische Studien.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Tiere 10:258–372.

Prahl, H von. 1983. *Hypolobocera gorgonensis* sp. nov. (Crustacea: Brachyura: Pseudothelphusidae) un nuevo cangrejo de agua dulce de la Isla de Gorgona, Colombia. Cespedesia XII(45/46): 105–110.

———. 1985. Distribución del cangrejo de agua dulce *Hypolobocera beieri* Pretzmann, 1968 y anatomía de su gonópodo.—Actualidades Biológicas 14:43–47.

———. 1987. *Hypolobocera dentata* sp. nov.: a new freshwater crab (Crustacea: Brachyura: Pseudothelphusidae) from the Cordillera Occidental, Colombia.—Revista de Biología Tropical 35: 93–95.

———. 1988. Fresh-water crabs (Crustacea: Decapoda: Pseudothelphusidae) of the Pacific Drainage of Colombia.—Zoologische Jahrbücher für Systematik 115:171–186.

———, & J. Giraldo. 1985. Un nuevo cangrejo de agua dulce de la Cordillera Central de Colombia.—Lozania 49:1–5.

Pretzmann, G. 1965. Vorläufiger Bericht über die Familie Pseudothelphusidae.—Anzeiger der Österreichischen Akademie der Wissenschaften Mathematische Naturwissenschaftliche Klasse (1)1:1–10.

———. 1968. Neue Südamerikanische Süsswasserkrabben der Gattung *Pseudothelphusa.*—Entomologisches Nachrichtenblatt, Wien 15:1–15.

———. 1971. Fortschritte in der Klassifizierung der Pseudothelphusidae.—Anzeiger der Mathematisch Naturwissenschaftliche der Österreichischen Akademie der Wissenschaften (1)179(1–4): 14–24.

———. 1972. Die Pseudothelphusidae (Crustacea Brachyura).—Zoologica 42(120) pt. 1: 1–182.

Rathbun, M. J. 1898. A contribution to a knowledge of the fresh-water crabs of America. The Pseudothelphusidae.—Proceedings of the United States National Museum 21(1158):507–537.

———. 1905. Les crabes d'eau douce (Potamonidae).—Nouvelles Archives du Muséum d'Histoire Naturelle, Paris 7:159–321.

———. 1915. New fresh-water crabs (*Pseudothelphusa*) from Colombia.—Proceedings of the Biological Society of Washington 28:95–100.

Rodríguez, G. 1966. The freshwater crabs of the genus *Pseudothelphusa* from northern Venezuela and Trinidad (Brachyura, Potamonidae).—Zoologische Mededelingen, Leiden 41(6):111–135, pl. 1–7.

———. 1967. New species of Pseudothelphusa from the Venezuelan Andes (Crustacea: Brachyura, Potamonidae).—Zoologische Mededelingen, Leiden 42(2):1–10, pl. 1–2.

———. 1980. Description préliminaire de quelques esp'eces et genres nouveaux de Crabes d'eau douce de l'Amérique tropicale (Crustacea: Decapoda: Pseudothelphusidae).—Bulletin du Muséum nationale d'Histoire naturelle, Paris (4) 2 Section A (3):889–894.

———. 1982a. Les crabes d'eau douce d'Amérique. Famille des Pseudothelphusidae.—Faune Tropicale 22:1–223.

———. 1992. The freshwater crabs of America. Family Trichodactylidae and supplement to the family Pseudothelphusidae.—Faune Tropicale 31: 1–189.

———. 1994. A revision of the type material of some species of *Hypolobocera* and *Ptychophallus* (Crustacea: Decapoda: Pseudothelphusidae) in the National Museum of Natural History, Washington D.C., with descriptions of a new species and a new subspecies.—Proceedings of the Biological Society of Washington 107:296–307.

———, & R. von Sternberg. 1998. A revision of the freshwater crabs of the family Pseudothelphusidae (Decapoda: Brachyura) from Ecuador.—Proceedings of the Biological Society of Washington 111:110–139.

———, M. R. Campos, & B. López. 2002. New species and records of pseudothelphusid crabs (Crustacea, Brachyura) from Colombia in the

Tulane Natural History Museum.—Tulane Studies in Zoology and Botany 31(2):1–17.

Schmitt, W. L. 1969. Colombian freshwater crab notes.—Proceedings of the Biological Society of Washington 82:93–112.

Smalley, A. 1964. A terminology for the gonopods of the American river crabs.—Systematic Zoology 13:28–31.

Smithe, F. B. 1975. Naturalist's color guide. The American Museum of Natural History, New York. Part 1: unnumbered pages.

Young, C. G. 1900. The stalk-eyed Crustacea of the British Guiana, West Indies and Bermuda. John M. Watkins, London, 514 pp.

Zimmer, C. 1912. Beitrag zur kentniss der Süsswasser dekapoden Kolumbiens. *In* O. Fuhrmann et E. Mayor, Voyage d'exploration scientifique en Colombie. Mémoires de la Société neuchateloise des Sciences naturelles 5:1–8.

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A new species of *Xenorhina* (Anura: Microhylidae) from western New Guinea

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Abstract.—We describe a new species of fossorial frog, *Xenorhina adisca,* from the Sudirman Mountains of western New Guinea. The new species is distinguished from its congeners in lacking discs on fingers and toes, having moderately long legs, large eyes, and a long, pointed snout, and having a red venter with black "pants" markings under the groin. It is currently known only from the type locality. The limited mobility of members of this genus make them highly susceptible to endemism, and it seems likely that additional species await discovery along the south versant of the Central Dividing Range of New Guinea.

Xenorhina is a genus of seven endemic New Guinea species (Zweifel 1972, Blum & Menzies 1988, Allison & Kraus 2000) closely allied with the equally endemic *Xenobatrachus,* from which it differs in lacking odontoid spikes. Clear synapomorphies distinguishing these two genera are lacking (Burton 1986) and further phylogenetic study may result in the synonymization of the latter with the former. Of the seven species of *Xenorhina* currently recognized, six are terrestrial or fossorial, and one has secondarily adopted an arboreal life style (Allison & Kraus 2000). All species are found in the western part of the island, ranging from western Papua New Guinea to the western end of Papua (formerly Irian Jaya). Most *Xenorhina* species occur at moderate to high altitudes (1000–3500 m), although *X. oxycephala* is a widespread lowland species.

During a biological survey in southwestern Papua in 1997 we discovered a new species of *Xenorhina* and describe it below.

Materials and Methods

Specimens were euthanized in the field by immersion in chlorotone, fixed in 10% buffered formalin, and then transferred to 70% ethanol for storage. All measurements were made to the nearest 0.1 mm with digital calipers or an optical micrometer, except that disc widths were measured to the nearest 0.03 mm. We follow the methodology and use the terminology of Zweifel (1972, 2000) and Kraus & Allison (2001): distance from anterior corner of eye to center of naris (EN); diameter of eye (EY); width of disc on third finger (FD); foot length from proximal edge of sole to tip of 4th toe (FT); hand length from proximal edge of palm to tip of 3rd finger (HD); head width at widest point, typically at the level of the tympana (HW); internarial distance, between centers of external nares (IN); distance from anterior corner of eye to tip of snout (SN); body length from snout to vent (SV); width of disc on fourth toe (TD); tibia length from heel to skin fold of knee (TL_{fold}); tibia length from heel to outer surface of flexed knee (TL_{knee}); tympanum diameter (TY). The two different measures of TL are provided because measurement technique varies in the literature: the latter measurement is generally the more reliable across a variety of microhylid genera and is the standard in more recent taxonomic

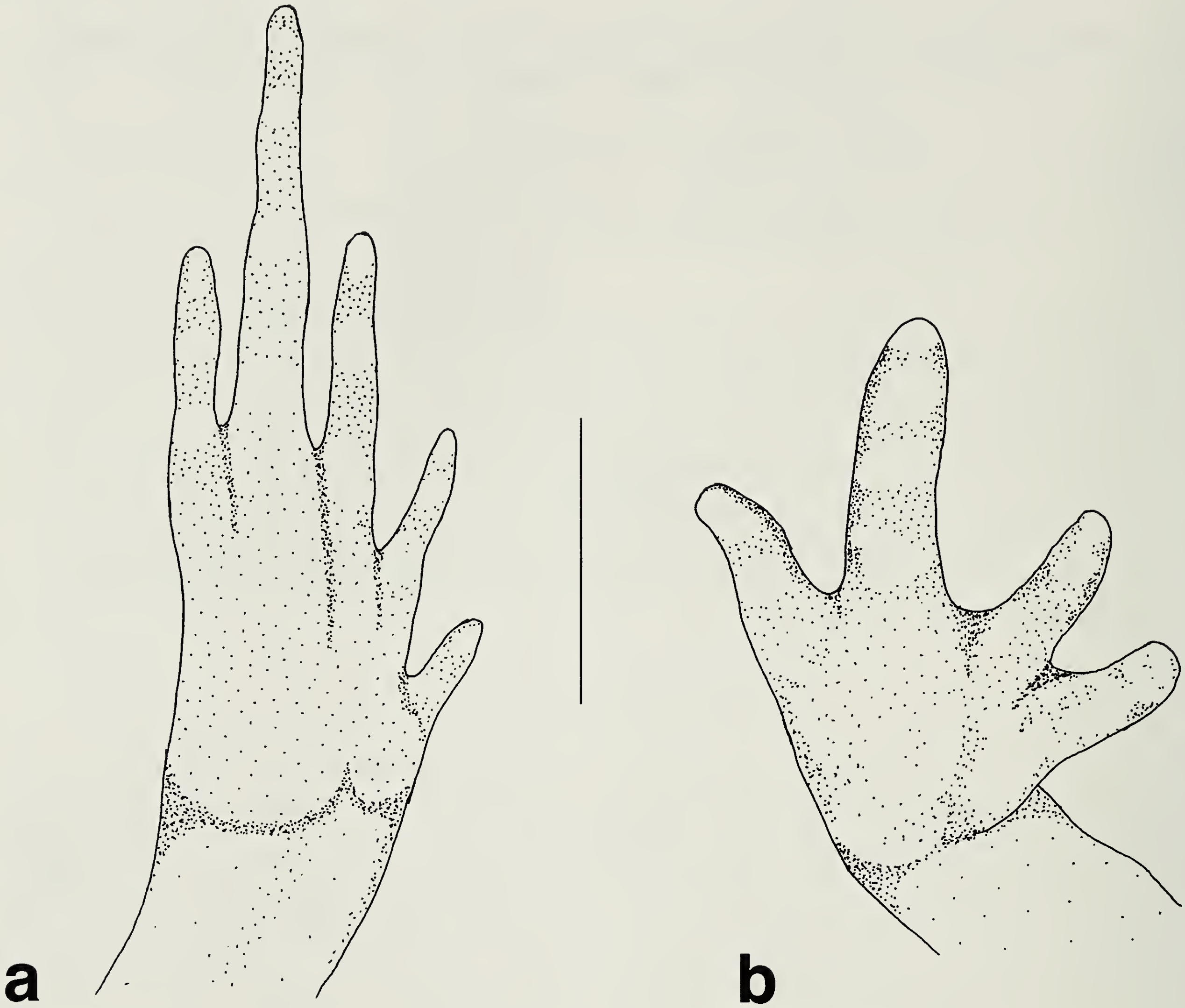

Fig. 1. Right foot (a), and hand (b) of holotype (MZB 8403) of *Xenorhina adisca,* showing absence of discs. Scale bar is 2 mm.

treatments, but the former measurement is published for a wider array of taxa (Zweifel 1972). Sex was determined by examination of gonads and vocal slits.

We confirmed generic assignment of the frogs by the presence of a symphygnathine jaw, absence of vomeropalatine spikes, lack of a broad subdermal sheet of bone behind the eye, absence of cutaneous turbercles on the eyelids, and presence of a pointed snout and small eyes. Type specimens are deposited in the Museum Zoologi Bogor, Indonesia (MZB) and the Bernice P. Bishop Museum, Honolulu (BPBM). Additional comparative material is housed in the collections of the University of Papua New Guinea (UPNG).

Xenorhina adisca, new species
Figs. 1–3

Holotype.—MZB 8403 (field no. AA 15395), adult female, collected by Allen Allison at Tembagapura, 4.14009°S, 137.09782°E, 2200 m elev., Sudirman Mountains, Papua (=Irian Jaya), Indonesia, on 17 March 1997.

Paratypes.—MZB 8404 and BPBM 14915, juvenile and adult female, respectively, same data as holotype.

Diagnosis.—A small (SV = 18.8–23.6 mm) species of *Xenorhina* lacking finger and toe discs (Fig. 1), and having moderately long legs (TL_{fold}/SV = 0.35–0.38, TL_{knee}/SV = 0.39–0.40), large eyes (EY/SV = 0.072–0.080), and a relatively long point-

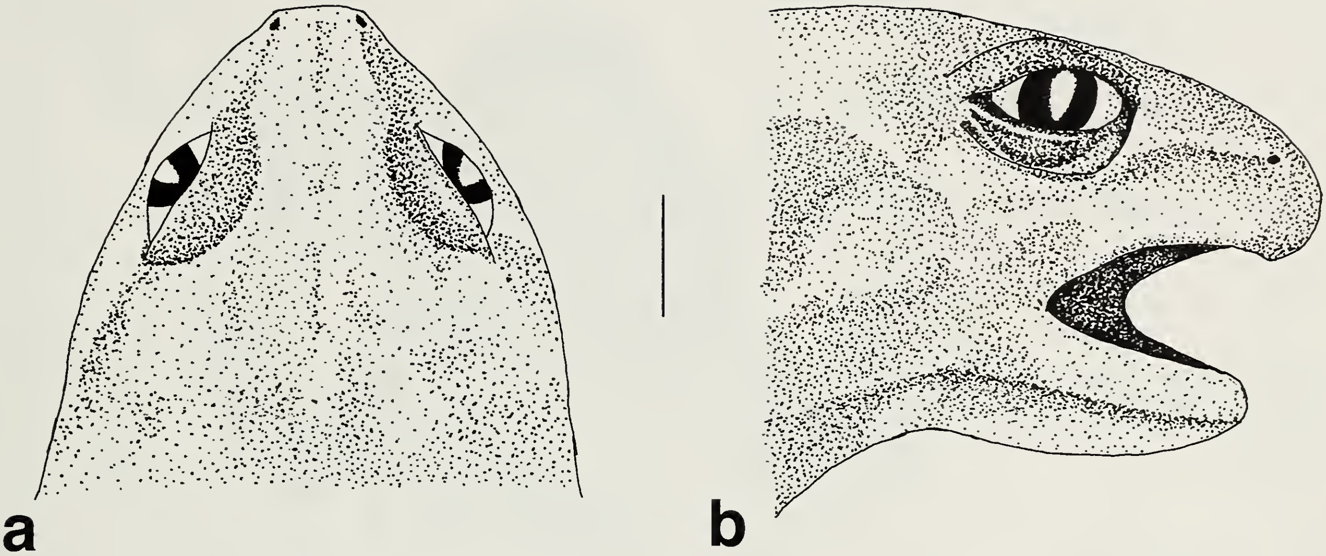

Fig. 2. Dorsal (a) and lateral (b) views of the head of holotype (MZB 8403) of *Xenorhina adisca.* Scale bar is 3 mm.

ed snout with a high EN/IN ratio (1.1–1.2, Fig. 2).

Description of holotype.—An adult female. Head moderately wide (HW/SV = 0.32), merging with body with no constriction at neck; oblique loreal region, no canthus rostralis; nostrils much closer to tip of snout than to eyes (Fig. 2); internarial distance less than distance from external naris to eye (EN/IN = 1.1, IN/SV = 0.068, EN/SV = 0.072); snout rounded when viewed from side and from above (Fig. 2); eyes of moderate size (EY/SV = 0.072), eyelid less than one-half width of interorbital distance; tympanic ring indistinct, horizontal diameter equal to width of eye.

Dorsal and lateral surfaces with scattered low rounded tubercles, especially concentrated on end of snout (Fig. 2). Supratympanic fold slight. Ventral surfaces smooth.

Fingers unwebbed, relative lengths $3 > 4 > 2 \approx 1$, tips somewhat flattened but lacking discs and circummarginal grooves (Fig. 1); very low areas of thickened skin on inner metacarpal surfaces, but not developed into actual tubercles. Toes unwebbed, relative lengths $4 > 3 > 5 > 2 > 1$; tips rounded and lacking discs and circummarginal grooves; low skin thickenings present on inner metatarsal surfaces, but not developed into tubercles. Hind legs moderately long ($TL_{fold}/SV = 0.35$, $TL_{knee}/SV = 0.40$).

The vomeropalatines lack enlarged odontoid spikes.

Ground color of dorsal surfaces of body and limbs brownish yellow in preservative, heavily and evenly suffused with dark brown, which is densest dorsally and lighter laterally. Obscure chocolate brown flecks are scattered on dorsum and sides. Tympanum somewhat lighter in color and with an obscure chocolate brown supratympanic stripe that extends across the dorsal margin of the tympanum and ends just anterior to the forelimb insertion. A chocolate brown patch surrounds the anus. Ventral ground color of body and limbs brownish yellow with many tiny dark brown flecks scattered throughout and most densely concentrated on chin, throat, groin, and undersides of limbs, forming "pants" in the groin and upper thighs (Fig. 3). Palms and soles mottled light gray and chocolate brown.

Measurements (in mm).—SV = 23.5, TL_{fold} = 8.3, TL_{knee} = 9.5, HW = 7.6, IN = 1.6, EN = 1.7, SN = 2.4, EY = 1.7, TY = 1.7, HL = 4.9, FL = 10.1, FD = 0.58, TD = 0.50.

Variation.—One of the paratypes is an adult female; the other is near adult size but of undetermined sex. Mensural variation in

Fig. 3. Underside of holotype (MZB 8403) of *Xenorhina adisca,* showing strongly melanized gular region and "pants" in the groin and upper thighs. Scale bar is 10 mm.

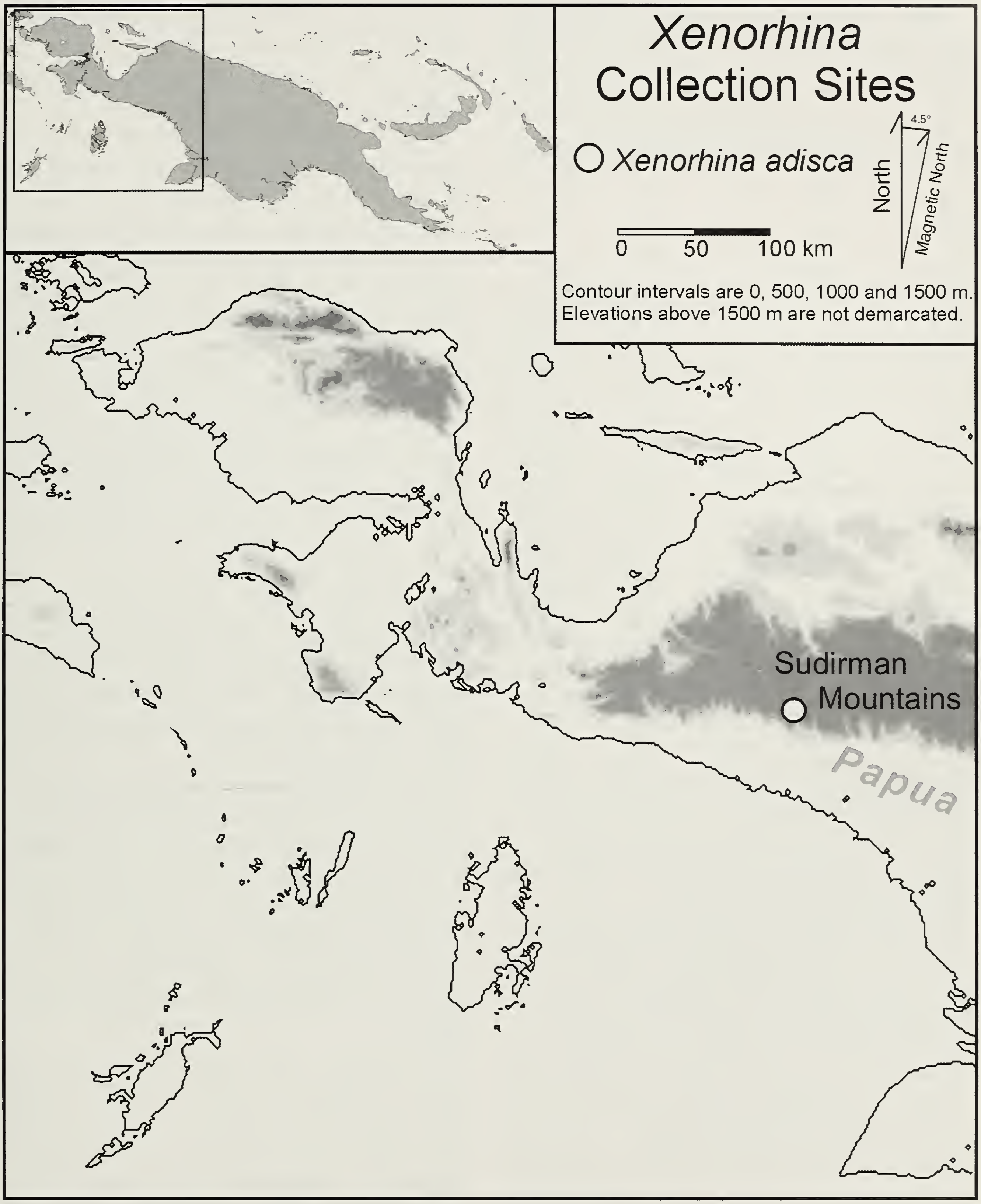

Fig. 4. Map of western New Guinea showing the type locality of *Xenorhina adisca*.

the small sample at hand is minor (Table 1) and there are no noteworthy differences in color pattern among the three specimens.

Color in life.—Dorsum dark brown; venter bright red.

Call.—Unknown. All available specimens are female or immature.

Comparisons to other species.—*Xenorhina adisca* may be distinguished from all other species of the genus except *X. similis*

Table 1.—Mensural measurements (in mm) and ratios of the holotype and two paratypes of *Xenorhina adisca*.

	Specimen			
Character	MZB 8403	MZB 8404	BPBM 14915	Mean
SV	23.5	18.8	23.6	22
TL_{fold}	8.3	6.7	8.9	8
TL_{knee}	9.5	7.3	9.5	8.8
EN	1.7	1.3	1.8	1.6
IN	1.6	1.2	1.5	1.4
SN	2.4	1.9	2.7	2.3
TY	1.7	1.5	1.5	1.6
EY	1.7	1.5	1.8	1.7
HW	7.6	6.3	8.2	7.4
HL	4.9	4.1	5.5	4.8
FL	10.1	8.2	10	9.4
FD	0.58	0.48	0.53	0.53
TD	0.5	0.38	0.53	0.47
TL_{fold}/SV	0.35	0.36	0.38	0.36
TL_{knee}/SV	0.4	0.39	0.4	0.4
EN/SV	0.072	0.069	0.076	0.073
IN/SV	0.068	0.064	0.064	0.065
SN/SV	0.1	0.1	0.11	0.11
TY/SV	0.072	0.08	0.064	0.072
EY/SV	0.072	0.08	0.076	0.076
HW/SV	0.32	0.34	0.35	0.34
HL/SV	0.21	0.22	0.23	0.22
FL/SV	0.43	0.44	0.42	0.43
FD/SV	0.025	0.026	0.022	0.024
TD/SV	0.021	0.02	0.022	0.021
EN/IN	1.1	1.1	1.2	1.1

and *X. minima* in lacking expanded discs on both the fingers and toes.

From *X. similis, X. adisca* may be distinguished by its considerably smaller size (SV = 18.8–23.6 in *X. adisca* vs. 48–51 mm in *X. similis*), larger eye (EY/SV = 0.072–0.080 in *X. adisca* vs. 0.058–0.072 in *X. similis*), and dark dorsal color pattern.

From *X. minima, X. adisca* may be distinguished by its longer legs (TL_{fold} = 0.35–0.38 in *X. adisca* vs. 0.29–0.34 in *X. minima*), longer and more pointed snout (EN/IN = 1.1–1.2 in *X. adisca* vs. 0.83–0.84 in *X. minima*), dark dorsal color pattern, and red (vs. cream) venter.

Xenorhina adisca is further distinguished from all other members of the genus by its ventral color pattern, which includes a dark chin and throat and dark "pants" in the groin and upper thighs (Fig. 3). Other *Xenorhina* species having melanized gular regions are either entirely dark below (*X. parkerorum*) or are mottled in the groin/thigh region (*X. arboricola, X. similis*).

Ecological notes.—*Xenorhina adisca* is fossorial. We collected our specimens during the day from within the surface litter of a heavily mossed montane closed-canopy forest on a steep southwest-facing slope drained by a small stream. The dominant trees at the collection site included *Elaeocarpus nubigenus, Saurauia calyptrate* and *Polyosma integrifolia.* Canopy height was 20–30 m. Treeferns, *Cyathea* sp., were common throughout the subcanopy, as was a species of *Pittosporum.* The ground flora included a dense array of tree saplings, gingers, *Elatostema,* ferns, and mosses (*Dawsonia* and *Sphagnum*).

Intermittent rainfall and temperature records maintained by P.T. Freeport Indonesia suggest that the mean monthly temperature at the collection site is around 11–12°C with little annual variation. Annual rainfall likely exceeds 6000 mm.

Xenorhina adisca occurred sympatrically with *Xenobatrachus macrops, X. ocellatus,* and an undescribed species of *Xenorhina,* all closely related frogs of similar habitus. Other members of the local herpetofauna included a treefrog, *Litoria angiana,* and a skink *Papuascincus stanleyanus,* both of which are widespread in montane New Guinea.

Etymology.—The name is a feminine compound adjective derived from the Greek "*a*", meaning "without", and the Greek noun "*disc*", meaning "a flat plate", in its adjectival combining form "*-disca*", and refers to the absence of digital discs in the species.

Distribution.—*Xenorhina adisca* is known only from the type locality (Fig. 4) but is likely to prove more widely distributed along the southern versant of the Central Dividing Range of western New Guinea.

Remarks

Thirteen of the 26 species now recognized in *Xenorhina* and *Xenobatrachus* have been described in the last quarter century (Menzies & Tyler 1977, Blum & Menzies 1988, Allison & Kraus 2000, Kraus & Allison 2002, this paper) and we are aware of additional undescribed species. Most recently described taxa of *Xenorhina* and *Xenobatrachus* have been discovered in the central valleys of the Central Dividing Range or in the outlying north coast ranges. In contrast, *Xenorhina adisca* is the first member of these genera described from the southern versant of New Guinea since *X. minima* (Parker 1934). Considering the large tracts of western New Guinea that have not been adequately surveyed, more species seem likely to occur. Our surveys confirmed the presence of at least six species of *Xenorhina* and *Xenobatrachus* along an altitudinal transect ranging from sea level to ca. 3000 m along the road from Timika to Tembagapura in southern Papua. We heard but were unable to collect what may be additional species. This appears to be the richest concentration of species yet reported for this clade; other sites have 3–4 species recorded (Blum & Menzies 1988, Allison & Kraus 2000, Kraus & Allison 2002).

Blum & Menzies (1988) have remarked that the rugged terrain of New Guinea, combined with the limited mobility of these fossorial frogs, has likely led to high levels of speciation and endemism—a view with which we agree. However, the degree of endemism varies in scale: several taxa may prove endemic to single valley or mountain complexes, but others inhabit broader, though geographically limited, regions encompassing several distinct mountain ranges. The taxa described from the Eipo Valley (Blum & Menzies 1988) may prove to fit the former pattern, whereas *Xenorhina arboricola, Xenobatrachus zweifeli,* and *Xenobatrachus tumulus* are already known to inhabit multiple discrete mountain ranges along the north coast of Papua New Guinea (Allison & Kraus 2000, Kraus & Allison 2002). What pattern generally holds for species along the southern versant of the Central Dividing Range remains to be seen but most known species from that region have broad distributions (Zweifel 1972).

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Literature Cited

Allison, A., & F. Kraus. 2000. A new species of frog of the genus *Xenorhina* (Anura: Microhylidae) from the North Coast Ranges of Papua New Guinea.—Herpetologica 56:285–294.

Blum, J. P., & J. I. Menzies. 1988. Notes on *Xenobatrachus* and *Xenorhina* (Amphibia: Microhylidae) from New Guinea with description of nine new species.—Alytes 7:125–163.

Burton, T. C. 1986. A reassessment of the Papuan subfamily Asterophryinae (Anura: Microhylidae).—Records of the South Australian Museum 19:405–450.

Kraus, F., & A. Allison. 2001. A review of the endemic New Guinea microhylid frog genus *Choerophryne*.—Herpetologica 57:214–232.

———, & ———. 2002. A new species of *Xenobatrachus* (Anura: Microhylidae) from northern Papua New Guinea.—Herpetologica 58:56–66.

Menzies, J. I., & M. J. Tyler. 1977. The systematics and adaptations of some Papuan microhylid frogs which live underground.—Journal of Zoology, London 183:431–464.

Parker, H. W. 1934. A monograph of the frogs of the family Microhylidae.—British Museum, London.

Zweifel, R. G. 1972. Results of the Archbold expeditions. No. 97. A revision of the frog subfamily Asterophryinae family Microhylidae.—Bulletin of the American Museum of Natural History 148:411–546.

———. 2000. Partition of the Austropapuan microhylid frog genus *Sphenophryne* with descriptions of new species.—Bulletin of the American Museum of Natural History 253:1–130.

Appendix
Specimens Examined

Xenorhina arboricola: BPBM 13745, 1.3 km S, 2.3 km E summit of Mt. Hunstein, Hunstein Mts., 1000 m, East Sepik Prov., Papua New Guinea; BPBM 13746–77, S slopes of Mt. Menawa, 8.5 km N, 14 km E Utai aerodrome, Bewani Mts., 1200 m, West Sepik Prov., Papua New Guinea.

Xenorhina bouwensi: BPBM 1015, Sibil Valley, Star Mts., 1250 m, Irian Jaya [= Papua], Indonesia; BPBM 3686, 3.2 km N Dasiga, New Guinea.

Xenorhina eiponis: UPNG 7406 (paratype), Munggona, 1800 m, Irian Jaya [= Papua], Indonesia.

Xenorhina minima: UPNG 7409, Serabum, 2400 m, Irian Jaya [= Papua], Indonesia.

Xenorhina oxycephala: BPBM 13756–57, 2 km W Utai aerodrome, 260 m, West Sepik Prov., Papua New Guinea; BPBM 14269, 8.7 km N, 9.8 km E Mt. Hunstein, 75 m, East Sepik Prov., Papua New Guinea.

Xenorhina parkerorum: UPNG 9358–59, Nogar Village, Keowagi, 2200 m, Simbu Prov., Papua New Guinea.

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Acanthochondria hoi, a new species of parasitic copepod (Poecilostomatoida: Chondracanthidae) on the California halibut, *Paralichthys californicus,* from Santa Monica Bay, California, with an amended key to the genus *Acanthochondria*

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Abstract.—A new species of parasitic copepod, *Acanthochondria hoi,* is described from specimens collected within the gill cavity of the California halibut, *Paralichthys californicus* (Ayers), from Santa Monica Bay, California. *Acanthochondria hoi* can be distinguished from its congeners by the combination of a Type B-V antennule and Type A leg 2, in addition to leg 1 ornamentation. A revision of the key of *Acanthochondria* prepared by previous authors is provided and includes three new species.

Santa Monica Bay is located in the Southern California Bight and is an open coastal embayment bounded by Point Dume to the north and Palos Verdes Point to the south. The Hyperion Treatment Plant (Bureau of Sanitation, Department of Public Works, City of Los Angeles) provides secondary treatment and disposal of treated wastewater through a 5-mile effluent outfall located in Santa Monica Bay. The Environmental Monitoring Division conducts quarterly otter trawls to monitor the effects of the effluent on the fishes and macroinvertebrates living in the vicinity of the outfall (Dojiri & Brantley 1991). During the July/August and November 1998, and February and May 1999 trawls, several specimens of California halibut, *Paralichthys californicus* (Ayers), were collected with parasitic copepods within the gill cavity. These parasites represent a new species of *Acanthochondria,* which is described below.

Materials and methods.—The fishes were collected in Santa Monica Bay, California. Quarterly otter trawls were made aboard the R/V *La Mer* in association with the Environmental Monitoring Division, Bureau of Sanitation, Department of Public Works, City of Los Angeles. Immediately after the catch was brought on board, the fishes were placed in plastic bags and kept on ice in a cooler for a later examination in the laboratory. The copepods were removed and preserved in 70% isopropyl alcohol, then cleared in 85% lactic acid. They were measured with an ocular micrometer and selected specimens were dissected. Illustration were drawn with the aid of a camera lucida. Holotype and paratypes were deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (1001623–1001628). Additional specimens are in the collection of the author.

Systematic Account

Order Poecilostomatoida Thorell, 1859
Family Chondracanthidae
Milne-Edwards, 1840
Genus *Acanthochondria* Oakley, 1927
Acanthochondria hoi, new species
Figs. 1–3

Material examined.—A total of seven nonovigerous and 22 ovigerous females

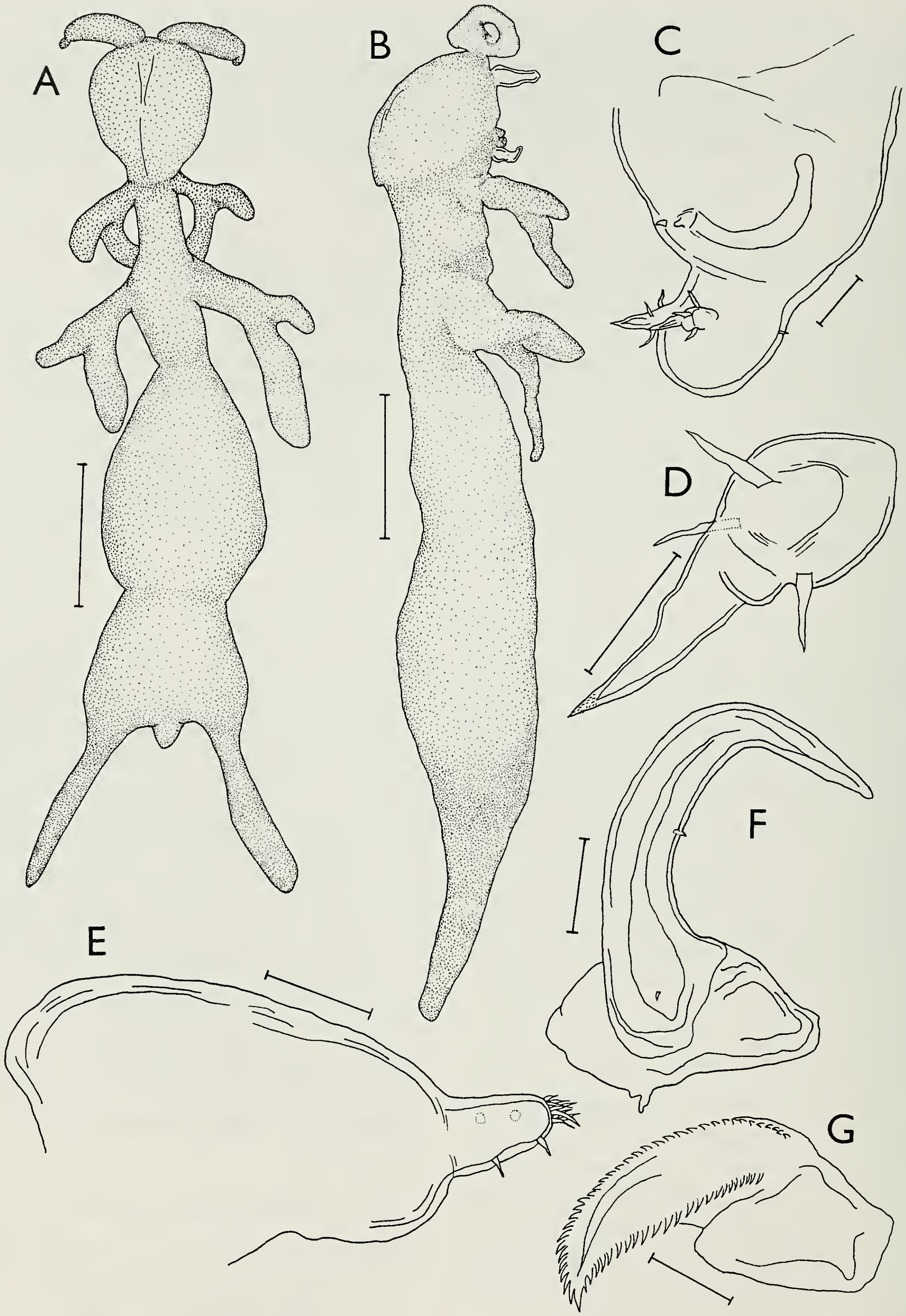

Fig. 1. *Acanthochondria hoi* n. sp., female. A, habitus, dorsal; B, habitus, lateral; C, genito-abdomen, lateral; D, caudal ramus; E, antennule; F, antenna; G, mandible. Scale: 1.0 mm in A, B; 0.1 mm in C, F; 0.05 mm in D, G; 0.2 mm in E.

(each with an attached male) was collected from within the gill cavity (inner side of operculum and floor of oral cavity at the base of gill arches) of the California halibut, *Paralichthys californicus* (Ayers).

Female.—The trunk (Fig. 1A, B) is long and slender. The cephalosome is slightly longer than wide. Neck region consisting of first and second pedigers. Trunk with a single mid-lateral indentation and bearing a pair of posterior processes, which are moderately long and slender. The genital segment (Fig. 1C) is longer than wide; and the abdomen (Fig. 1C) is shorter than the genital segment and bears two dorsal setules. The caudal ramus (Fig. 1D) has three setae, a knob, and a large spinulated terminal process. The antennule (Fig. 1E) is of Type B-V (Ho & Kim 1995), consisting of a large unarmed basal portion and a small cylindrical distal portion with an armature formula of 2-2-8. The antenna (Fig. 1F) is 2-segmented; the basal segment is large and unarmed; the terminal claw possesses a small mid-lateral seta and a minute basal setule. The mandible (Fig. 1G) is 2-segmented; convex margin armed with 31–35 teeth, concave margin has 21–24 teeth.

The maxillule (Fig. 2A) is a lobe bearing two processes produced at the distal margin of the appendage. The maxilla (Fig. 2B) is 2-segmented, with the basal segment unarmed. The terminal segment carries a small seta, a large seta, and a large process armed with 15 teeth along its posterior margin. The maxilliped (Fig. 2C) is 3-segmented; the first segment is unarmed; the second segment bears a protruded portion on which one patch of spinules is located and a row of 12 teeth on the distal margin; the terminal segment is clawlike, bearing a proximal patch of small spinules and a subterminal accessory process. Leg 1 (Fig. 2D) is biramous with the exopod bearing an outer seta. The anterior surface is covered with irregular patches of spinules. Leg 2 (Fig. 2E) is biramous with long rami. The exopod carries an outer seta. The rami bear spinules at the distal tips of the anterior surfaces in addition to several setules.

Measurements.—Total length (tip of cephalosome to tip of posterior process) 6.84 mm; trunk width 0.44 mm; cephalosome 0.39 mm × 0.35 mm; genital segment 0.47 mm × 0.44 mm; abdomen 0.19 mm × 0.16 mm; posterior process 1.32 mm.

Male.—The body (Fig. 3A), 0.67 mm × 0.34 mm, is ventrally flexed. The cephalosome and the first pedigerous segment comprise more than half the total length. The antennule (Fig. 3B) is slender and bears an armature formula of 1-1-2-2-8. The antenna (Fig. 3C) is 2-segmented. The basal segment possesses a rounded knob near the articulation with the terminal claw. The terminal segment bears two setae on the basal portion. The mandible (Fig. 3D) is 2-segmented; terminal segment armed with 20 teeth along convex margin, 9 teeth along concave margin. The maxilla (Fig. 3E) is 2-segmented and exhibits the usual sexual dimorphism for this genus by possessing a naked terminal process. Leg 1 (Fig. 3F) is larger than leg 2 (Fig. 3G). Both legs are similarly armed, with the protopod bearing a long outer seta, the exopod with two small elements, and the endopod a smaller unarmed lobe. However, the two elements on the exopod of leg 2 are unequal in size.

Etymology.—This species is named after Dr. Ju-Shey Ho, an expert in parasitic copepod research and my mentor and former advisor.

Remarks.—*Acanthochondria hoi,* new species, was previously reported by Dojiri (1977) as *Acanthochondria* sp. C. However, a literature search revealed that a description of this species was never published. Ho (1975) tentatively identified a badly damaged specimen of *Acanthochondria* from the California halibut as *A. soleae* (?). In addition, Haaker (1975) and Allen (1990) reported *A. soleae* to occur on the California halibut, directly and indirectly citing Ho (1975), respectively. Ho's (1975) specimen is probably identifiable with *A. hoi.* Kabata (1979) comments that the literature contains

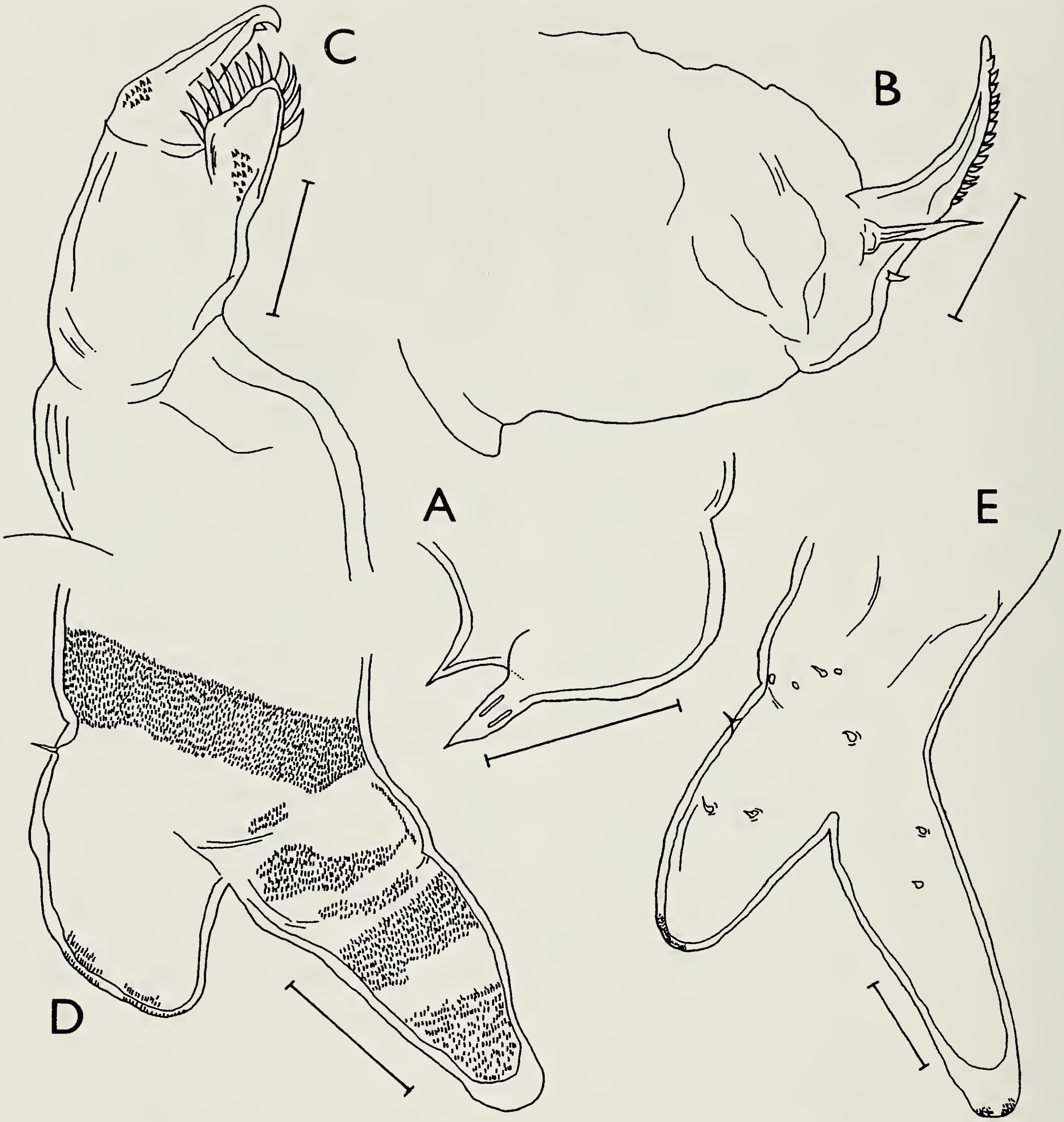

Fig. 2. *Acanthochondria hoi* n. sp., female. A, maxillule; B, maxilla; C, maxilliped; D, leg 1; E, leg 2. Scale: 0.05 mm in A, B, C; 0.3 mm in D, E.

a number of erroneous host listings of *A. soleae. A. soleae* is parasitic mainly on the sole, *Solea solea,* and its distribution is restricted to the Atlantic Ocean (Kabata 1979). *A. hoi* differs from *A. soleae* in the relative lengths of the endopod and exopod, leg 1 ornamentation, and structure of the maxilliped.

Acanthochondria hoi is distinguished from its congeners by the combination of a Type B-V antennule and Type A leg 2 (Ho & Kim 1995), in addition to leg 1 ornamentation. Legs 1 and 2 have relatively long rami with the endopod noticeably longer than the exopod. A check into the key of *Acanthochondria* prepared by Ho and Kim (1995) revealed that this specimen collected from the California halibut is new to science. This specimen keyed out to step 33a, which is equivalent to *A. exilipes* (Ho 1971). Table 1 lists differences between *A. hoi* and *A. exilipes.*

Key to the Species of *Acanthochondria*

The following revised key includes all accepted species of *Acanthochondria* (Ho & Kim 1995). Three new species were add-

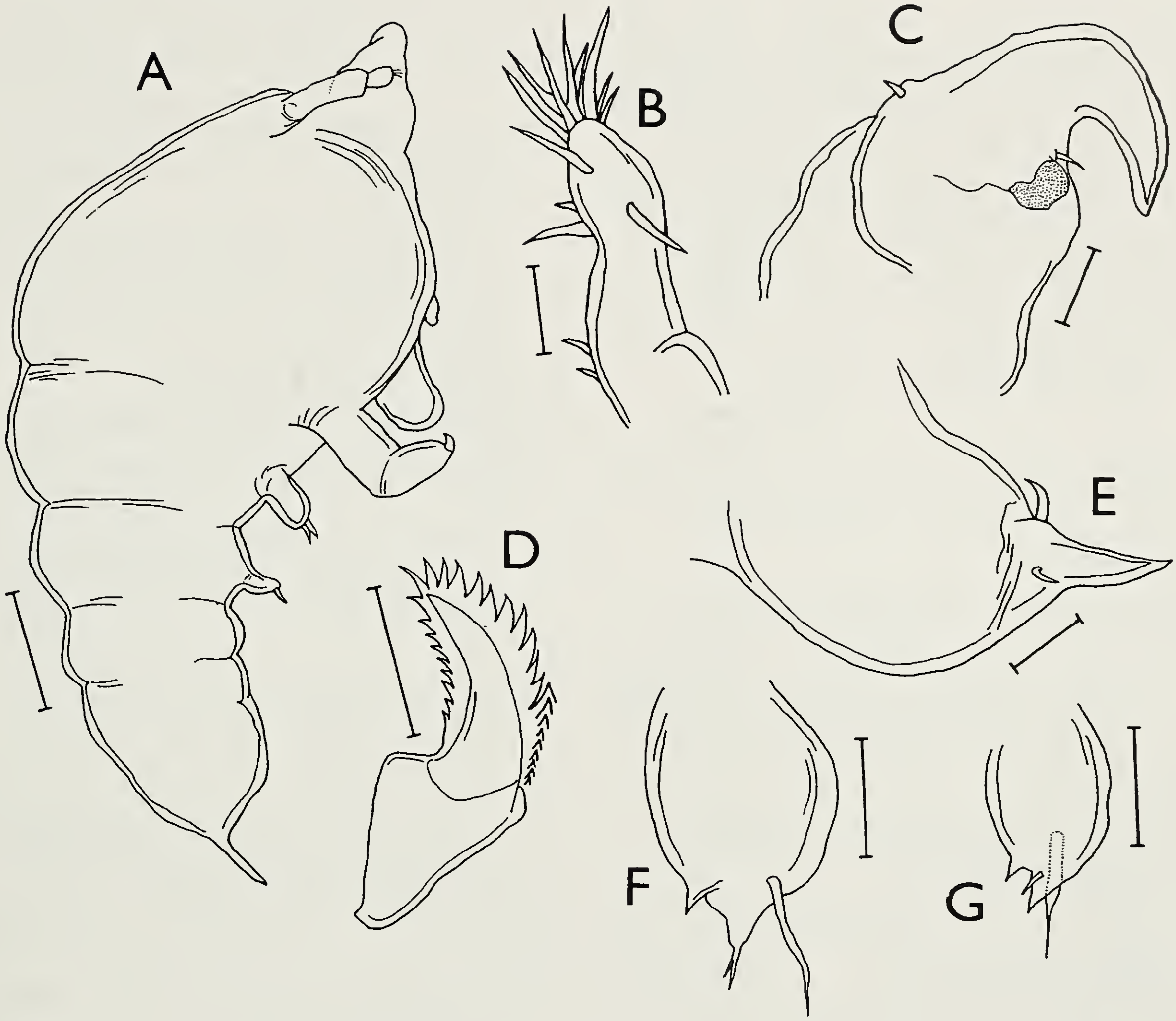

Fig. 3. *Acanthochondria hoi* n. sp., male. A, habitus, lateral; B, antennule; C, antenna; D, mandible; E, maxilla; F, leg 1; G, leg 2. Scale: 0.1 mm in A; 0.02 mm in B, C, D, E, F, G.

ed, *A. kajika* (Ho & Kim 1996), *A. zebriae* (Ho et al. 2000), and *A. hoi* (Kalman, this report), increasing the number of species to 46. In addition, all typographical errors have been corrected (most notable, from Ho and Kim (1995): step 16b should lead to step 29, not step 28 as previously noted; *A. cyclopsetta, A. exilipes, A. galerita,* and *A. physidis* should all be cited as Ho 1971, not Ho 1970 as previously noted).

Poly and Mah (2001) deeply criticize some of the characters used in the key by Ho and Kim (1995). However, this revised key is still valid and useful until further morphological characters can be discovered for some nominal species where the host

Table 1.—Differences between *Acanthochondria exilipes* and *A. hoi.*

	A. exilipes	*A. hoi*
Antennule type	B-III	B-V
Teeth on mandible	37–41 on convex margin 32–34 on concave margin	31–35 on convex margin 21–24 on concave margin
Maxillule	2 patches of spinules	naked
Leg 1 ornamentation	naked	patches of spinules
2nd segment of maxilliped	2 patches of spinules	1 patch of spinules and 12 teeth on outer margin

family is used as a "character". Thus, the publication containing the best information to aid in species identification is provided in parentheses after each species name.

The males of *Acanthochondria* do not show species differences; therefore, the characters used in this key refer strictly to adult ovigerous females (Ho 1970). For types of antennule and leg 2 found in this key, refer to Ho and Kim (1995).

1a Neck region consisting of first pediger only 2

b Neck region consisting of first and second pedigers 4

c Neck region consisting of second pediger only; first pediger incorporated into head region .... *triglae* (Herrera-Cubilla & Raibaut 1990:82–87)

2a Second pediger indistinguishably fused to trunk 3

b Second pediger distinctly separated from trunk and bearing a pair of large rounded swellings .... *limandae* (Kabata 1979:127–128)

3a Antenna of B-VII type ..... *laemonemae* (Capart 1959:102–103)

b Antenna of B-III type .... *lepidionis* (Ho 1972a:147–149)

c Antenna of B-I type .... *zebriae* (Ho et al. 2000:711–713)

4a Neck very long, at least 8 times longer than wide 5

b Neck moderately long, at most about 3 times as long as wide; leg 2 with extremely long protopod (Type E) 6

c Neck short; at most slightly longer than wide; protopod of leg 2 not greatly elongated 8

5a Posterolateral processes short and blunt; terminal process of maxilla bearing a short row of fine denticles .... *diastema* (Ho & Dojiri 1988:273–279)

b Posterolateral processes long and slender; terminal process of maxilla bearing a long row of large teeth .. *uranoscopi* (Ho & Kim 1995:48–51)

6a Endopod of leg 2 much reduced, represented by a little knob .... *tchangi* (Shiino 1959:361)

b Endopod of leg 2 at least half as large as exopod 7

7a Cephalosome about as long as wide; parasite of Platycephalidae .. *platycephali* (Ho 1973:127–130)

b Cephalosome distinctly longer than wide; parasite of fishes other than Platycephalidae .... *inimici* (Dojiri & Ho 1988:47–53)

8a Trunk cylindrical, long (at least twice longer than wide), and without lateral indentations 9

b Trunk appearance otherwise 11

9a Posterolateral processes shorter than head; caudal ramus shorter than abdomen 10

b Posterolateral processes longer than head; caudal ramus distinctly longer than abdomen .... *elongata* (Pillai 1985:125–127)

10a Cephalosome with small rounded knob at each anterior corner; hook-like antenna curved in distal region .... *fraseri* (Ho 1972b:523–527)

b Cephalosome with large anterolateral swellings; hook-like antenna curved in basal region .... *pingi* (Yü & Wu 1932:66–68)

11a Trunk trapezoidal; postoral region elongated .... *dilatata* (Shiino 1955:107–110)

b Trunk shaped otherwise; leg 1 close to oral region 12

12a Cephalosome bearing a pair of lateral horn-like projections; trunk without lateral indentations .... *bicornis* (Shiino 1955:103–107)

b Cephalosome without such projections; trunk mostly with lateral indentations 13

13a Leg 2 long and slender (Type D) ... 14

b Leg 2 shaped otherwise 15

14a Posterolateral processes long, as long as or longer than 4th pediger .... *soleae* (Kabata 1979:128–129)

b Posterolateral processes short, distinctly shorter than 4th pediger ... *cyclopsetta* (Ho 1971:3)

15a Legs 1 and 2 indistinctly bilobated (Type B) .... *physidis* (Ho 1971:11–15)

b Legs 1 and 2 distinctly bilobated ... 16

16a Antennule without inflated basal part (Type A) 17

b Antennule with inflated basal part (Type B) ... 30

17a Leg 2 slightly larger than leg 1 ... 18

b Leg 2 distinctly larger than leg 1 ... 24

18a Both legs 1 and 2 covered with spinules ... 19

b Both legs 1 and 2 without spinules or bearing at most only patches of spinules ... 20

19a First pediger with lateral protuberance ... *sixteni* (Dojiri & Ho 1988:53–56)

b First pediger without such protuberance ... *dojirii* (Kabata 1984:1708–1910)

20a Cephalosome distinctly longer (at least 1.38 times) than wide ... 21

b Cephalosome about as long as wide .. 22

21a Distal part of leg rami covered with spinules ... *vancouverensis* (Kabata 1984:1710)

b Distal part of leg rami not covered with spinules ... *glandiceps* (Shiino 1955:93–96)

22a Trunk about as long as wide ... 23

b Trunk distinctly longer than wide ... *spirigera* (Shiino 1955:100–103)

23a Parasitic on Sillaginidae ... *shawi* (Yü 1935:7–9)

b Parasitic on Gobiidae ... *yui* (Shiino 1964:30–33)

24a Terminal process of maxilla armed with a long row of teeth (about 15) .. 25

b Terminal process of maxilla armed with a short row of teeth (at most 11) ... 26

25a Cephalosome round in dorsal view ... *brevicorpa* (Yamaguti 1939:535)

b Cephalosome pear-shaped in dorsal view ... *longifrons* (Shiino 1955:86–89)

26a Both legs bearing large, prominent patches of spinules ... *margolisi* (Kabata 1984:1705)

b Both legs naked or with small patches of spinules ... 27

27a Trunk distinctly longer than wide and with prominent lateral indentations ... 28

b Trunk about as long as wide with slight lateral indentations ... 29

28a Parasitic on Serranidae ... *constricta* (Shiino 1955:96–100)

b Parasitic on Pleuronectidae .. *hippoglossi* (Kabata 1987:215)

29a Labrum with lateral protrusion, legs 1 and 2 tipped with spinules on both rami .. *kajika* (Ho & Kim 1996:276–279)

b Labrum without lateral protrusion, legs 1 and 2 naked ... *fissicauda* (Shiino 1955:90–93)

30a Cephalosome with two lateral round swellings on ventral surface of head; antennule with prominent ventral protuberance ... *clavata* (Kabata 1979:126–127)

b Cephalosome and antennule without such features ... 31

31a Both rami of leg 2 large, coniform (Type C); a pair of large protuberances lateral to labrum in oral area ... *galerita* (Ho 1971:8–11)

b Leg 2 and oral area without such features ... 32

32a Leg 2 distinctly larger than leg 1 ... 33

b Leg 2 only slightly larger than leg 1 ... 37

33a Trunk wider than long; posterolateral processes short and blunt ... *tasmaniae* (Heegaard 1962:154–155)

b Trunk about as long as wide; posterolateral processes long ... *priacanthi* (Ho & Kim 1995:53–56)

c Trunk distinctly longer than wide; posterolateral processes either long or short ... 34

34a Endopod of leg 2 about as long as protopod ... 35

b Endopod of leg 2 distinctly shorter than protopod ... 36

35a Antennule of B-III type; leg 1 naked ... *exilipes* (Ho 1971:3–7)

b Antennule of B-V type; leg 1 with patches of spinules ... *hoi* (Kalman this report)

36a Terminal process of maxilla bearing less than 10 teeth ... *epachthes* (Kabata 1968:339–344)

b Terminal process of maxilla armed with at least 15 teeth ... *oralis* (Yamaguti 1939:536–537)

37a Trunk as long as wide or slightly longer than wide ... 38

b Trunk distinctly longer than wide ... 40

38a Cephalosome large, as wide as trunk and bearing a pair of anterolateral protuberances ... *macrocephala* (Ho & Kim 1995:46–48) b Cephalosome distinctly narrower than trunk, without protuberance 39

39a Cephalosome slightly longer than wide; endopod of leg 2 distinctly longer than exopod .... *incisa* (Shiino 1955:83–86)

b Cephalosome distinctly longer than wide; endopod of leg 2 about as long as exopod ... *ophidii* (Ho 1977:158–160)

40a Cephalosome about as long as wide; both legs covered with spinules .... *rectangularis* (Kabata 1984:1705)

b Cephalosome wider than long; both legs with spinules on rami only 41

41a Cephalosome with two prominent lateral protrusions; antennule of Type B-II .... *sicyasis* (Ho 1977:160–164)

b Cephalosome with swollen oral region; antennule of Type B-V .... *cornuta* (Ho 1970:121–127)

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Literature Cited

Allen, M. J. 1990. The biological environment of the California halibut, *Paralichthys californicus.* Pp. 7–29 *in* C. W. Haugen, ed., The California halibut, *Paralichthys californicus,* resource and fisheries. California Department of Fish and Game, Fish Bulletin 174.

Capart, A. 1959. Copépodes parasites. *In* Results Expedition oceanographique Belge dans les Ezux Cotieres Africines de l'Atlantique sud (1948–1949).—Institut Royal des Sciences naturelles de Belgique 3(5):57–126.

Dojiri, M. 1977. Copepod parasites of Orange County sewer outfall. M.A. thesis, California State University, Long Beach, 295 pp.

———, & J. S. Ho. 1988. Two species of *Acanthochondria* (Copepoda: Poecilostomatoida) parasitic on fishes of Japan.—Report of the Sado Marine Biological Station Niigata University 18:47–56.

———, & R. A. Brantley. 1991. *Lepeophtheirus spatha,* a new species of copepod (Siphonostomatoida: Caligidae) parasitic on the California halibut from Santa Monica Bay, California.—Proceedings of the Biological Society of Washington 104:727–735.

Haaker, P. L. 1975. The biology of the California halibut, *Paralichthys californicus* (Ayres), in Anaheim Bay, California. Pp. 137–151 *in* E. D. Lane and C. W. Hill, eds., The marine resources of Anaheim Bay. California Department of Fish and Game, Fish Bulletin 165.

Heegaard, P. E. 1962. Parasitic Copepoda from Australian waters.—Records of Australian Museum 25(9):149–234.

Herrera-Cubilla, A., & A. Raibaut. 1991. *Acanthochondria triglae* n. sp., copépode parasite des fosses nasals de poisons Triglidae.—Crustaceana 59(1):82–88.

Ho, J. S. 1970. Revision of the genera of the Chondracanthidae, a copepod family parasitic on marine fishes.—Beaufortia 17(229):105–218.

———. 1971. Parasitic copepods of the family Chondracanthidae from fishes of Eastern North America.—Smithsonian Contributions to Zoology 87:1–39.

———. 1972a. Copepods of the family Chondracanthidae (Cyclopoida) parasitic on south African marine fishes.—Parasitology 65:147–158.

———. 1972b. Four new parasitic copepods of the Family Chondracanthidae from California inshore fishes.—Proceedings of the Biological Society of Washington 85:523–540.

———. 1973. Chondracanthid copepods parasitic on platycephalid fishes of Australia, with discussion of known species occurring on flatheads.—Parasitology 67:123–131.

———. 1975. Parasitic Crustacea. Pages 69–72 *in* E. D. Lane and C. W. Hill, eds., The marine resources of Anaheim Bay. California Department of Fish and Game, Fish Bulletin 165.

———. 1977. Parasitic copepods of the family Chondracanthidae from fishes of the south-eastern Pacific (Crustacea, Copepoda).—Steenstrupia 4(13):157–166.

———, & M. Dojiri. 1988. Copepods of the family Chondracanthidae parasitic on Australian marine fishes.—Australian Journal of Zoology 36: 273–291.

———, & I. H. Kim. 1995. *Acanthochondria* (Copepoda: Chondracanthidae) parasitic on fishes of Sado Island in the Sea of Japan, with a preliminary review of the genus.—Report of the Sado

Marine Biological Station, Niigata University 25:45–67.

———, I. H. Kim, & A. B. Kumar. 2000. Chondracanthid copepods parasitic on flatfishes of Kerala, India.—Journal of Natural History 34:709–735.

Kabata, Z. 1968. Some Chondracanthidae (Copepoda) from fishes of British Columbia.—Journal Fisheries Research Board of Canada 25(2):321–345.

———, 1979. Parasitic Copepoda of British Fishes. Ray Society, London, 468 pp.

———, 1984. A contribution to the knowledge of Chondracanthidae (Copepoda: Poecilostomatoida) parasitic on fishes of British Columbia.—Canadian Journal of Zoology 62:1703–1713.

———, 1987. *Acanthochondria hippoglossi* sp. nov. (Copepoda, Chondracanthidae), a crustacean parasitic of some flatfishes off the Pacific coast of North America.—Canadian Journal of Zoology 65:213–216.

Pillai, N. K. 1985. The fauna of India—copepod parasites of marine fishes.—Zoological Survey of India 900 pp.

Poly, W. J., and C. L. Mah. 2001. New host distribution records for parasitic copepods in the Northeast Pacific Ocean with a discussion of taxonomy of the genus *Acanthochondria.*—Bulletin of Marine Science 69(3):1121–1127.

Shiino, S. M. 1955. Copepods parasitic on Japanese fishes, 9. Family Chondracanthidae, subfamily Chondracanthinae.—Report of Faculty of Fisheries, Prefectural University of Mie 2(1):70–111.

———. 1959. Sammlung der parasitischen Copepoden in der Prafekturuniversitat von Mie.—Report of Faculty of Fisheries, Prefectural University of Mie 3(2):334–374.

———. 1964. On two new species of the genus *Acanthochondria* Oakley (Crustacea Copepoda) found in Japan.—Zoologische Mededelingen 34:30–36.

Yamaguti, S. 1939. Parasitic copepods from fishes of Japan. 6, Lernaeopodida I.—Volumen Jubilare Professor Sadao Yoshida 2:529–578.

Yü, S. C. 1935. Studies on the parasitic copepods of China belonging to the family Chondracanthidae.—Bulletin of the Fan Memorial Institue of Biology 6(1):1–15.

———, & H. W. Wu. 1932. Parasitic copepods of the flatfishes from China.—Bulletin of the Fan Memorial Institue of Biology 3(4):55–75.

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116(3):820–826. 2003.

Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 11. Documentation of an intergeneric woodstar hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant*

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Abstract.—A specimen in the Museum Alexander Koenig collected in Colombia is shown to be a hybrid between *Calliphlox mitchellii* and *Chaetocercus mulsant.* This is the first known example of intergeneric hybridization between species in these presumably closely related genera. External measurements of the hybrids are consistent with the proposed parental hypothesis.

As far as I am aware, the sole reference to intergeneric hybridization between miniature woodstars currently placed in *Chaetocercus* and *Calliphlox* (sensu Schuchmann 1999) is buried in the published catalog of the Otto Kleinschmidt Collection, which is now deposited in the Museum Alexander Koenig, Bonn, Germany (Kleinschmidt 1943:226):

> "***Chaetocercus***—? 9837 ♂ ohne Orig.-Etik., wohl CC, höchst interessanter Vogel, Zwischenglied oder Mischling bzw. Bastard zwischen *Chaetocercus mulsanti* und *Calliphlox mitchelli.* Schwerlich Aberration von *mulsanti. C. harterti* scheint ähnlich, ist aber kleiner."

Kleinschmidt's brief entry was accompanied by an inked drawing of the rectrices of the specimen and those of its proposed parental species. This record was overlooked in subsequent catalogs of hummingbird hybrids (Meyer de Schauensee 1949, Gray 1958, Panov 1989, Schuchmann 1999). In any case, Kleinschmidt's presentation was insufficient to determine the taxonomic status of the specimen or to make a convincing case for a particular hybrid combination. Here I provide an assessment of the specimen employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990), as modified by the findings of Graves (1998, 1999).

Methods

The specimen (Museum Alexander Koenig 9837) was obtained by the Fassl brothers in Colombia, possibly from the Cordillera Central, but little else is known about its provenance except that Anton and Eduard Fassl collected natural history specimens in Colombia from 1908 to 1911. The specimen, which was sexed as ♂ on one of the three attached labels (November 2001), appears to be in definitive plumage as judged by the absence of striations on the maxillary ramphotheca, the absence of distinctive buffy feather tips on the dorsal plumage or white spots in the rectrices, and the presence of a strongly iridescent gorget. Descriptions in this paper refer to definitive male plumage.

I compared the specimen with all species in the subfamily Trochilinae, the typical hummingbirds (Zusi & Bentz 1982, Sibley & Monroe 1990, Bleiweiss et al. 1997), deposited in the Museum Alexander Koenig. Color photographs of the specimen were compared with all trochiline species in the National Museum of Natural History, Smithsonian Institution. The diminutive specimen was similar in size and general appearance to several of the small woodstars. For assessing the possibility of hybridization, I considered all species cur-

Table 1.—Ranges (mean ± standard deviation) of measurements (mm) of wing chord, bill length, and rectrix length (R1–R5) of adult males of *Calliphlox mitchellii, Chaetocercus amethystina, Chaetocercus mulsant,* and a probable hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant* (Museum Alexander Koenig 9837).

Character	*Calliphlox mitchellii* (N = 13–15)	*Calliphlox amethystina*[a] (N = 10–11)	*Chaetocercus mulsant* (N = 18–19)	Hybrid
Wing	34.3–37.2 (35.6 ± 0.6)	30.4–33.1 (32.0 ± 0.4)	37.6–40.6 (39.3 ± 0.9)	38.9
Bill	12.9–14.3 (13.7 ± 0.4)	11.4–13.6 (12.5 ± 0.8)	15.5–17.3 (16.3 ± 0.4)	16.2
R1	11.9–13.1 (12.5 ± 0.4)	13.3–15.1 (14.2 ± 0.6)	14.4–17.2 (15.8 ± 0.7)	15.1
R2	16.0–17.5 (16.7 ± 0.5)	16.1–17.4 (16.9 ± 0.5)	17.3–20.4 (19.1 ± 0.9)	18.8
R3	23.3–27.7 (25.3 ± 1.3)	20.8–25.0 (23.0 ± 1.1)	22.8–27.8 (25.1 ± 1.3)	28.3
R4	30.0–34.3 (32.0 ± 1.3)	28.0–31.1 (29.7 ± 0.9)	22.8–26.6 (24.7 ± 0.9)	31.2
R5	29.9–33.1 (31.6 ± 1.0)	32.2–36.9 (33.8 ± 1.4)	19.3–22.2 (20.4 ± 0.8)	27.5

[a] Bahia (n = 1), "Brazil" (n = 3), Minas Gerais (n = 3), Rio de Janeiro (n = 4).

rently placed by Schuchmann (1999) in *Calliphlox* (*mitchellii, amethystina*) and *Chaetocercus* (*mulsant, bombus, heliodor, astreans, jourdanii*) that occur in Colombia (Hilty & Brown 1986) as potential parental species (see Graves 1997).

Measurements were taken with digital calipers and rounded to the nearest 0.1 mm: wing chord; bill length (from anterior extension of feathers); and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix) (Table 1). Pairs of rectrices are numbered from the innermost (R1) to the outermost (R5). Scatter plots of measurements were used to illustrate size differences among specimens.

General color descriptions presented in Appendix 1 were made under natural light. I evaluated crown color with a calibrated colorimeter (CR-221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture. The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicular to the specimen surface is collected for color analysis. Colorimetric data from iridescent feathers are acutely dependent on the angle of measurement, the curvature of plumage surfaces in museum skins, and the degree of pressure applied to the plumage surface by the Chroma Meter aperture. In order to reduce measurement variation, I held the aperture flush with the rectrix surface without depressing it. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements.

Colorimetric characters were described in terms of opponent-color coordinates (L, a, b) (Hunter & Harold 1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (L), red-green (a), and yellow-blue (b). The rationale is that a color cannot be perceived as red and green or yellow and blue at the same time. Therefore "redness" and "greenness" can be expressed as a single value a, which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by b for yellows and $-b$ for blues. The third coordinate, L, ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage, the higher the L value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans and the relevance of opponent color coordinates to colors perceived by hummingbirds is unknown. In any case, the L, a, b color system permits plumage color to be unambiguously characterized for taxonomic purposes.

Results and Discussion

I considered the hypotheses that the specimen represents (*i*) a geographic variant or genetic color morph of a valid species; (*ii*) a hybrid; or (*iii*) an undescribed species. Hybrids lack formal standing in zoological nomenclature. Therefore, hybridity must be ruled out before species status is conferred. Because the specimen differed significantly in size and shape from all species of *Calliphlox* or *Chaetocercus,* it does not appear to represent a previously undiscovered color morph or geographic variant of a known species. All evidence is consistent with Kleinschmidt's hypothesis that the specimen represents an intergeneric hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant.* Several characters of the hybrid facilitate the identification of its parental species (Figs. 1, 2): (a) purplish-rose gorget with a few scattered white barbs on the chin; (b) white pectoral band; (c) broad white midline from pectoral band to vent; (d) absence of rufous or buff pigmentation on the rectrices; (e) the presence of cinnamon or rufus tipping on lower flank feathers; and (f) the unusual shape of the tail (rectrix length: R4 >R3 > R5 > R2 > R1).

Here I present a synopsis of the critical steps of the hybrid diagnosis (see Appendix). The pool of potential parental species may first be narrowed by focusing on absence of rufus or buff pigmentation in the rectrices in the hybrid. Because brown and reddish-brown pigments appear to exhibit consistent penetrance in hummingbird hybrids (Banks & Johnson 1961, Graves & Newfield 1996), *Chaetocercus bombus* (buff pectoral band) and *C. jourdanii* (rufus pigmentation on rachii and vanes of rectrices) can be eliminated from further consideration as parental species. *Chaetocercus astreans* can also be eliminated because its geographic range in the Sierra Nevada de Santa Marta does not overlap that of other potential parental species (Graves 1986) and because it possesses a dark red gorget and bluish-green dorsal plumage, neither of which is expressed in the hybrid. Similarly, *Chaetocercus heliodor* can be eliminated because hybridization between it and any of the remaining species would likely produce offspring with a grayish-white pectoral band, dark green dorsal plumage toned with

Fig. 1. Lateral views of males in definitive plumage (top to bottom): *Chaetocercus mulsant,* a probable hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant* (Museum Alexander Koenig 9837), and *Calliphlox mitchellii.*

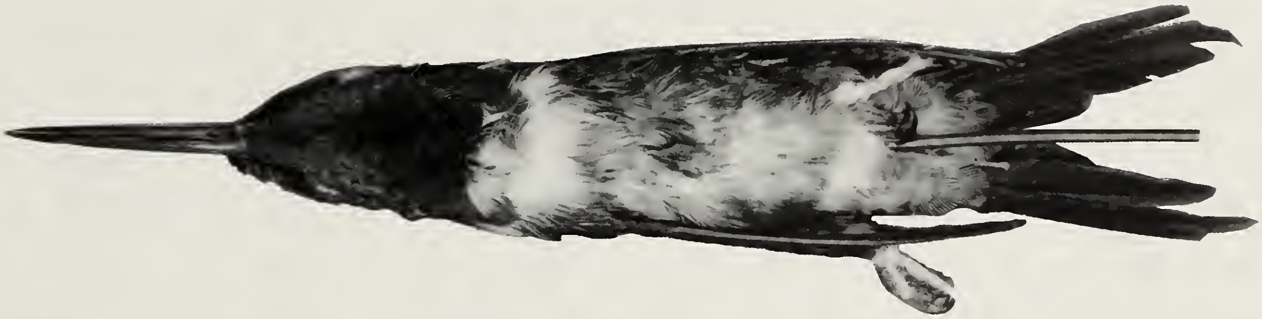

Fig. 2. Ventral view of a probable hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant* (Museum Alexander Koenig 9837).

bluish-green, and dark greenish flanks (Graves 1997). Based on plumage characters, the hybrid could be the product of two possible combinations of species: *Calliphlox mitchellii* × *Chaetocercus mulsant* and *Calliphlox amethystina* × *Chaetocercus mulsant.* On geographical grounds the hybrid must represent the former combination because *Calliphlox amethystina* and *Calliphlox mitchellii* have allopatric distributions east and west of the Cordillera Oriental (Hilty and Brown 1986). The hybrid was collected in the Cordillera Central (Kleinschmidt 1943). Colorimetric measurements of crown color (Table 2) are consistent with the hypothesis that the specimen represents an intergeneric hybrid between *Calliphlox mitchellii* and *Chaetocercus mulsant.*

As a second step, I tested the restrictive hypothesis with an examination of size and external proportions (Fig. 3). Measurements of trochiline hybrids fall within the mensural ranges exhibited by their parental species as a consequence of the polygenic mode of inheritance (Banks & Johnson 1961). Measurements of *Calliphlox mitchellii* and *Chaetocercus mulsant* overlap for only two of the seven characters but the percent difference in character means (larger species divided by smaller) is moderate except for the outermost rectrix (R5): wing chord (10.4%), bill length (18.9%), R1 (26.4%), R2 (14.4%), R3 (0.8%), R4 (29.6%), and R5 (54.9%). Measurements of the hybrid fall within the cumulative range of parental measurements for six of the seven measurements. The third rectrix (R3) of the hybrid was 0.5 mm (1.8%) longer than the largest value recorded for that character in the parental species. There have been no well-documented cases of morphological luxuriance (where the size of hybrid offspring exceeds that of the parental species) among avian hybrids (Graves 1990, 1996). I suspect that the cumulative range of measurements for R3 in the parental species would overlap the hybrid value if the sample size was increased.

I note for comparative purposes that *Cal-*

Table 2.—Minima, maxima, and means (± standard deviation) of opponent color coordinates (*L, a, b*) of crown color of adult males of *Calliphlox mitchellii, Chaetocercus mulsant,* and a probable hybrid, *Calliphlox mitchellii* × *Chaetocercus mulsant* (Museum Alexander Koenig 9837).

	L darkness			*a*/−*a* red/green			*b*/−*b* yellow/blue		
	Min.	Max.	Mean ± *SD*	Min.	Max.	Mean ± *SD*	Min.	Max.	Mean ± *SD*
Calliphlox mitchellii	29.9	32.2	31.3 ± 0.8	0.5	2.7	1.1 ± 0.8	8.8	12.1	9.8 ± 1.3
Chaetocercus mulsant	13.6	20.2	16.9 ± 1.7	−0.3	4.4	1.9 ± 1.4	−4.3	1.6	−1.6 ± 1.8
Hybrid		22.2			−1.6			7.7	

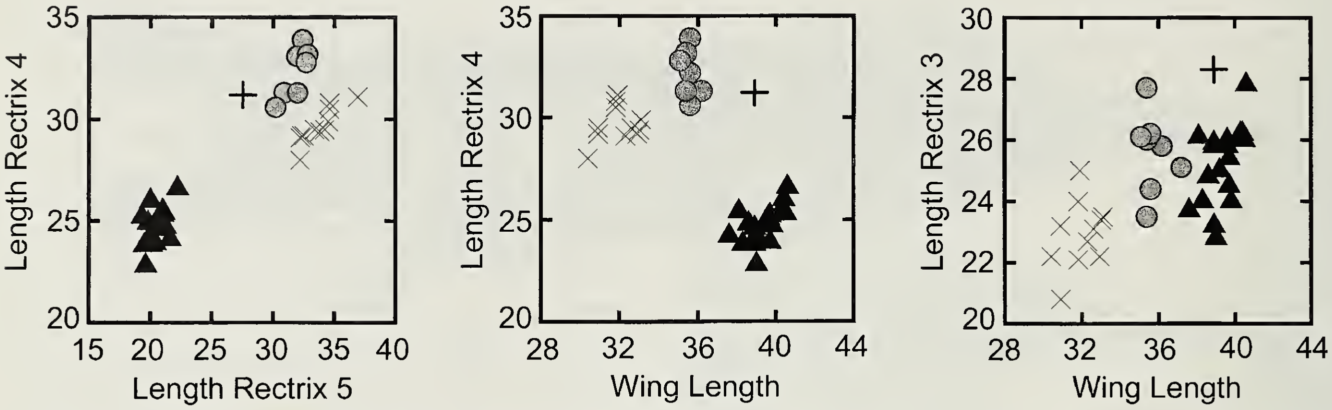

Fig. 3. Bivariate plots of selected measurements (see Table 1) of males in definitive plumage: *Calliphlox mitchellii* (●), *Calliphlox amethystina* (×), *Chaetocercus mulsant* (▲), and a probable hybrid (+), *Calliphlox mitchellii* × *Chaetocercus mulsant* (Museum Alexander Koenig 9837).

liphlox amethystina × *Chaetocercus mulsant* was not excluded as a parental combination by mensural measurements (Table 1). However, inspection of bivariate plots of the wing and rectrix measurements suggest that *Calliphlox mitchellii* was the most likely *Calliphlox* parent (Fig. 3). In summary, evidence obtained from plumage color and pattern, as well as from external size and shape, is consistent with the hypothesis that Kleinschmidt's specimen represents a hybrid between *Calliphlox mitchellii* and *Chaetocercus mulsant.*

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Literature Cited

Banks, R. C., & N. K. Johnson. 1961. A review of North American hybrid hummingbirds.—Condor 63:3–28.

Bleiweiss, R., J. A. W. Kirsch, & J. C. Matheus. 1997. DNA hybridization evidence for the principal lineages of hummingbirds (Aves: Trochilidae).—Molecular Biology and Evolution 14: 325–343.

Goldsmith, T. H., & K. M. Goldsmith. 1979. Discrimination of colors by the black-chinned hummingbird, *Archilochus alexandri.*—Journal of Comparative Physiology A 130:209–220. Colombia.—Condor 92:754–760.

Graves, G. R. 1986. Systematics of the Gorgeted Woodstars (Trochilidae: *Acestrura*). Proceedings of the Biological Society of Washington 99:218–224.

———. 1990. Systematics of the "green-throated sunangels" (Aves: Trochilidae): valid taxa or hybrids?—Proceedings of the Biological Society of Washington 103:6–25.

———. 1996. Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes.—Proceedings of the Biological Society of Washington 109:373–390.

———. 1997. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 4. Hybrid origin of *Calothorax decoratus* Gould. Proceedings of the Biological Society of Washington 110:320–325.

———. 1998. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 6. An intergeneric hybrid, *Aglaiocercus kingi* × *Metallura tyrianthina,* from Venezuela.—Proceedings of the Biological Society of Washington 111:511–520.

———. 1999. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 8. A provisional hypothesis for the hybrid origin of *Zodalia glyceria* (Gould, 1858).—Proceedings of the Biological Society of Washington 112:491–502.

———, & N. L. Newfield. 1996. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 1. Characterization of *Calypte anna* × *Stellula calliope* and the possible effects of egg volume on hybridization potential. Proceedings of the Biological Society of Washington 109:755–763.

———, & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* × *Heliangelus amethysticollis*) from northern Colombia.—Condor 92:754–760.

Gray, A. P. 1958. Bird hybrids. Commonwealth Agricultural Bureaux, Bucks, England, 390 pp.

Hilty, S. L., and W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, 836 pp.

Hunter, R. S., & R. W. Harold. 1987. The measurement of appearance, 2nd edition. Wiley, New York, 411 pp.

Kleinschmidt, O. 1943. Katalog meiner ornithologischen Sammlung. Gebauer-Schwetschke, Halle, Germany. I–XII + 236 + A–H pages.

Meyer de Schauensee, R. M. 1949. Birds of the Republic of Colombia, part 2.—Caldasia 5:381–644.

Panov, E. N. 1989. Natural hybridisation and ethological isolation in birds (in Russian). Nauka, Moscow, 510 pp.

Schuchmann, K. L. 1999. Family Trochilidae. Pp. 468–680 *in* J. del Hoyo, A. Elliott, & J. Sargatal, eds., Handbook of the birds of the world, vol. 5. Barn-owls to hummingbirds. Lynx Edicions, Barcelona, 759 pp.

Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.

Zusi, R. L., & G. D. Bentz. 1982. Variation of a muscle in hummingbirds and swifts and its systematic implications.—Proceedings of the Biological Society of Washington 95:412–420.

Appendix

Comparative description of selected characters of adult male *Calliphlox mitchellii, Chaetocercus mulsant,* and a probable hybrid, *C. mitchellii* × *C. mulsant* (Museum Alexander Koenig 9837). Descriptions of structural colors are unusually subjective, as color seen by the observer varies according to the angle of inspection and direction of light. For this reason I use general color descriptions.

The dorsal plumage in *mitchellii,* from forecrown to uppertail coverts, is weakly iridescent and dark green in coloration. When viewed head-on, the dorsum is sooty green. The dorsal plumage of *mulsant* is significantly more iridescent than in *mitchellii,* appearing bluish-green, particularly on the rump and uppertail coverts. When viewed head-on, the dorsum of *mulsant* exhibits a moderate degree of green iridescence which becomes progressively bluer from crown to uppertail coverts. The color and intensity of dorsal iridescence in the hybrid were intermediate in appearance to that of the parental species. Both parental species and the hybrid possess silky white tufts of flank feathers.

In *mitchellii* the central rectrices (R1) are black, toned with dull bronze, the outer vanes glossed with dark green. The remainder of the rectrices (R2–R5) are black, toned with bronze or purplish-bronze at certain angles of inspection under intense light. In *mulsant,* the central rectrices are black, glossed with dull green on the proximal two-thirds of the inner and outer vanes; the outer rectrices (R2–R5) are black. Rectrices of the hybrid are intermediate in color and shape (width of R4 = ~1.3 mm, width of R5 = ~1.1 mm; both measured 5 mm from the feather tip).

In *mulsant,* dark green wing coverts contrast with dull black secondaries and primaries. The contrast between wing coverts and flight feathers in *mitchellii* is negligible. Wing coverts and flight feathers in the hybrid are intermediate in color between those of *mulsant* and *mitchellii.*

In *mitchellii,* a white post-ocular spot elongates to form a tenuous connection to the side of the white pectoral band. The postocular facial stripe (obscured by lateral gorget feathers in Fig. 2) in *mulsant* and in the hybrid is more pronounced.

The purplish-rose gorget of *mitchellii* extends laterally to the lower edge of the eyering and posteriorly to the lower throat. Gorget feathers are pale gray basally (with a few dark gray lateral barbs near the base of the feather), banded distally by a narrow transitional band of dark gray, and tipped with a purplish-rose disk. The gorget is bordered posteriorly by a creamy-white pectoral band. The abdomen and sides are dull green. Feather tips along the midline are tipped with gray. Feathers of the lower flanks are tipped with cinnamon or rufus. Vent feathers are white, whereas undertail coverts are dull green narrowly fringed with gray or buff.

The purplish-rose gorget of *mulsant* does not extend laterally to the eyering. A small white chin spot speckled with iridescent disks is found in most specimens. The gorget is bordered posteriorly by a white pectoral band (whiter than in *mitchellii*). Gorget feathers are pale gray, grayish-white or creamy white, banded distally by a narrow transitional band of dull bronzy-green, and tipped with a purplish-rose disk. A broad white stripe extends along the midline from the pectoral band to the vent (also white). The flanks and sides of the breast below the pectoral band are bluish-green. Undertail coverts are white with an indistinct grayish or bluish-gray lanceolate subterminal spot. Lower flank feathers lack cinnamon or rufus tips.

The ventral plumage of the hybrid is intermediate in appearance between that of *mitchellii* and *mulsant.* A few feathers on the chin have scattered white barbs.

The gorget extends laterally to the lower margin of the eyering as in *mitchellii.* The gray basal portions of gorget feathers are intermediate in darkness between those of *mitchellii* and *mulsant*; the narrow subterminal band of gorget feathers exhibits dull bronze reflections. The remainder of the underparts are nearly intermediate in appearance between that of the parental species although the elongated preparation of the skin makes it difficult to compare homologous parts efficiently. The hybrid possesses a distinctive pectoral band (darker than in *mulsant*) and a white midline stripe extending to the vent area (Fig. 2). Feathers on the lower flanks are tipped with cinnamon or rufus. The undertail coverts are creamy white or buff with a subterminal grayish-green spot. Longer coverts are narrowly tipped with gray whereas shorter ones are tipped with buff or rufus. The maxillary and mandibular ramphotheca of *mitchellii, mulsant,* and the hybrid are black.

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A new burrowing crayfish of the genus *Cambarus* Erichson, 1846 (Decapoda: Cambaridae) from the lower Flint River basin in the Dougherty Plain of Georgia, with notes on *C.* (*D.*) *harti* Hobbs, 1981

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Abstract.—*Cambarus* (*Depressicambarus*) *doughertyensis* is a new species of obligate burrowing crayfish known from a single locality in the lower Flint River basin in the Dougherty Plain of the East Gulf Coastal Plain, Dougherty County, Georgia. It appears to be most closely related to *Cambarus* (*D.*) *harti* Hobbs, which is known from two localities in the western Piedmont Plateau, Meriwether County. Although the two species are morphologically similar in many respects, *C.* (*D.*) *doughertyensis* differs from *C.* (*D.*) *harti* in having a longer areola; a plethora of tubercles on the carpus and ventral surface of the palm; more tubercles on the opposable surfaces of both fingers of the chela, and differences in the morphology of those surfaces; a lack of spines or tubercles on the proximal podomere of the uropod; a radically different color pattern; and in a number of other characters. Spines on the ventral keel of the rostrum of crayfishes other than certain Mexican crayfishes of the genus *Procambarus* Ortmann are reported for the first time. Inadvertent errors in the description of *C.* (*D.*) *harti* are corrected.

Five similar species of highly specialized, obligate burrowing crayfishes of the genus *Cambarus* Erichson, 1846, subgenus *Depressicambarus* Hobbs, 1981, *latimanus* Group Bouchard 1978, are known to occupy limited, widely separated ranges in Georgia (Hobbs 1981). *Cambarus* (*D.*) *cymatilis* Hobbs, 1970, occurs in the Conasauga-Coosa River basin in the Ridge and Valley physiographic province; *Cambarus* (*D.*) *harti* Hobbs, 1981, is known from the Flint-Chattahoochee River basin in the western Piedmont Plateau; *Cambarus* (*D.*) *reflexus* Hobbs, 1981, occupies parts of the Savannah and Ogeechee River basins in the Atlantic Coastal Plain and eastern Fall Line Hills District; *Cambarus* (*D.*) *strigosus* Hobbs, 1981, is limited to the Savannah River basin in the eastern Piedmont Plateau; and *Cambarus* (*D.*) *truncatus* Hobbs, 1981, is known only from the Oconee River basin in the Fall Line Hills District. Of these five crayfishes, *C.* (*D.*) *harti,* which is cobalt blue, occupies the southwesternmost range, and is known only from wetlands at two localities in Meriwether County. Its type locality is within the Cold Spring Creek subdrainage of the upper Flint River, the other is within the Flat Shoal Creek subdrainage of the Chattahoochee River, about 18.4 air km northwest of the type locality.

On 20 May 1999, CES excavated a number of chimneyed burrows in a seasonally flooded swamp forest adjacent to the floodplain of Kiokee Creek, a tributary of the lower Flint River in the Dougherty Plain of the East Gulf Coastal Plain in Dougherty County. This locality is about 147 air km south-southeast of the type locality of *C.* (*D.*) *harti.* The initial digging efforts produced four specimens of a relatively drab, brownish crayfish that superficially resembled *C.* (*D.*) *harti* except in color pattern. Additional specimens have since been collected, and it is apparent that this animal is an undescribed species related to *C.* (*D.*) *harti* and the four other previously mentioned species. Examination of these specimens also revealed the presence of spines on the ventral keel of the rostrum, a character that has been reported only in some Mexican crayfishes of the genus *Procambarus,* subgenera *Paracambarus* Ortmann, 1906, and *Villalobosus* Hobbs, 1972 (Villalobos 1955, 1983). Confusing statements in the original description of *C.* (*D.*) *harti* are clarified, based on a recent examination of the primary types.

Measurements of crayfish structures were made to the nearest 0.1 mm with a Fowler precision dial caliper, following the methods of Hobbs (1981:9–10) except where noted. Abbreviations used in the paper are: GMNH, University of Georgia Museum of Natural History, Athens; j, juvenile; NCSM, North Carolina State Museum of Natural Sciences, Raleigh; PCL, postorbital carapace length; TCL, total carapace length; USGS, United States Geological Survey; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UTM, Universal Transverse Mercator.

Cambarus* (*Depressicambarus*) *doughertyensis, new species

Fig. 1, Table 1

Diagnosis.—Body and eyes pigmented, eye small ($\bar{x}$ adult diam. 1.2 mm, $n = 15$). Rostrum with slightly thickened, elevated margins, subparallel or moderately converging to base of short acumen, which not delimited by tubercles or spines; margins constricted at base of acumen, strongly converging and concave from there to small, dorsally directed apical tubercle; acumen comprising 28.6–42.9% ($\bar{x}$ = 34.6%) of rostrum length, latter constituting 11.7–13.3% ($\bar{x}$ = 12.5%) of TCL; floor (dorsal surface) of rostrum broadly concave, cephalic half cuplike; ventral keel of rostrum bearing 1–4 corneous spines. Areola obliterated or nearly so, length constituting 40.9–45.6% ($\bar{x}$ = 43.7%) of TCL and 46.2–51.2% ($\bar{x}$ = 48.9%) of PCL. Thoracic section of carapace dorsally crowded with punctations, dorsolaterally and laterally granulate or with small tubercles; cephalic section laterally with many, usually small, tubercles. Cervical spines reduced to tubercles, one to several each side of carapace. Postorbital ridge moderate, cephalic margin rounded and without spine or tubercle. Suborbital angle obsolete to broadly obtuse, without tubercle or spine; branchiostegal spine vestigial or a small tubercle. Antennal scale 2.5–3.1 ($\bar{x}$ = 2.8) times as long as wide, greatest width at midlength; lateral margin thickened and terminating distally in long spine, lamella narrow, cephalic margin moderately or strongly declivous, mesial margin subparallel to lateral margin; antennal peduncle without tubercles or spines.

Palm of chela inflated, 1.7–1.9 ($\bar{x}$ = 1.8) times wider than deep, depth 89.5–98.6% ($\bar{x}$ = 95.2%) of length of mesial margin, width 1.6–1.9 ($\bar{x}$ = 1.7) times length of mesial margin; latter constituting 26.3–31.3% ($\bar{x}$ = 28.9%) of total chela (propodus) length, bearing subserrate mesial row of 6 (rarely 5 or 7) large, semierect tubercles, row subtended dorsally by second row of 5 or 6 (rarely 3 or 4) smaller ones, and other smaller but produced tubercles dorsolateral to this row; 1 or 2 small, produced tubercles ventral to mesial row. Fixed finger of chela costate laterally, with strong median ridge dorsally and weak submedian ridge ventrally; opposable surface of finger with row

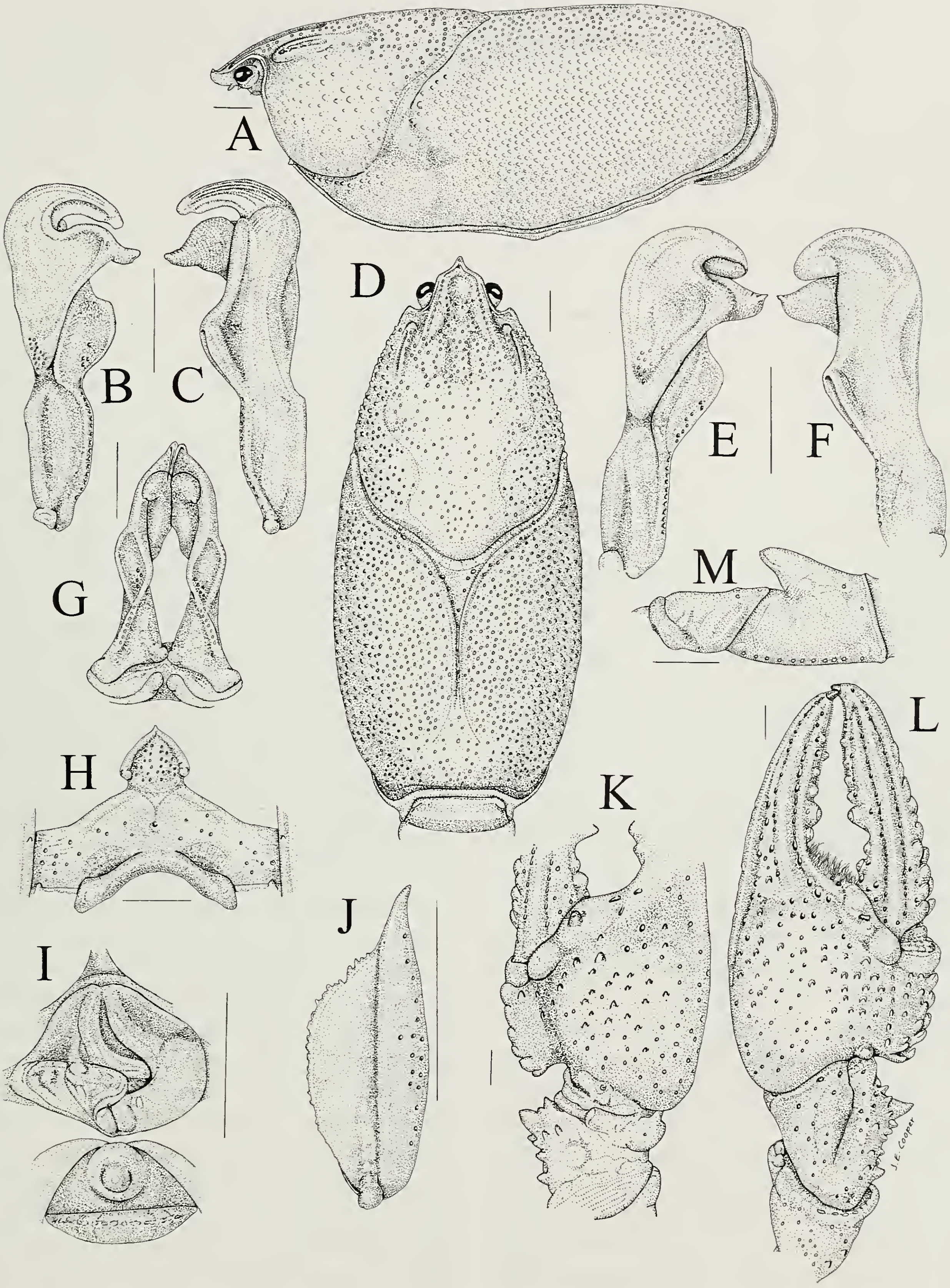

Fig. 1. *Cambarus* (*Depressicambarus*) *doughertyensis,* new species; all from holotypic male, form I (NCSM 7997), except E, F, from morphotypic male, form II (NCSM 7999), and I from allotypic female (NCSM 7998): A, lateral aspect of carapace; B, E, mesial aspect of gonopod (first pleopod); C, F, lateral aspect of gonopod; D, dorsal aspect of carapace; G, caudal aspect of in situ gonopods; H, epistome; I, annulus ventralis and postannular sclerite; J, antennal scale; K, ventral aspect of left palm; L, dorsal aspect of distal podomeres of left cheliped; M, basis and ischium of third pereiopod. Scale line = 2 mm.

Table 1.—Measurements (mm) of types of *Cambarus* (*Depressicambarus*) *doughertyensis*, new species.

	Holotypic male, form I	Allotypic female	Morphotypic male, form II
Carapace			
Total length	28.5	29.0	29.4
Postorbital length	25.7	25.8	26.2
Width	14.5	14.5	14.7
Depth	11.0	11.4	11.2
Length rostrum	3.4	3.7	3.8
Length acumen	1.2	1.4	1.3
Length areola	12.7	12.7	13.0
Width areola	0.2	oblit	oblit
Antennal scale			
Length	3.2	3.2	3.4
Width	1.1	1.3	1.1
Abdomen			
Length	25.5	26.4	26.0
Width	10.1	10.7	10.3
Cheliped			
Length propodus	22.1	21.5	24.4
Length mesial margin palm	6.5	6.4	7.0
Width palm	11.5	11.1	12.6
Depth palm	6.0	6.3	6.9
Length dactyl	14.6	14.0	15.8
Gonopod length	6.8	N/A	7.1

of 5–7 (rarely 8) tubercles, in addition to subconical tubercle ventral to denticles, third tubercle from base usually very large; dactyl length 2.2–2.6 ($\bar{x}$ = 2.3) times length of mesial margin of palm, with very strong median dorsal ridge and weak submedian ventral ridge; mesial surface of dactyl with strong, broad tubercles on proximal two-thirds or more; opposable surface with row of 9–12 (usually 9 or 10) tubercles, fourth from base usually very large. Carpus with weak dorsomesial tubercles; large, stout, conical spine at distal margin of mesial surface; 2 low, subconical distal mounds at distal margin of ventral surface; and multiple strong tubercles on mesial and ventral surfaces; merus with 2–4 small subdistal dorsal tubercles, 4–6 (usually 5) tubercles on ventrolateral ridge, and 7–11 (usually 9 or 10) tubercles on ventromesial ridge.

Abdomen shorter and considerably narrower than carapace; proximal podomere of uropod without tubercles or spines; mesial ramus with small caudolateral and caudomedian spines, latter submarginal.

Hook on ischium of third pereiopod of males, that of holotypic male, form I (Fig. 1M) uniramous, tapered, oblique, overreaching basioischial articulation by most of length, opposed by very weak tubercle on basis; coxa of fourth pereiopod of males with vertically disposed, caudomesial boss.

In situ gonopods (first pleopods) of form I male (based on holotypic male; Fig. 1G) symmetrical; proximomesial apophyses moderate, partly rounded; pair of bulbosities on base below apophyses; central projection directed caudally; mesial process inflated at base, tip extruded, directed caudally and inclined slightly proximally; in lateral aspect (Fig. 1C), central projection curved over 90° to plane of shaft, slightly tapered, not recurved, with moderate, proximally directed subapical notch; tip extending proximally nearly to distal margin of mesial process but not as far caudally as tip of latter; mesial process subglobose, distal margin arched; tip of process extruded, subacute, caudally directed; caudal process represented by small, rounded protuberance; in mesial aspect (Fig. 1B), setae at midlength of shaft and some near proximocaudal margin of caudal curvature.

Annulus ventralis (based on allotypic female; Fig. 1I) about 1.5 times wider than long, subovate in ventral outline; cephalic half moderately depressed, with broad, uneven median trough flanked each side by strong ridge; cephalomedian margin domed, with median concavity; sinistral ridge of cephalic half descending obliquely to join upper arm of reverse C-shaped caudosinistral wall, dextral ridge slightly curved, descending to cephalic margin of caudodextral wall; caudosinistral wall inflated, rounded caudally and laterally, caudodextral wall long, nearly horizontal, less inflated but broad; transverse tongue originating at broad median end of caudodextral wall, proceeding horizontally to plunge into deep fossa beneath sinistral wall; sinus not dissecting caudal margin. Mirror image of this configuration observed in 7 of 10 females.

Measurements of type specimens provided in Table 1.

Description of holotypic male, form I.—Body and eyes pigmented, eye 1.4 mm diameter. Cephalothorax (Fig. 1A, D) subcylindrical, thoracic section 1.3 times wider than deep. Areola nearly obliterated, 1 punctation in narrowest part, length constituting 44.6% of TCL (49.4% of PCL). Rostrum with relatively thick, strongly elevated margins slightly converging to base of short acumen, where sharply constricted, more convergent and concave to small, dorsally directed apical tubercle; latter reaching midlength of penultimate podomere of antennular peduncle; acumen comprising 35.3% of rostrum length, latter constituting 11.9% of TCL; floor of rostrum excavate, cephalically cuplike, sparsely punctate, with usual row of deep punctations along inner surface of dorsal ridge; subrostral ridge strong, visible to base of acumen in dorsal aspect; ventral keel of rostrum with 2 corneous spines.

Postorbital ridge fairly strong, poorly defined ventrally, inflated caudally; groove shallow, lateral; cephalic margin rounded. Suborbital angle obsolete, margin without tubercle or spine; branchiostegal spine reduced to small tubercle. Thoracic section of carapace dorsally crowded with deep punctations, dorsolaterally and laterally granulate; row of small tubercles along ventral margin of anterior section of cervical groove; cephalic section of carapace 1.2 times longer than areola, constituting 55.5% of TCL; laterally with many scattered, small to moderate, tubercles, gastric region with scattered punctations. Cervical spine region with 1 tubercle and several granules.

Antennal peduncle devoid of spines or tubercles; tip of adpressed antennal flagellum reaching caudal margin of third tergite; antennular peduncle with very small, subdistal median spine on ventral surface of basal podomere. Antennal scale (Fig. 1J) 2.9 times as long as wide, broadest near midlength; lateral margin slightly convex, thickened, terminating in long spine, tip of which reaching distal margin of penultimate podomere of antennular peduncle; lamella 1.2 times width of thickened lateral portion, distal margin strongly declivous from base of spine, mesial margin subparallel to lateral.

Abdomen narrow, greatest width 69.7% of greatest carapace width; length 89.5% of TCL; abdominal pleura fairly short, rounded ventrally and caudally; terga with many large punctations, except articular surfaces glabrous. Proximal podomere of uropod without spines or tubercles; mesial ramus of uropod with weak median ridge bearing very small, submarginal caudomedian spine; caudolateral spine of ramus very small; cephalic section of right lateral ramus of uropod with weak ridge, caudal margin of transverse flexure bearing total of 19 fixed spines and 1 long, articulated sublateral spine (15 fixed and 1 sublateral on left). Telson with 2 spines in right caudolateral corner of cephalic section, innermost articulated, left corner with single fixed and 2 articulated spines; transverse flexure strong, caudal margin broadly rounded.

Epistome (Fig. 1H) with subcordiform to subtriangular cephalic lobe bearing short cephalomedian projection; margins of lobe relatively narrow, moderately elevated, lateral corners produced as tuberclelike protuberances; floor (ventral surface) broadly convex, very punctate; central depression shallow, with deep median fovea; lamellae very broad, moderately punctate, laterally truncate, with 1 small tubercle and 1 strong caudal tubercle each side; zygoma well arched, cephalolateral margins flanked by deep pit.

Third maxilliped with tip reaching midlength of penultimate podomere of antennal peduncle; exopodite very hirsute, tip reaching nearly to midlength of merus of endopodite; distolateral corner of ischium subacute, lateral half apunctate, glabrous; mesial section very broad, with clumps of long bristles, mesial margin of right ischium with 21 denticles, 20 on left; incisor ridge of right mandible with 8 denticles, 7 on left.

Right cheliped regenerated; left chela (Fig. 1L) 1.9 times longer than wide, palm 1.9 times as wide as deep, width 1.8 times length of mesial margin; latter 29.4% of total chela (propodus) length, 44.5% of dactyl length. Dorsal surface of palm covered with mostly deep punctations, those on mesial half and some on lateral half with small basal tubercles; longitudinal dorsomesial sulcus weak, with row of small, produced tubercles; dorsolateral margin of palm costate for much of length (continuous onto fixed finger), with slight impression and large punctations, some with tubercles at proximal bases; articular ridge strong, lateral eminence with dense, short setae on distolateral margin, continuing onto base of opposable surface of fixed finger; lateral margin of palm with row of large punctations. Ventral surface of palm (Fig. 1K) very punctate, mesial portion sharply set off from greatly inflated portion; distolaterally with weak depression (continuous onto fixed finger); lateral eminence of strong articular ridge with large, depressed, subconical subdistal tubercle; 3 strong and 3 weaker tubercles proximal to ridge (total of 13 obvious, produced tubercles on ventral surface). Mesial margin of palm with subserrate mesial row of 6 strong tubercles, row subtended dorsolaterally by row of 6 generally smaller tubercles, and 4 others dorsal to this row; 1 strong distal tubercle ventral to mesial row.

Fingers gaping except at tips, greatest width of gape slightly more than width of dactyl base, largest tubercles on opposable surfaces of fingers separated when fingers closed. Fixed finger costate laterally, inner margin of proximal fourth scalloped; dorsal surface with very strong, glabrous median ridge, flanked each side by deep punctate groove; lateral surface with row of large punctations; ventral surface with fairly strong ridge, closer to opposable margin than median in position, flanked mesially by row of coalescing punctations, laterally by slanted surface crowded with large punctations; opposable surface with relatively small subconical tubercle ventral to denticles at base of distal third or so of finger, and row of 5 other tubercles dorsal to or interrupting denticles, second from base largest; denticles in 1 or 2 rows. Dorsal surface of dactyl with very strong, glabrous median ridge, flanked each side by deep, punctate groove; mesial surface with very strong, broad tubercles on proximal three-fourths, basal tubercles in 3 rows, strongly encroaching dorsally, weakly encroaching ventrally; ventral surface with moderate, glabrous ridge, flanked each side by row of punctations; opposable surface with 9 tubercles, third from base largest, and excision in surface proximal to this tubercle; denticles in 1 row.

Carpus (Fig. 1L) 1.4 times as long as wide, 1.4 times as long as mesial margin of palm; dorsal surface of carpus with narrow, deep sulcus, lateral to which surface punctate, mesial to which surface with 3 dorsomesial tubercles; mesial margin with short, stout distal spine, 1 moderate tubercle close to its proximal margin, and 9 other strong, often subacute, tubercles; ventral surface with 2 subconical distal mounds, and 1 strong and 1 smaller proximomesial tubercle. Merus 1.7 times longer than deep, distodorsal surface with 1 large, broad adpressed tubercle and 1 smaller tubercle; ventrolateral ridge with 6 small, rounded tubercles, none on articular condyl, which rounded, glabrous; ventromesial ridge with 8 subacute tubercles and short, stout distal spine; ischium with 4 small, subacute tubercles on ventral ridge.

See "Diagnosis" for description of gonopods.

Description of allotypic female.—Except for secondary sexual characters, differing from holotypic male in following respects: Areola obliterated, constituting 43.8% of TCL (49.2% of PCL). Acumen comprising 37.8% of rostrum length, latter constituting 12.8% of TCL. Postorbital ridge fairly weak, nowhere sharply defined. Cephalic section of carapace 1.3 times longer than areola, constituting 56.2% of TCL. Cervical spine region with 5 small tubercles and several granules. Greatest width of abdomen 73.8% of greatest carapace width, length 91.0% of TCL. Telson with single fixed spine in each caudolateral corner of cephalic section, transverse flexure weak, caudal margin domed.

Palm of chela 1.8 times broader than deep, width 45.7% of length of mesial margin, latter 29.8% of total chela length, 45.7% of dactyl length; dorsomesial sulcus of palm obliterated; ventral surface with total of 10 obvious, produced tubercles. Opposable surface of right fixed finger with broken subconical tubercle ventral to denticles at base of distal fourth of finger, row of 8 other tubercles (6 on left finger), third from base massive. Opposable surface of right dactyl with 10 tubercles, fourth from base massive. Carpus 1.3 times as long as wide, mesial surface with 10 tubercles of varying sizes and shapes in addition to short, stout distal spine. Right merus with 1 moderate and 4 weak, rounded distodorsal tubercles (3 moderate tubercles on left); ventromesial ridge with 10 tubercles (9 on left), in addition to distal spine; ischium with 2 small ventral tubercles each limb.

First pleopods strong, distally hirsute; preannular sternite relatively narrow, walls steep (see "Affinities"); ventral surface of postannular sclerite (Fig. 1I) with large, subconical papilla.

See "Diagnosis" for description of annulus ventralis.

Description of morphotypic male, form II.—Differing from holotype in following respects: Areola obliterated, constituting 44.2% of TCL (49.6% of PCL). Ventral keel of rostrum with single spine near base. Branchiostegal spine obsolete. Cephalic section of carapace 1.3 times longer than areola, constituting 55.8% of TCL. Greatest width of abdomen 69.7% of greatest width of carapace, abdomen length 88.4% of TCL. Telson with 1 very small fixed spine and 1 minuscule articulated spine in right caudolateral corner of cephalic section, all spines congenitally absent from left. Lateral corner of lamella of epistome devoid of tubercles; zygoma moderately arched.

Right cheliped regenerated; palm of left chela 1.8 times broader than deep; length of mesial margin 28.7% of total chela length, 44.3% of dactyl length; ventral surface of palm covered with tubercles of various sizes; subconical tubercle on lateral eminence of articular ridge originating at proximal margin of ridge, not adpressed; 3 large tubercles proximal to ridge. Largest tubercle on opposable surface of fixed finger second from base, largest on opposable surface of dactyl fourth from base. Carpus length 1.5 times length of mesial margin of palm; dorsal sulcus short, flanked mesially by row of 3 tubercles; mesial surface with total of 11 tubercles in addition to usual stout subdistal spine; ventral surface with single proximomesial tubercle. Distodorsal surface of left merus with 1 moderate, subconical and 2 smaller, rounded tubercles; ventrolateral ridge with 5 very small tubercles, none on distal condyl; ventromesial ridge with 11 small, conical tubercles.

Hook on ischium of third pereiopod moderate, not overreaching articulation, opposed by extremely weak tubercle on ventral surface of basis. In situ gonopods with moderate, nearly abutted proximomesial apophyses; in lateral aspect (Fig. 1F), central projection broad, slightly tapered, not reaching as far caudally as tip of mesial process; latter inflated nearly entire length, directed caudally, tip subtruncate and with small, spiniform protuberance directed caudomesially; juvenile suture absent; in mesial aspect (Fig. 1E), short setae at midlength of shaft.

Color notes.—Most specimens discolored by ferrous deposits; the following based on a live adult female.

Ground color of carapace brown, fading ventrally to pale greenish-brown, ventral margin orangish; cephaloventral area of lateral surface of cephalic section of carapace creamy orange. Coxa, basis, and ischium of cheliped orangish; merus brownish, fading to orangish ventrally and proximally; carpus brown dorsally, orangish ventrally, with orangish dorsomedian furrow. Large distal tubercle on mesial surface of carpus orange, all others orange-cream. Dorsal surface of chela greenish-brown, articular ridge orange; tips of both fingers orange, not subtended by black band; tubercles on mesial margin of palm and dactyl orangish; lateral surface of propodus orangish. Largest tubercle on opposable surface of dactyl and fixed finger cream; other tubercles on both fingers orange-cream. Proximodorsal part and merus of second through fifth pereiopods orangish, fading to brownish on basis and ischium; ventral surfaces of these pereiopods orangish. Dorsal surface of abdomen brown; cephalic part of all pleura pinkish-orange, color most obvious on cephalic two-thirds of second abdominal segment; uropods and telson light brown.

Type locality.—Georgia, Dougherty County, burrows in wetland just south of access road near western boundary Albany Nursery Wildlife Management Area, ca. 12.8 km W of Albany (Pretoria 7.5″ USGS quadrangle, UTM Zone 16, coord. 751779E, 3496706N). Locality within subdrainage of Kiokee Creek, Flint River basin, Apalachicola River drainage.

Disposition of types.—The holotypic male, form I, allotypic female, and morphotypic male, form II, are in the NCSM crustacean collection (7997, 7998, and 7999, respectively). The following are designated paratopotypes: 1 j♂, 3 ♀ (5253), 22 Jul 1999, coll. CES, S. E. Cammack, E. E. Van De Genachte; 4 ♀, 2 j♀ (7987), 25 Feb 2001, coll. CES; 1 ♂ I (7988), 13 Aug 1999 (was ♂ II when collected), coll. CES, S. K. Berckman; 1 ♂ I, 1 ♀ (USNM 1004610), 2 Jun 1999, coll. CES, M. C. Freeman (MCF); 1 ♀ (GMNH 6239), 2 Jun 1999, coll. CES, MCF; 1 ♀ (23692); 14 May 2002, coll. CES.

Variations.—Some variations other than those previously addressed have been observed. In dorsal aspect, the margins of the rostrum are usually rather straight, and subparallel or only moderately convergent to the base of the acumen. In several specimens, though, the margins are slightly concave between the orbits, and in two very small females the rostrum is triangular. These juveniles also have marginal spines on the rostrum. In all specimens, the mesial (lamellar) portion of the antennal scale is only slightly wider than the thickened lateral portion, and the distomesial margin is moderately or strongly declivous from the base of the spine to the widest point. In some specimens the distomesial margin is deeply incised, bearing decidedly spinelike protuberances. In ventral outline, the cephalic lobe of the epistome varies in shape from subcordiform or subtriangular to subpentagonal, and in some specimens the margins are erose, with small angular protrusions. The central depression of the epistome is obsolete in 10 specimens, very shallow in the others, and always displays a deep fovea.

The greatest width of the abdomen varies from 69.1–74.8% ($\bar{x}$ = 72.2%) of carapace width, and is only slightly wider in females than in males. The length of the abdomen varies from 86.5–95.2% ($\bar{x}$ = 90.3%) of TCL. The number of spines in the caudolateral corner of the cephalic section of the telson is highly variable. Four specimens have a single fixed lateral spine and a single articulated inner spine in each corner. Four have two spines in one corner, and either a single fixed or articulated spine in the other. One specimen has no spines in one corner, two in the other; another has two spines in one corner, three in the other; and two specimens have a single fixed spine in each corner. In most specimens the articulated spines are very small.

In most specimens the punctations on at least the mesial half or third of the ventral surface of the palm have small basal tubercles, but the surface also bears from 6–13 prominent, produced tubercles, several of which may be very large. The largest tubercle on the opposable surface of the fixed finger is almost always the third (rarely the second or fourth) from the base; the largest tubercle on the corresponding surface of the dactyl is usually the fourth from the base, but often is the third, and occasionally the first and fourth tubercles are equally large. The total number of tubercles or spines on the carpus, excluding the stout distal spine of the mesial surface and the two stout distal tubercles or mounds of the ventral surface, ranges from 7–13 (usually 10–13). The ventral surface of the ischium of the cheliped bears from 2–4 (usually 3 or 4) small, subacute tubercles. The total length of the chela of adult males averages about 85% of TCL (94% of PCL), while the average for adult females is about 75% of TCL (84% of PCL).

Size.—The largest specimen is a female measuring 34.5 mm TCL (31.0 mm PCL). The largest form I male measures 31.0 mm TCL (27.5 mm PCL), the smallest 28.5 mm TCL (25.7 mm PCL). The smallest specimens yet collected are two females with TCLs of 7.0 and 7.7 mm.

Life history notes.—Form I males were collected in May and July. A form II male, collected in August 1999, underwent two molts in the laboratory, became form I in January 2000. No ovigerous females or those with attached young have yet been found. The two very small females, possibly representative of recruitment size, were dug from the same burrow on 25 February 2001.

Ecological notes.—The type locality of *C.* (*D.*) *doughertyensis* is in a swamp forest dominated by an overstory of *Quercus* spp., *Nissa biflora,* and *Acer rubrum,* while the understory has abundant *Crataegus aestivalis, Sebastiana fruticosa, Rhus radicans,* and a variety of graminoids. The area is seasonally flooded, and in very wet periods produces a shallow outflow to Kiokee Creek. Burrows are typically found just above the standing water mark among roots of small trees and *Serenoa repens.* The soils in the area are Grady clay loams and provide easy digging for the first 25 cm. Below that, the soil becomes much more dense and is more difficult to excavate. When the water table is high, burrows are anastomosed and usually have four or five openings, often marked by well developed chimneys approximately 10 cm high and 15 cm across. In this situation, the animals are most often found in one of the horizontal passages about 30 cm below the surface. As the water table drops, burrows are marked by only two or three openings, with chimneys, that angle down to a single subvertical passage that penetrates the water table. The animals are then found in the vertical passage, 5 to 10 cm below the water level. When a burrow is excavated, the crayfish can rarely be induced to come to the air-water interface, and when encountered they are unmoving and rarely try to escape.

Crayfish associates.—*Faxonella clypeata* (Hay, 1899) was collected in open water in the swamp forest when flooded, and was dug from simple burrows when the water table dropped. Two female *Cambarus* (*Depressicambarus*) cf. *C.* (*D.*) *striatus* Hay, 1902 (5157, 23691) and a female *Cambarus* (*Lacunicambarus*) *diogenes* Girard, 1852 (23690) were dug from separate burrows in the floodplain of Little Kiokee Creek, not far from the *C.* (*D.*) *doughertyensis* site.

Affinities.—Cambarus (*D.*) *doughertyensis* shares so many similarities with *C.* (*D.*) *harti* and several of the other small Georgia burrowers that, although some of them can undoubtedly be attributed to convergence and the channeling effect of adaptation to an obligate burrowing existence, it seems reasonable these species have descended from a common proximate ancestor. The annuli ventrales of some of the species are very similar, as are their narrow abdomens, many aspects of their chelipeds, rostra, antennal scales, suborbital angles, and branchiostegal spines, and other features. Some, including *C.* (*D.*) *harti,* also have spines on the ventral keel of the rostrum. They differ significantly, however, in many ways.

In *C.* (*D.*) *doughertyensis* the areola constitutes 40.9–45.6% ($\bar{x}$ = 43.7%) of TCL and 46.2–51.2% ($\bar{x}$ = 48.9%) of PCL, while in *C.* (*D.*) *harti* it constitutes 38.2–40.3% ($\bar{x}$ = 39.4%) of TCL and 44.2–45.8% ($\bar{x}$ = 44.8%) of PCL. Correspondingly, the cephalic section of the carapace in the former species is 1.2–1.4 times as long as the areola, while in the latter it is 1.5–1.6 times as long. The proximal podomere of the uropod in *C.* (*D.*) *harti* usually bears a small spine on both the lateral and mesial lobes, but such spines are lacking in *C.* (*D.*) *doughertyensis.* In *C.* (*D.*) *harti,* the preannular sternite of the female is broader and flatter than that of *C.* (*D.*) *doughertyensis,* which is narrow and steep. The width of this sternite, i.e., the distance between the ventral angles of the walls at their articulations with the mesial surfaces of the fourth coxae, is about 38% of carapace width in the former species, about 31% in the latter.

The ventral surface of the palm of the cheliped of *C.* (*D.*) *doughertyensis* (Fig. 1K), proximal to the articular ridge, bears many prominent, produced tubercles, whereas only a few such tubercles are present in *C.* (*D.*) *harti.* The opposable surface of the fixed finger of *C.* (*D.*) *doughertyensis* bears a row of from 5–8 tubercles in addition to the usual subconical tubercle ventral to the denticles, and there is a wide space between the base of the finger and the proximalmost tubercle. In *C.* (*D.*) *harti,* the number of tubercles that lie dorsal to the denticles is 4 or 5 (6 in one specimen). The opposable surface of the dactyl of *C.* (*D.*) *doughertyensis* bears 9–12 (usually 9 or 10) tubercles, whereas that of *C.* (*D.*) *harti* bears 5–7 tubercles. When the fingers of the chela are closed in *C.* (*D.*) *doughertyensis,* the largest tubercles on the opposable surfaces are separated from each other, but in *C.* (*D.*) *harti* the largest tubercles either abut or overlap. The carpus of *C.* (*D.*) *doughertyensis* usually bears from 7–13 spines or tubercles in addition to the large, stout distomesial spine and the two broad distoventral structures, whereas that of *C.* (*D.*) *harti* has 3 or 4 tubercles in addition to the usual. The former species has a shorter, deeper merus, in which the length averages 1.7 times the greatest depth, whereas in *C.* (*D.*) *harti* the merus averages twice as long as deep.

The following species differ from *C.* (*D.*) *doughertyensis* as indicated: *C.* (*D.*) *cymatilis* has a strong, usually subacute suborbital angle, the caudomedian spine on the mesial ramus of the uropod extends well beyond the caudal margin, and the color is blue; *C.* (*D.*) *reflexus* has a long, strongly recurved central projection and a well-defined caudal knob, both on the form I male gonopod, and the color is reddish or blue; *C.* (*D.*) *strigosus* has a row of plumose setae on the caudal border of the mesial process of the form I male gonopod, and a single spine in each cephalolateral corner of the telson; and *C.* (*D.*) *truncatus* usually lacks both caudomedian and caudolateral spines on the mesial ramus of the uropod and a transverse flexure in the telson, and the form I male gonopod has a very short central projection.

The members of some Georgia populations of *C.* (*D.*) *striatus* and *Cambarus* (*Depressicambarus*) *latimanus* (LeConte, 1856) display multiple strong tubercles on the carpus and the ventral surface of the chela. In these species, however, there is no excision in the opposable surface of the dactyl; there is a tubercle or spine on the ischium of the antennal peduncle; both lobes of the proximal podomere of the uropod bear a spine; the rostrum is longer, and the abdomen is longer and much broader; the antennal scale is subquadrate, with a broader lamella; and the annulus is subrhomboidal rather than subovate in outline.

Remarks.–As far as we can determine, the presence of spines or acute tubercles on the ventral keel of the rostrum, while a not uncommon feature in some Malacostraca, has never been reported in freshwater crayfishes except, as mentioned, some Mexican *Procambarus* of the subgenera *Paracambarus* and *Villalobosus.* An investigation of the presence or absence of this character in other U.S. species is just getting underway, but it has to date been found in several other members of subgenus *Depressicambarus,* including *C.* (*D.*) *harti,* and in one species of subgenus *Erebicambarus.*

Etymology.—This species is named for both the physiographic province and the county in which it appears to be endemic.

Suggested vernacular name: Dougherty burrowing crayfish.

Cambarus (*Depressicambarus*) *harti* Hobbs, 1981

Some inadvertent errors appeared in the description of this species (Hobbs 1981: 104–109). On page 104, column 2, paragraph 2, part of the first sentence has been omitted. It should read: *Cephalic* lobe of epistome (Figure 45g) subrhomboidal with short cephalomedian projection and scalloped margins; *main body with broad, shallow central depression* lacking distinct fovea. . . . On page 107, column 1, paragraph 1, line 10 says "ventrolateral row of setae on carpus reduced to 2. . . ." This should read: ventrolateral row of *tubercles* on *merus* reduced to 2. The next line says "mesial surface of ischium of cheliped devoid of tubercles," which should read: mesial *and ventral* surface of ischium. . . . These latter statements (p. 107) apply to the "morphotypic male, form II," but the specimen actually appears to be a juvenile rather than an adult male of the second form.

Acknowledgments

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Literature Cited

Bouchard, R. W. 1978. Taxonomy, ecology, and phylogeny of the subgenus *Depressicambarus,* with the description of a new species from Florida and redescriptions of *Cambarus graysoni, Cambarus latimanus,* and *Cambarus striatus* (Decapoda: Cambaridae).—Alabama Museum of Natural History Bulletin 3:26–60.

Erichson, W. F. 1846. Uebersicht der Arten der Gattung *Astacus.*—Archiv für Naturgeschichte 12(1): 86–103.

Girard, C. 1852. A revision of the North American Astaci, with observations on their habits and geographical distribution.—Proceedings of the Academy of Natural Sciences of Philadelphia 6: 87–91.

Hay, W. P. 1899. Description of two new species of crayfish.—Proceedings of the United States National Museum 22(1187):121–123.

———. 1902. Observations on the crustacean fauna of Nickajack Cave, Tennessee, and vicinity.—

Proceedings of the United States National Museum 25(1291):417–439.

Hobbs, H. H., Jr. 1969. On the distribution and phylogeny of the crayfish genus *Cambarus*. Pp. 93–178 *in* P. C. Holt, R. L. Hoffman, and C. W. Hart, Jr., eds., The distributional history of the biota of the southern Appalachians, Part I: Invertebrates. Research Division Monograph 1, Virginia Polytechnic Institute, Blacksburg, 295 pages.

———. 1970. New crayfishes of the genus *Cambarus* from Tennessee and Georgia (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 83(23):241–259.

———. 1972. The subgenera of the crayfish genus *Procambarus* (Decapoda: Astacidae).—Smithsonian Contributions to Zoology 117:1–22.

———. 1981. The crayfishes of Georgia.—Smithsonian Contributions to Zoology 318:1–549.

LeConte, J. 1856. Descriptions of new species of *Astacus* from Georgia.—Proceedings of the Academy of Natural Sciences of Philadelphia 7:400–402.

Ortmann, A. E. 1905. *Procambarus,* a new subgenus of the genus *Cambarus.*—Annals of the Carnegie Museum 3(3):435–442.

———. 1906. Mexican, Central American and Cuban Cambari.—Proceedings of the Washington Academy of Sciences 8:1–24.

Villalobos, A. 1955. Cambarinos de la Fauna Mexicana: Crustacea Decapoda. Tesis, Facultad de Ciencias, Universidad Nacional Autonoma de Mexico, 290 pp.

———. 1983. Crayfishes of Mexico (Crustacea: Decapoda). Translation of Villalobos 1955 by H. H. Hobbs, Jr. Smithsonian Institution Libraries and National Science Foundation, Washington, D.C., 276 pp.

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The rare deep-sea shrimp *Bitias brevis* (Rathbun, 1906) (Crustacea: Decapoda: Pandalidae) from the western Pacific

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Abstract.—During recent deep-sea expeditions in Taiwan, Japan and New Caledonia seven specimens were collected of the rare pandalid shrimp *Bitias brevis* (Rathbun, 1906), a species previously known from only two specimens. The study of this new material showed that characters used in separating *B. brevis* from its sole congeneric species, *B. stocki* Fransen, 1990, are variable. This study provides additional information on this rare shrimp, including coloration.

The recently established pandalid genus *Bitias* Fransen, 1990 contains two species: *B. stocki* Fransen, 1990, type species of the genus, and *B. brevis* (Rathbun, 1906). Both are rare and small species that occur in deep waters from 550 to 1350 m. *Bitias stocki* is known based only on four specimens from the North Atlantic (Fransen 1990, González 1995, González & Santana 1996, González et al. 2001). *Bitias brevis* is known from the holotype originally described as *Pandalus brevis* Rathbun, 1906, collected in Hawaii, and another specimen from Madagascar (Crosnier & Fransen 1994). These two species are very similar, and only slight differences in the shape of rostrum, and length of telson, have been proposed to separate them (see Crosnier & Fransen 1994). However, the limited number of known specimens renders the evaluation of these distinguishing characters difficult.

During recent deep-water expeditions in Taiwan, Japan and New Caledonia, seven more specimens of this genus were obtained. Careful examination showed that they can be assigned to *B. brevis.* The present report provides additional information on this rare shrimp, including a color photograph. The shape of the rostrum and the length of the telson proved to be variable in the Indo-West Pacific material examined of this species. It is possible that *B. stocki* may be synonymous with *B. brevis,* but more material from the Atlantic is needed for a full evaluation.

The specimens are deposited in the National Taiwan Ocean University, Keelung (NTOU), Natural History Museum and Institute, Chiba (CBM), and the Muséum national d'Histoire naturelle, Paris (MNHN). The following abbreviations are used: cl, postorbital carapace length, measured from the orbital margin to the posterodorsal margin of the carapace; BT, bottom trawl; CP, beam trawl; DW, Warén dredge; stn, station. Expeditions names used are: TAIWAN 2000, joint Taiwanese-French cruise; BATHUS, French expedition named after the Greek word for deep, *bathys*; and HALIPRO, French expedition named from "halieutique profonde".

Bitias brevis (Rathbun, 1906)
Figs. 1–3

Pandalus brevis Rathbun, 1906:916 (in part), fig. 65, pl. 21–fig. 3 (type-locality: Hawaii).—Chace, 1985:44.

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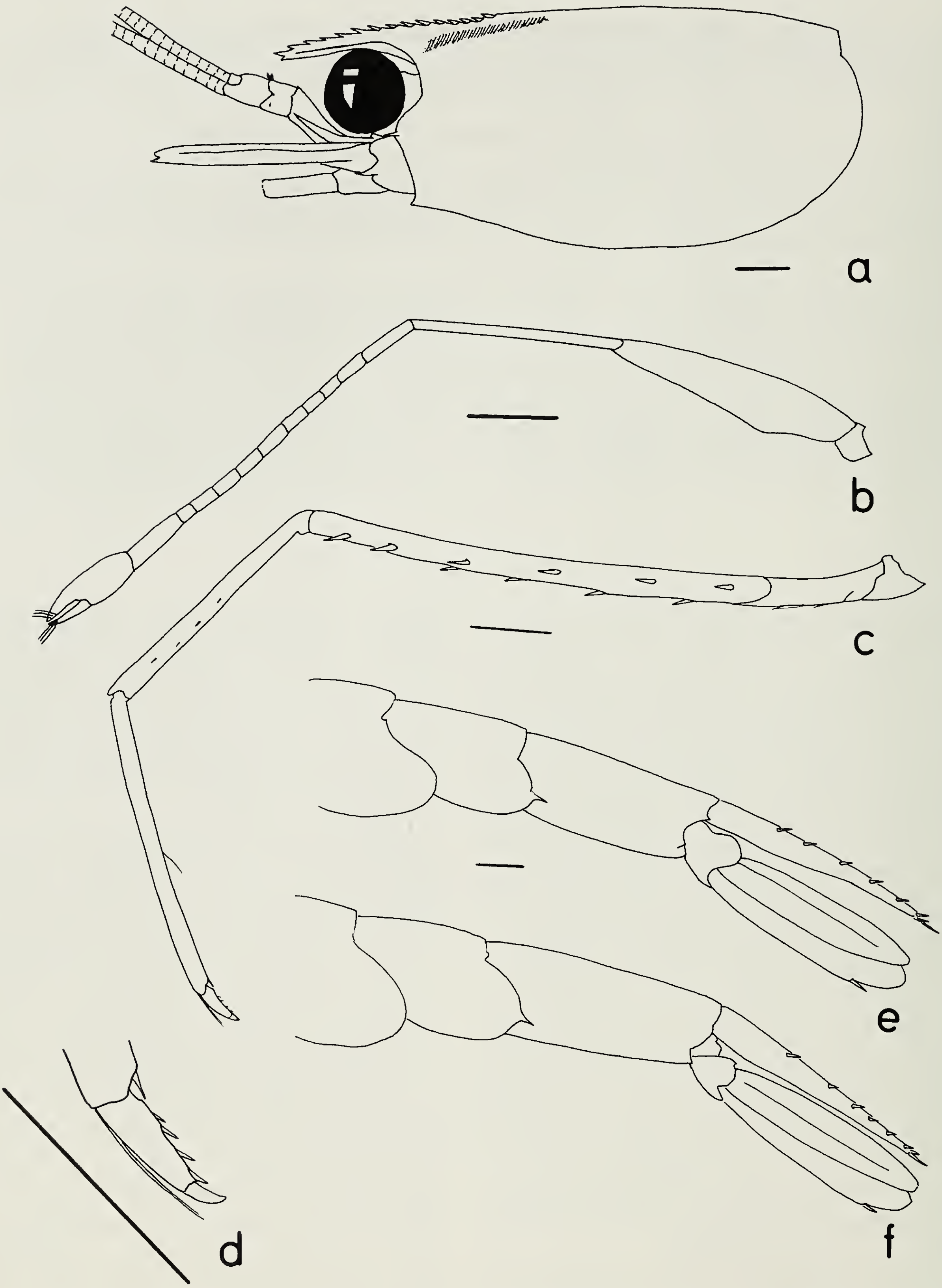

Fig. 1. *Bitias brevis* (Rathbun, 1906). a, b, e, Taiwan, TAIWAN 2000 stn CP 55, female 7.2 mm cl, NTOU 2000-55; c, d, Taiwan, TAIWAN 2000 stn CP 55, 6.3 mm cl, NTOU 2000-55; f, New Caledonia, HALIPRO 2 stn BT 58, female 6.8 mm cl, MNHN-Na. 14970. a, carapace lateral view; b, left second pereiopod; c, left third pereiopod; d, dactylus of left third pereiopod; e, f, posterior abdomen and tail fan, lateral view. Scales equal 1 mm.

Bitias brevis—Crosnier & Fransen, 1994: 46, figs. 1, 2a–f, 3a–b.

Material examined.—Taiwan. TAIWAN 2000, R/V *Fishery Researcher 1*, stn CP 55, 24°26.9′N, 122°18.1′E, 638 m, 4 Aug 2000, 1 female 7.2 mm cl, 1 carapace 6.3 mm cl, NTOU 2000-55.

Japan. KT 02-03 cruise, R/V *Tansei-maru*, stn B4, SE of Amami-Oshima Island, Ryukyu Islands, 27°56.94′N, 129°31.40′E, 3 m beam trawl, 751–810 m, 16 Apr 2002, 1 male 5.5 mm cl, 2 females 5.3, 6.0 mm cl, CBM-ZC 6469.

New Caledonia. BATHUS 3, stn DW 809, 23°39.39′S, 167°58.94′E, 650–730 m, 27 Nov 1993, 1 female (posterior part of abdomen missing) 6.8 mm cl, MNHN-Na. 14969; HALIPRO 2, stn BT 58, 25°4.13′S, 168°45.21′E–25°4.99′S, 168°44.86′E, 1303–1500 m, 17 Nov 1996, 1 female 6.8 mm cl, MNHN-Na. 14970.

Description.—Tegumental scales absent. Rostrum short, slightly shorter than half carapace length, nearly horizontal, extending to second segment of antennular peduncle, dorsal margin densely serrated with 11–16 teeth, including 4–6 on carapace posterior to level of orbital margin; dorsal rostral teeth generally movable but distal 1–6 teeth may lack complete basal suture; ventral margin of rostrum usually armed with 1 subdistal fixed tooth (rarely unarmed); rostral lateral carina well marked and continuous with orbital margin. Carapace with orbital margin concave; suborbital lobe poorly developed; antennal spine well developed, pterygostomian spine small.

Eye pyriform, with well developed, darkly pigmented cornea, lacking ocellus. Antennule with peduncle slightly overreaching midlength of scaphocerite; stylocerite terminating sharply, extending nearly to distal margin of basal segment of peduncle; basal segment with plumose setae and bristles on dorsodistal margin, ventromesial ridge without tooth; second segment with 3 or 4 spinules on dorsodistal margin. Antenna with scaphocerite about 0.7 as long as carapace, lateral margin nearly straight, distolateral tooth reaching distal margin of lamella; basicerite with moderately large ventrolateral distal spine extending to proximal end of outer margin of scaphocerite.

Third maxilliped with endopod overreaching scaphocerite by about half length of ultimate segment; penultimate segment slightly longer than ultimate segment; ultimate segment with several slender spinules on lateral and dorsal surfaces; exopod absent. Pereiopods slender, but not extremely elongate. First pereiopod not chelate, exceeding scaphocerite by 0.3–0.4 length of propodus; ischium not expanded ventrally, lacking spinules on ventral margin; carpus with few spinules on lateral surface; propodus shorter than carpus, with few spinules on lateral surface; dactylus minute. Second pereiopods subequal, overreaching scaphocerite by length of chela and 0.5–0.1 length of carpus; carpus composed of 10 or 11 articles; chela rather large, about half length of carpus; dactylus slightly shorter than palm, terminating in 2 unguis corresponding to simple unguis of fixed finger. Third to fifth pereiopods similar, but decreasing in length posteriorly. Third pereiopod overreaching scaphocerite by length of dactylus, propodus about 0.1 length of carpus; ischium with 2 ventral spines; merus almost as long as carapace, armed with 5–7 lateral and 4 ventral spines; carpus slightly shorter than propodus, with few minute spinules on lateral surface and 6–8 (rarely 0) slender spinules on ventral surface; dactylus about 0.2 as long as propodus, laterally compressed, not notably curved ventrally, bearing 4 or 5 accessory spinules on ventral margin. Fourth pereiopod overreaching scaphocerite by length of dactylus and 0.8 length of propodus; ischium with 2 ventral spines; merus slightly shorter than carapace, armed with 6 lateral and 4 or 5 ventral spines; carpus with 3 or 4 ventral spinules. Fifth pereiopod overreaching scaphocerite by length of dactylus and 0.4 length of propodus; ischium without ventral spine; merus about 0.7 of carapace length,

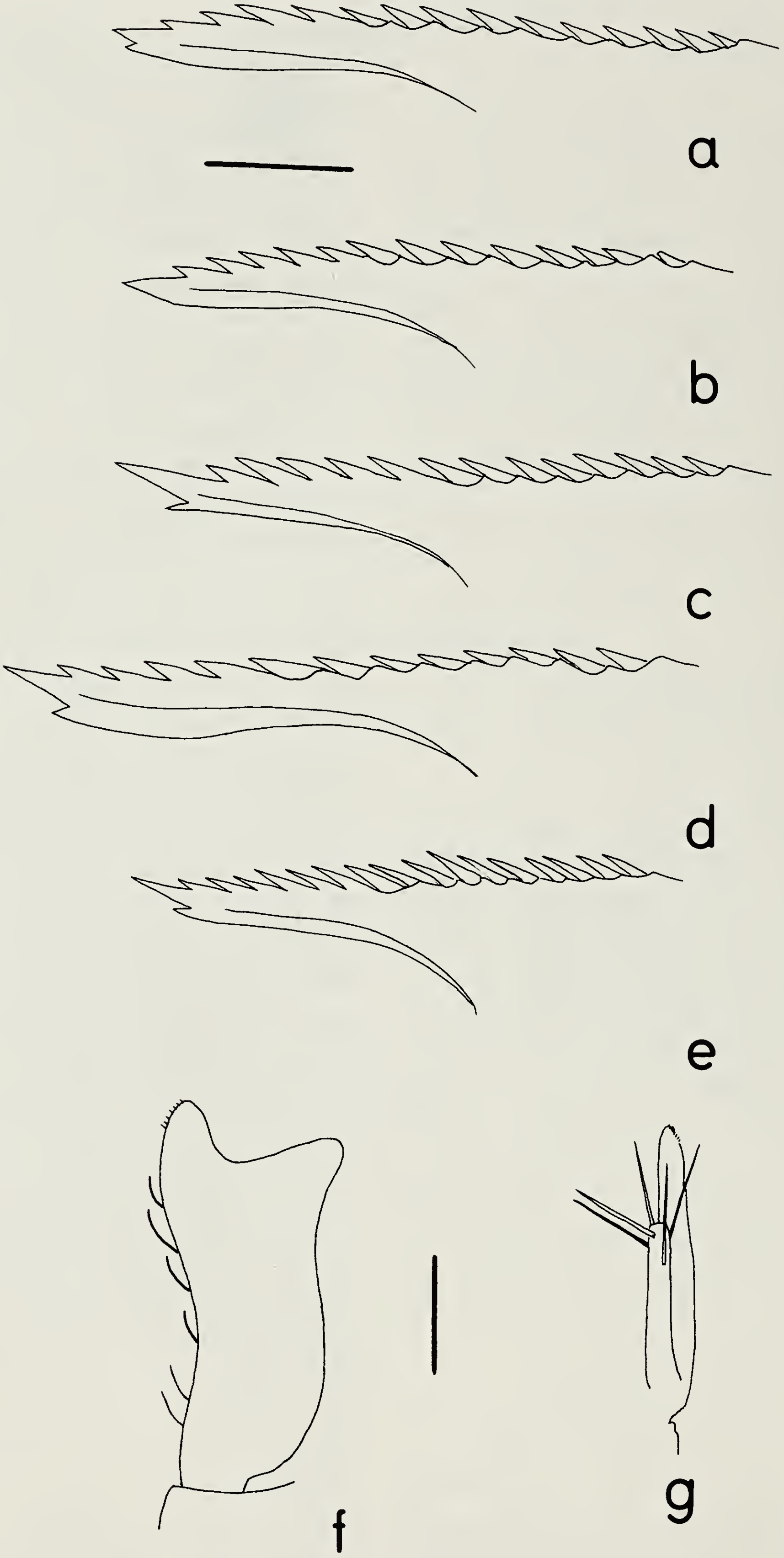

Fig. 2. *Bitias brevis* (Rathbun, 1906). a, Taiwan, TAIWAN 2000 stn CP 55, female 7.2 mm cl, NTOU 2000-55; b, Taiwan, TAIWAN 2000 stn CP 55, 6.3 mm cl, NTOU 2000-55; c, New Caledonia, BATHUS 3 stn DW 809, female 6.8 mm cl, MNHN-Na. 14969; d, New Caledonia, HALIPRO 2 stn BT 58, female 6.8 mm cl, MNHN-Na. 14970; e, Japan, KT 02-03 stn B4, female 6.0 mm cl, CBM-ZC 6469; f, g, Japan, KT 02-03 stn B4, male 5.5 mm cl, CBM-ZC 6469: a–e, lateral view of rostrum; f, endopod of first pleopod; g, appendix masculina and appendix interna of second pleopod. Scales a–d = 1 mm, f, g = 0.5 mm.

Fig. 3. *Bitias brevis* (Rathbun, 1906), Taiwan, TAIWAN 2000 stn CP 55, female 7.2 mm cl, NTOU 2000-55.

armed only with 2–4 lateral, and 0 or 1 ventral spines; carpus with 2 ventral spinules.

Strap-like epipods on third maxilliped through fourth pereiopods, and corresponding setobranchs on first to fifth pereiopods. Gill formula identical to that of *B. stocki* (see Fransen 1990: table 1).

Abdomen with third somite dorsally rounded, without posterior spine. Fourth abdominal pleuron rounded, fifth abdominal pleuron bearing distinct posteroventral denticle. Sixth somite 2.2–2.5 times as long as height, distinctly shorter than telson. Telson reaching or falling short of posterior end of uropods, armed with 6 pairs (sometimes 7 on one side) of dorsolateral spines and 2 pairs of terminal spines (inner pair shorter). Uropod with endopod slightly shorter than exopod; exopod with movable spinule just mesial to small posterolateral tooth.

Coloration (Fig. 3).—Carapace reddish except translucent rostrum. Eyes black. Antennules and antennae translucent except basal parts of latter somewhat reddish. Thoracic appendages reddish. Abdomen including tail fan translucent.

Size.—Males ranging 5.5–7.8 mm cl, and females 5.3–7.2 mm cl.

Distribution.—Indo-West Pacific; known from Madagascar, Taiwan, Japan, Hawaii and New Caledonia, at depths of 580–1500 m.

Remarks.—Crosnier & Fransen (1994) reported that *B. brevis* can be distinguished from *B. stocki* by the shape of the rostrum, and the length of the telson. The seven specimens of *B. brevis* reported here all have complete rostrum, but the telson and/or uropods are broken off in four specimens. One specimen from Taiwan (Fig. 2a), and one from New Caledonia (Fig. 2d), have the rostrum moderately deep, and with the ventral margin convex, somewhat similar to those of the holotype and allotype of *B. stocki* (Fransen 1990: fig. 1a, c; Crosnier & Fransen 1994: fig. 3c, d). The rostrum of the other specimens (Fig. 2b, c, e) are rather slender, and similar to those of the holotype of *B. brevis,* and the Madagascar specimen of this species reported by Crosnier & Fransen (1994: fig. 3a, b). The lateral carina of the rostrum is distinct in all the material reported in the present study. Moreover, the rostrum of the paratype of *B. stocki* is also rather slender (Crosnier & Fransen 1994: fig. 3e). Therefore, the shape of the rostrum can not be used to separate *B. brevis* from *B. stocki* as suggested by Crosnier & Fransen (1994).

The other distinguishing character proposed by Crosnier & Fransen (1994) is the length of the telson, being shorter than the uropods in *B. stocki,* and reaching the posterior end of the uropods in *B. brevis.* The three specimens of *B. brevis* reported herein with complete tail fan have the telson (excluding the terminal spines) falling short of the posterior end of the uropods (Fig. 1e, f). Crosnier & Fransen (1994) had only one specimen of *B. brevis* and one of *B. stocki* with a complete telson. It should be pointed out that the paratype of *B. stocki* mentioned by Crosnier & Fransen (1994) as having the telson broken, is illustrated with a complete telson in Holthuis (1993: fig. 261), and the telson does not reach the posterior end of the uropods.

Although both characters proposed by Crosnier & Fransen (1994) for separating *B. brevis* from *B. stocki* are variable, careful comparison of our specimens with the original description of *B. stocki* shows that there are still minor differences between them. The specimens of the type series of *B. stocki* have 13–18 dorsal teeth on the rostrum (Fransen 1990, but Crosnier & Fransen 1994: fig. 3c–e illustrated a maximum of 17 dorsal teeth on the rostrum), which are slightly more numerous than the 11–16 dorsal rostral teeth in *B. brevis.* The carpi of the third to fifth pereiopods bear only a few minute spinules on the lateral surfaces in our specimens, while the carpi are armed with numerous spinules in *B. stocki* (Fransen 1990: fig. 3a–c). The shape of the endopod of the male first pleopod seems to be quite different in our male specimen, and the male holotype of *B. stocki.* In our male specimen, the endopod is narrower, the distal part is distinctly bilobed with a well differentiated appendix interna, and a mesially directed rounded lobe (Fig. 2f). In the holotype of *B. stocki,* the endopod is noticeably broadened distally and not bilobed (Fransen 1990: fig. 3g). However, our male (5.5 mm cl) is considerably smaller than the holotype of *B. stocki* (7.9 mm cl), and the appendix masculina is distinctly shorter than the appendix interna (Fig. 2g), whereas the appendix masculina and the appendix interna are subequal in length in the holotype of *B. stocki* (Fransen 1990: fig. 3h). Therefore, the observed differences in the shape of the endopod of the first pleopod may merely reflect the maturity of the specimens. More material from the Atlantic is needed to determine whether or not *B. stocki* is distinct from *B. brevis.* A specimen of *B. stocki* has been reported from the Canary Island by González (1995), González & Santana (1996) and González et al. (2001). However, only a photograph of a preserved specimen probably with a broken rostrum was provided by González (1995: Foto 41), without any descriptive details. An attempt to borrow this Canary Island specimen has been unsuccessful.

As mentioned by Crosnier & Fransen (1994), it is often difficult to determine whether the small anterior, dorsal teeth on the rostrum are movable or not. In our specimens, the anterior four to six dorsal rostral teeth appear to lack a complete basal suture, and are probably fixed (Fig. 2a–e). Therefore, it is necessary to modify the key characters of *Bitias* given in Holthuis (1993: 262) to "Rostrum short, not reaching the end of antennular peduncle; dorsal teeth densely packed and more or less movable. Second pereiopods equal. Stylocerite pointed. Proximal lobe of scaphognathite truncate."

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Literature Cited

Chace, F. A., Jr. 1985. The caridean shrimps (Crustacea Decapoda) of the *Albatross* Philippines expedition, 1907–1910, part 3. Families Thalassocarididae and Pandalidae.—Smithsonian Contributions to Zoology (411):1–143.

Crosnier, A., & C. H. J. M. Fransen. 1994. Découverte de *Bitias brevis* (Rathbun, 1906) à Madagascar (Decapoda, Pandalidae).—Crustaceana 66(1): 45–52.

Fransen, C. H. J. M. 1990. *Bitias stocki,* a new genus and new species of Pandalid shrimp (Crustacea, Decapoda, Caridea) in the Eastern Atlantic Ocean.—Beaufortia 41(10):67–73.

González, J. A. 1995. Catálogo de los Crustáceos Decápodos de las Islas Canarias. Publicaciones Turquesa, Santa Cruz de Tenerife, 282 pp.

González, J. A., J. A. Quiles, V. M. Tuset, M. M. García-Díaz, & J. I. Santana. 2001. Data on the family Pandalidae around the Canary Islands, with first record of *Plesionika antigai* (Caridea).—Hydrobiologia 449:71–76.

González, J. A., & J. I. Santana. 1996. Shrimps of the family Pandalidae (Crustacea, Decapoda) off the Canary Islands, eastern central Atlantic.—South African Journal of Marine Science 17: 173–182.

Holthuis, L. B. 1993. The recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda), with an appendix on the order Amphionidacea. Nationaal Natuurhistorisch Museum, Leiden, 328 pp.

Rathbun, M. J. 1906. The Brachyura and Macrura of the Hawaiian Islands.—Bulletin of the United States Fish Commission (1903), 23(3):827–930, pls. 1–24.

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Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 12. *Amazilia bangsi* Ridgway, 1910, is an intrageneric hybrid, *Amazilia tzacatl* × *Amazilia rutila*

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Abstract.—*Amazilia bangsi* Ridgway, 1910, collected at Volcan de Miravalles, Costa Rica, is shown to be a hybrid between *Amazilia tzacatl* and *Amazilia rutila.*

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The unique type of *Amazilia bangsi* Ridgway, 1910, was collected by C. F. Underwood (1896) at Volcan de Miravalles, Costa Rica, on 7 September 1895. Early references treated *A. bangsi* as a valid species (Ridgway 1911, Cory 1918) until Simon (1921) suggested that it represents an aberrant specimen of *A. rutila.* Bangs (1930:218) later noted in a catalog of avian types in the Museum of Comparative Zoology:

> "Simon (1921, p. 106) gives it as his opinion, without, however, having seen the type, that *bangsi* is simply an example of *rutila* with an undue amount of green feathers on the sides of the breast. I do not think that this is so, but regard the type, which is unique, as a hybrid. The type in its coloring is nearly intermediate between *A. rutila* and *A. tzacatl,* both of which are common birds in the region whence it came."

Although Bangs' brief comment was insufficient to verify the taxonomic status of *A. bangsi,* subsequent authors accepted this treatment without additional comment (Peters 1945, Gray 1958, Panov 1989, Weller 1999). Here I provide a more comprehensive assessment of *A. bangsi* employing the methods and assumptions outlined in Graves (1990) and Graves & Zusi (1990), as modified by the findings of Graves (1998, 1999).

Methods

The type of *Amazilia bangsi,* originally part of the E. A. and O. Bangs Collection (No. 16682), was eventually cataloged in the Museum of Comparative Zoology, Harvard University (No. 116682). Sexed as ♂ on the Bangs Collection label, the specimen appears to be adult as judged by the absence of striations on the maxillary ramphotheca. I compared the type with all trochiline species (n = 26) that occur in the Cordillera de Guanacaste and adjacent lowlands of northwestern Costa Rica (see Underwood 1896, Carriker 1910, Slud 1964, Stiles & Skutch 1989) in the Museum of Comparative Zoology (Appendix 1). Detailed descriptions and photographs of the type were compared with series of Costa Rican species in the National Museum of Natural History, Smithsonian Institution. Descriptions in this paper refer to definitive male plumage.

Measurements of selected specimens (Table 1) were taken with digital calipers and rounded to the nearest 0.1 mm: wing chord; bill length (from anterior extension of feathers); and rectrix length (from point of insertion of the central rectrices to the tip of each rectrix). Rectrices (R1–R5) and primaries (P1–P10) are numbered from the innermost to the outermost.

General color descriptions presented in Appendix 2 were made under natural light. I evaluated the color of the lower back and abdominal plumage (3 mm lateral of the midline) with a calibrated colorimeter (CR-

Table 1.—Range (mean ± standard deviation) of measurements (mm) of wing chord, bill length, and rectrix length (R1–R5) of adult male *Amazilia tzacatl, A. rutila,* and probable hybrid, *A. tzacatl* × *A. rutila* (= type of *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

	Amazilia tzacatl[a] (*n* = 13–15)	*Amazilia rutila*[b] (*n* = 10–14)	"*Amazilia bangsi*" MCZ 116682
Wing	54.6–58.7	54.9–57.0	58.8
	(56.9 ± 1.3)	(56.2 ± 0.8)	
Bill	18.5–22.7	18.2–20.7	20.7
	(20.4 ± 1.2)	(19.3 ± 0.8)	
R1	30.7–32.9	30.4–34.0	32.1
	(31.8 ± 0.7)	(31.9 ± 1.3)	
R2	32.3–35.1	32.1–35.9	34.2
	(33.8 ± 0.7)	(33.8 ± 1.3)	
R3	33.3–35.7	33.2–36.9	35.7
	(34.6 ± 0.6)	(34.9 ± 1.2)	
R4	33.1–36.2	33.1–37.2	36.7
	(35.0 ± 0.8)	(35.3 ± 1.4)	
R5	32.4–35.9	32.7–36.4	35.7
	(34.5 ± 1.1)	(34.7 ± 1.3)	

[a] Costa Rica.

[b] Costa Rica (*n* = 8), Honduras (*n* = 6).

221 Chroma Meter, Minolta Corporation) equipped with a 3.0 mm aperture (Table 2). The measuring head of the CR-221 uses 45° circumferential illumination. Light from the pulsed xenon arc lamp is projected onto the specimen surface by optical fibers arranged in a circle around the measurement axis to provide diffuse, even lighting over the measuring area. Only light reflected perpendicularly from the specimen surface is collected for color analysis. To reduce measurement variation, I held the aperture flush with the plumage without depressing the surface. The default setting for the CR-221 Chroma Meter displays mean values derived from three sequential, in situ measurements. I repeated this procedure twice (five times for the type of *A. bangsi*), removing the aperture between trials. Thus, each datum summarized in Table 2 represents the mean of 6 (parental species) or 15 (type of *A. bangsi*) independent colorimetric measurements.

Colorimetric characters are described in terms of opponent-color coordinates (*L, a, b*) as per Hunter & Harold (1987). This system is based on the hypothesis that signals from the cone receptors in the human eye are coded by the brain as light-dark (*L*), green-red (+*a*/−*a*), and blue-yellow (+*b*/−*b*). The rationale is that a color cannot be perceived as red and green or as yellow and blue at the

Table 2.—Minima, maxima, and means (± standard deviation) of opponent color coordinates (*L, a, b*) of rectrix 1 (R1) of adult male *Amazilia tzacatl, A. rutila,* and probable hybrid, *A. tzacatl* × *A. rutila* (= type of *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

		Amazilia tzacatl (*n* = 15)			*Amazilia rutila* (*n* = 8)			"*Amazilia bangsi*" MCZ 116682
		Min.	Max.	Mean (± SD)	Min.	Max.	Mean (± SD)	
Back	*L*	28.7	35.4	32.9 (± 1.7)	32.8	37.4	35.5 (± 1.6)	35.0
	a	−10.3	1.1	−3.4 (± 3.1)	−3.0	1.0	−1.0 (± 1.5)	1.9
	b	16.7	29.5	23.8 (± 3.9)	14.7	21.5	18.1 (± 2.3)	24.7
Abdomen	*L*	35.3	47.7	40.6 (± 3.0)	42.5	49.1	46.8 (± 2.3)	42.6
	a	−1.2	3.0	1.3 (± 1.5)	5.0	14.6	10.4 (± 2.7)	10.5
	b	7.7	18.5	12.3 (± 3.1)	16.5	28.3	24.4 (± 3.5)	23.1

same time. Therefore "redness" and "greenness" can be expressed as a single value *a,* which is coded as positive if the color is red and negative if the color is green. Likewise, "yellowness" or "blueness" is expressed by $+b$ for yellows and $-b$ for blues. The third coordinate, *L,* ranging from 0 to 100, describes the "lightness" of color; low values are dark, high values are light. The more light reflected from the plumage, the higher the *L* value will be. Visual systems in hummingbirds (e.g., Goldsmith & Goldsmith 1979) differ significantly from those of humans, and the relevance of opponent color coordinates to colors perceived by hummingbirds is unknown. In any case, the *L,a,b* color system permits plumage color to be unambiguously characterized for taxonomic purposes.

Results and Discussion

I considered three hypotheses proposed by previous authors: *Amazilia bangsi* represents (1) a subdefinitive plumage, color morph, or geographic variant of *Amazilia rutila* or some other species (Simon 1921); (2) a hybrid, *Amazilia tzacatl* × *Amazilia rutila* (Bangs 1930); or (3) a valid species (Ridgway 1910). For brevity I use the epithet, *bangsi,* in the remainder of the paper.

Populations of *Amazilia tzacatl* and *A. rutila* from northwestern Costa Rica are adequately represented in museum collections (Carriker 1910). I found no evidence that *bangsi* represented a subdefinitive plumage, color morph, or geographic variant of either of these species or any other taxon. Rather, all evidence suggests that *bangsi* represents an intrageneric hybrid.

The hybrid diagnosis focuses on the identification of apomorphic character states in putative hybrids (Graves 1990). However, complete dominance and polygenic inheritance of plumage characters may preclude or obscure the expression of parental apomorphies in hybrids. When parental apomorphies are not identifiable, the parentage of a hybrid may be indicated, although less conclusively, by the presence or absence of a suite of plesiomorphic characters. Plumage and soft-part characters of *bangsi* that facilitated the identification of its parental species include: (a) ventral plumage from chin to undertail coverts predominately cinnamon-buff (Fig. 1); (b) feathers along the sides of the throat and breast spangled with dull pale green subterminal spots; (c) rectrices (R1–R5) dark rufous tipped with bronze; (d) mandibular ramphotheca predominately yellowish-brown (probably reddish-orange or red in life); and (e) shallowly forked tail (fork depth = 5.6 mm). Perhaps as informative, *bangsi* lacks several conspicuous traits that are present in some potential parental species (Appendix 1): (a) contrasting rump band; (b) brilliant frontlet or coronal patch; (c) brilliant gorget; (d) pronounced blue or violet iridescence on body plumage; (e) white spots on rectrices; and (f) thickened rachises of primaries (P8–P10).

The combination of plumage characters observed in *bangsi* can be derived from only a single pair of species—*A. tzacatl* × *A. rutila* (see Appendix 2 for comparative description of plumages). Other pairwise combinations of species can be eliminated from consideration because they either lack characters found in *bangsi,* or possess one or more distinctive characters that are not expressed, even subtly, in *bangsi.* Colorimetric values largely corroborate the visual impression that plumage color of *bangsi* is intermediate between that of the postulated parental species (Table 2, Fig. 2).

I tested the parental hypothesis by examining size and external proportions (Table 1). Measurements of trochiline hybrids invariably fall within the mensural ranges exhibited by their parental species as a consequence of a polygenic mode of inheritance (Banks & Johnson 1961; Graves 1990, 1996). *Amazilia tzacatl* and *A. rutila* are very similar in size and the percent difference in character means is negligible (larger species divided by smaller): wing chord (1.2%), bill length (5.7%), R1

Fig. 1. Lateral views of adult males: *Amazilia tzacatl* (top), *A. rutila* (bottom), and probable hybrid (middle), *A. tzacatl* × *A. rutila* (= type of *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

(0.3%), R2 (0.0%), R3 (0.9%), R4 (0.9%), and R5 (0.6%). Measurements of *bangsi* fall within the cumulative range of parental measurements for six of the seven measurements (the wing chord of *bangsi* was 0.1 mm longer than the largest value recorded for that character in the parental species). There have been no well-documented cases of morphological luxuriance (where the size of hybrid offspring exceeds that of the parental species) among avian hybrids (Graves 1990, 1996). I suspect that the cumulative range of measurements for wing chord in the parental species would overlap the hybrid value if the sample size was increased. Had the measurements of *bangsi* occurred well outside (e.g., >3% larger) the range of those of *A. tzacatl* and *A. rutila,* this particular hybrid hypothesis would have been rejected.

In summary, concordance of results from analyses of plumage color and external measurements provides strong support for the hypothesis that *bangsi* is an intrageneric hybrid between *A. tzacatl* and *A. rutila. Amazilia bangsi* Ridgway, 1910, is thus available in taxonomy only for the purposes of homonymy. The parental species are sympatric from the Yucatan Peninsula (Howell & Webb 1995) south to northwestern Costa Rica, particularly in the transition zone between dry thorn forest and semi-humid forest (Underwood 1896, Carriker 1910, Slud 1964, Stiles & Skutch 1989).

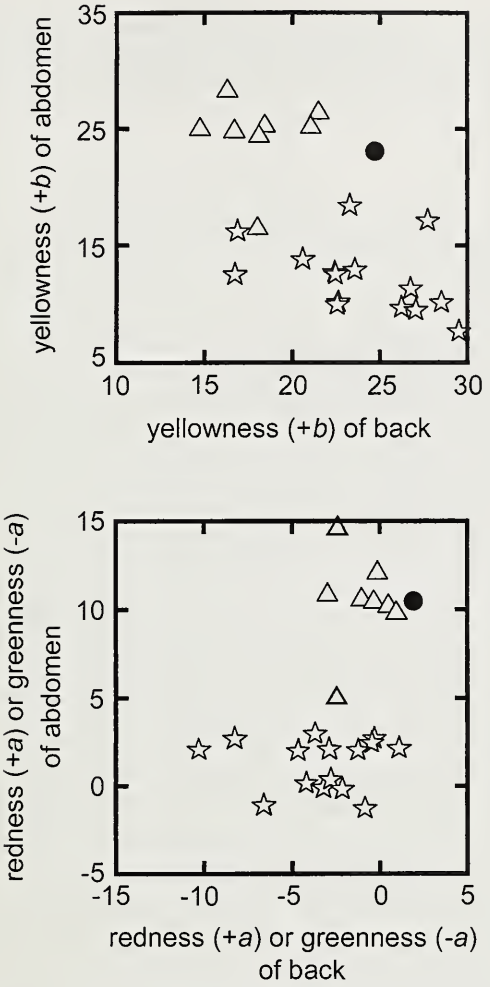

Fig. 2. Bivariate relationships of *L, a, b* color coordinates: *Amazilia tzacatl* (☆), *A. rutila* (△), and probable hybrid (●), *A. tzacatl* × *A. rutila* (= type of *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

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Literature Cited

Bangs, O. 1930. Types of birds now in the Museum of Comparative Zoology.—Bulletin of the Museum of Comparative Zoology 70:145–426.

Banks, R. C., & N. K. Johnson. 1961. A review of North American hybrid hummingbirds.—Condor 63:3–28.

Carriker, M. A., Jr. 1910. An annotated list of the birds of Costa Rica including Cocos Island.—Annals of the Carnegie Museum 6:314–915.

Cory, C. B. 1918. Catalogue of birds of the Americas. Part 2, No. 1.—Field Museum of Natural History Zoological Series 13:1–315.

Goldsmith, T. H., & K. M. Goldsmith. 1979. Discrimination of colors by the black-chinned hummingbird, *Archilochus alexandri.*—Journal of Comparative Physiology A 130:209–220.

Graves, G. R. 1990. Systematics of the "green-throated sunangels" (Aves: Trochilidae): valid taxa or hybrids?—Proceedings of the Biological Society of Washington 103:6–25.

———. 1996. Hybrid wood warblers, *Dendroica striata* × *Dendroica castanea* (Aves: Fringillidae: Tribe Parulini) and the diagnostic predictability of avian hybrid phenotypes.—Proceedings of the Biological Society of Washington 109:373–390.

———. 1998. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 6. An intergeneric hybrid, *Aglaiocercus kingi* × *Metallura tyrianthina,* from Venezuela.—Proceedings of the Biological Society of Washington 111:511–520.

———. 1999. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 8. A provisional hypothesis for the hybrid origin of *Zodalia glyceria* (Gould, 1858).—Proceedings of the Biological Society of Washington 112:491–502.

———, & R. L. Zusi. 1990. An intergeneric hybrid hummingbird (*Heliodoxa leadbeateri* × *Heliangelus amethysticollis*) from northern Colombia.—Condor 92:754–760.

Gray, A. P. 1958. Bird hybrids. Commonwealth Agricultural Bureaux, Bucks, England, 390 pp.

Howell, S. N. G., & S. Webb. 1995. The birds of Mexico and northern Central America. Oxford University Press, Oxford, UK, 851 pp.

Hunter, R. S., & R. W. Harold. 1987. The measurement of appearance, 2nd edition. Wiley, New York, 411 pp.

Panov, E. N. 1989. Natural hybridisation and ethological isolation in birds (in Russian). Nauka, Moscow, 510 pp.

Peters, J. 1945. Check-list of birds of the world, vol. 5. Museum of Comparative Zoology, Cambridge, Massachusetts, 306 pp.

Ridgway, R. 1910. Diagnosis of new forms of Micropodidae and Trochilidae.—Proceedings of the Biological Society of Washington 23:53–55.

Ridgway, R. 1911. Birds of North and Middle America.—Bulletin of the United States National Museum 50, part 5.

Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.

Simon, E. 1921. Histoire naturelle des Trochilidae (synopsis et catalogue). Encyclopedia Roret, L. Mulo, Paris.

Slud, P. 1964. The birds of Costa Rica.—Bulletin of the American Museum of Natural History 128: 1–430.

Stiles, F. G., & A. F. Skutch. 1989. A guide to the birds of Costa Rica. Christopher Helm, London, 511 pp.

Underwood, C. F. 1896. A list of birds collected on the lower, southern, and southwestern slopes of the Volcano of Miravalles and on the lower lands extending to Bagaces in Costa Rica, with a few observations on their habits.—Ibis (seventh series) 8:431–451.

Weller, A.-A. 1999. Rufous-tailed Hummingbird, *Amazilia tzacatl*. P. 595 *in* J. del Hoyo, A. Elliott, & J. Sargatal, eds., Handbook of the birds of the world, vol. 5. Barn-owls to hummingbirds. Lynx Edicions, Barcelona, 759 pp.

Appendix 1

Species of trochiline hummingbirds that occur regularly in the Cordillera de Guanacaste and adjacent lowlands of northwestern Costa Rica (see Underwood 1896, Carriker 1910, Slud 1964, Stiles & Skutch 1989). Taxonomy follows Sibley & Monroe (1990). Parentheses enclose a representative list of characters or traits that would probably be expressed in hybrid progeny of these species, but that do not occur in the type of *Amazilia bangsi* Ridgway, 1910 (MCZ 116682): *Phaeochroa cuvierii* (white spots on R4–R5; thickened rachises of P8–P10); *Campylopterus hemileucurus* (purple head and breast; white spots on R3–R5; thickened rachises of P8–P10); *Florisuga mellivora* (blue head and breast; white collar; R1–R5 white with black tips); *Colibri delphinae* (violet auricular patch); *Anthracothorax prevostii* (black throat; purple rectrices); *Klais guimeti* (violet crown and throat; white tips on R2–R5); *Lophornis helenae* (elongated black head plumes; white rump band); *Chlorostilbon canivetii* (black tail); *Thalurania colombica* (purplish-black rectrices; violet crown, lower breast, flanks, and abdomen); *Panterpe insignis* (brilliant coppery-orange throat; blue crown; bluish-black rectrices); *Hylocharis eliciae* (golden-green tail; blue throat); *Amazilia amabilis* (bluish-violet upper breast; black rectrices); *Amazilia saucerrottei* (steel-blue tail); *Amazilia cyanura* (blackish-violet rectrices); *Amazilia rutila; Amazilia tzacatl; Eupherusa eximia* (white medial vanes of R2–R5); *Elvira cupreiceps* (R2–R5 white); *Microchera albocoronata* (white crown; white vanes on R2–R5; deep maroon body plumage); *Chalybura urochrysia* (bronzy-black rectrices; pale feet in dried skin); *Lampornis castaneoventris* (brilliant green crown; purple gorget; bluish-black rectrices); *Heliodoxa jacula* (brilliant green crown; small blue gorget spot; bluish-black rectrices); *Heliothryx barroti* (R3–R5 white; violet crown; white ventral plumage); *Heliomaster constantii* (red gorget; white facial stripe; white tips on R3–R5); *Heliomaster longirostris* (reddish-violet gorget; white facial stripe; brilliant bluish-green crown; white tips on R4–R5); *Philodice bryantae* (purple gorget; white pectoral band; white flank tufts).

Appendix 2

Abridged description of adult male *Amazilia tzacatl, A. rutila,* and a probable hybrid, *A. tzacatl* × *A. rutila* (= *Amazilia bangsi* Ridgway, 1910; MCZ 116682).

The forecrown and crown of *tzacatl* are dark bronze becoming dark green on the hind neck, lesser and median wing coverts, and back, changing to bronzy-green or bronze on the upper tail coverts. The dorsum of *rutila* is similar in color but slightly paler and less iridescent (particularly on the lower back and rump) owing to narrow buffy feather margins. The color and quality of iridescence of the dorsum in *bangsi* are intermediate to those of *tzacatl* and *rutila.* The rectrices (R1–R5) of *tzacatl, rutila,* and *bangsi* share a similar color pattern. Rectrices are chestnut broadly tipped with bronze in *rutila,* slightly darker in *tzacatl.* The rectrices of *bangsi* are intermediate in appearance between those of *rutila* and *tzacatl.* Likewise, the greater wing coverts, secondaries, and primaries of *bangsi* are intermediate in appearance between those of the postulated parental species. Underwing coverts are dark glossy green in *tzacatl,* dull green broadly tipped with buff or rufous in *rutila,* and intermediate in appearance in *bangsi.* Primaries and secondaries of *tzacatl, rutila,* and *bangsi* lack rufous or chestnut pigmentation. Rachises of *tzacatl, rutila,* and *bangsi* are unmodified.

The chin, throat, breast, and flanks of *tzacatl* are dark green (the throat and upper breast are glowing golden-green when viewed head-on). Grayish feather margins on the abdomen become progressively wider from the sides to the ventral midline; the center of the abdomen is buffy-gray. Undertail coverts are chestnut or dark rufous. The ventral plumage of *rutila* from chin to undertail coverts is buffy-cinnamon, palest on the throat (feathers with narrow buffy margins in many individuals). Ventrally, *bangsi* is most similar to *rutila* but shows the influence of a "green breasted" parental species, particularly along the sides of the throat and upper breast where feathers have dull, pale green, subterminal disks which are broadly margined with buff. Feather of the chin and upper throat of *bangsi* are cinnamon-buff margined with very pale buff. Scattered feathers across the center of the lower throat have small greenish-bronze subterminal disks. The midline of the abdomen of *bangsi* is cinnamomeous as in *rutila* but duller with grayish tones. Undertail coverts of *bangsi* are intermediate in color but closer to *rutila* than to *tzacatl.* The maxillary and mandibular ramphotheca of *tzacatl, rutila,* and *bangsi* are pale yellowish-brown (red in life) tipped with dark brown or blackish-brown (20–30% of the bill length).

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A new small-eared shrew of the *Cryptotis nigrescens*-group from Colombia (Mammalia: Soricomorpha: Soricidae)

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Abstract.—*Cryptotis colombiana* Woodman & Timm, 1993 previously was known from few specimens from two isolated regions in the Cordillera Central and Cordillera Oriental of Colombia. Recent collecting in the northern Cordillera Central and review of older collections from the central Cordillera Oriental in the vicinity of Bogotá yielded additional specimens that permit reevaluation of the two geographic populations of these small-eared shrews. Morphological and morphometrical studies indicate that the population inhabiting the Cordillera Oriental represents a distinct, previously unrecognized species that I describe herein as *Cryptotis brachyonyx.* Study of 54 specimens of shrews from the Cordillera Oriental in systematic collections in North America, South America, and Europe yielded only four specimens of the new species, all collected before 1926. The paucity of modern specimens suggests that *C. brachyonyx* may be extremely restricted in distribution, or possibly extinct.

Small-eared shrews of the genus *Cryptotis* occur from eastern North America south through Central America to the Andes Mountains of South America. Recent systematic studies on these shrews generally partition the species among four informal, groupings originally defined by Choate (1970) and modified by Woodman & Timm (1993, 1999, 2000). Only two of these groups have members that occur in South America. The *C. nigrescens*-group is primarily a Central American group, but with two species occurring in South America: *Cryptotis mera,* along the Panama/Colombia border (Woodman & Timm 1993), and *Cryptotis colombiana,* reported from the Cordillera Central and Cordillera Oriental of Colombia (Woodman 1996). The *C. thomasi*-group is comprised entirely of Andean species. The *C. nigrescens*-group and the *C. thomasi*-group can be distinguished using a combination of external, cranial, and postcranial characters. Two of the more reliable external characters are the relative size of the forefeet and length of the foreclaws: members of the *C. thomasi*-group tend to have large forepaws with notably elongate foreclaws, whereas species in the *C. nigrescens*-group have smaller forefeet and foreclaws.

Cryptotis colombiana Woodman & Timm, 1993 originally was described from a single specimen collected in 1950 from Río Negrito on the Cordillera Central of Colombia and now housed in the Field Museum, Chicago. A second specimen, collected in 1925 from San Juán de Ríoseco on the Cordillera Oriental of Colombia, subsequently was identified in the collection of the American Museum of Natural History, New York. At that time, I (Woodman 1996) noted differences between the two specimens, but indicated that the taxonomic significance of this variation was difficult to interpret based on only two specimens. Field work during the past few years in the Cordillera Central by Colombian colleagues has added a number of important new specimens of *C. colombiana* that permit more comprehensive evaluation of the characteristics of this species (Woodman et al. 2003). However, its presence in the Cordillera Oriental has continued to be based on the single American Museum specimen. Recently, I studied available collections of Colombian shrews from the Cordillera Oriental, among them a series of ten specimens in The Natural History Museum, London, and the National Museum of Natural History, Washington, that were collected from April to November 1895 at or near La Selva. These specimens include at least five of the individuals Merriam (1897) used when he described *C. thomasi,* the first valid species of shrew identified from South America. The pelage of each of the skins is faded, and most are irregularly and somewhat overly stuffed, obscuring external differences. However, among the ten are three specimens that possess small forepaws, short claws, and distinctive cranial features that mark them as members of the *C. nigrescens*-group, rather than *C. thomasi.* This conclusion is supported by morphological and morphometrical characters of the skull. Additional morphological and morphometrical analyses of the four specimens from the Cordillera Oriental show them to be distinct from the population of *C. colombiana* on the Cordillera Central. Herein, I describe the population from the Cordillera Oriental as a new species and report on variation within and between the two species based on the available specimens from the two Colombian cordilleras.

Materials and Methods

Regional names, place names, and map coordinates derive from original collector tags, field notes, and field catalogs supplemented with additions, corrections, and alternative readings based on my review of published localities, maps, and gazetteers of Colombia (Paynter & Traylor 1981, USBGN 1988). Capitalized lifezone names follow Espinal and Montenegro (1963) and IGAC (1988). The species synonomy lists only the first use of published names.

Information from personal correspondence is based on my inspection of original letters from George O. Child to Oldfield Thomas [# Df 232/1/55–56] and photocopies of correspondence from Clinton Hart Merriam to Thomas [# Df 232/1/252–257] in the Official Archives of The Natural History Museum, London, and from microfilm of correspondence from Thomas to Merriam in The Bancroft Library, University of California, Berkeley [BANC Film 1958].

Terminology of dentition and dental characteristics follows Choate (1970). Capitalized color names for pelage hues are from Ridgway (1912). Pelage coloration was determined only from museum specimens. All four specimens of the new species were collected more than 80 years ago, and their pelages are faded and do not accurately represent those of live or newly-captured specimens.

Measurements used in my analyses follow Woodman & Timm (1993, 1999) and are in mm, weights in g. Abbreviations are explained in Table 1. External measurements were recorded from skin tags or original field notes, except for head-and-body length, which was calculated by subtracting length of tail from total length. Measurements of the skull were taken to the nearest 0.1 mm using either an ocular micrometer in a binocular microscope or a hand-held dial caliper (for CBL and CB). Univariate statistics include mean ± *SD* and total range. Ratios of measurements were multiplied by 100 to calculate percentages (Table 2). In describing species of *Cryptotis,* I compare them primarily with other members of the genus, unless stated otherwise. Comparative terms used for measurements and ratios reflect this context. A feature of "moderate" length or width is one whose mean value for the species falls within the range of plus or minus one standard deviation (*SD*) of the mean value for the genus. A "long" or "wide" feature is one greater than the mean plus one *SD*; a "short" or "narrow" feature is less than the mean minus one *SD*.

Principal components analysis (PCA) of a correlation matrix of 16 log-transformed craniomandibular variables (ZP, IO, M2B, PL, TR, UTR, MTR, M1W, ML, HCP, HCV, HAC, AC3, TRM, Lm1, BAC—Table 3) was used to investigate relationships in overall shape of the skull among 6 *C. colombiana* from the Cordillera Central, 6 *C. mera,* 32 *C. thomasi,* and 4 individuals of the new species. I carried out a second PCA to determine morphometrical relationships between just *C. colombiana* and the new species using a correlation matrix of 8 log-transformed cranial variables (ZP, IO, U3B, PL, TR, UTR, MTR, M1W—Table 4). Values of the variable M2B do not overlap between the two species (Table 1), and it was excluded from the second PCA to determine whether the two samples would continue to be separated using combinations of other variables.

In my investigations of *Cryptotis,* I operate under a systematic framework for the genus outlined previously (Woodman 2002). My comprehension of the biological species is under the philosophical influence of the evolutionary species concept as redefined by Wiley (1978) and characterized by Wiley & Mayden (2000). In application, a species represents the largest monophyletic entity whose constituent parts interact, that maintains its own identity, and that has an independent evolutionary trajectory (Frost & Hillis 1990). In practice, I use unique distributional patterns of morphological characters among populations to distinguish individual, presumably genetically-cohesive groups from other genetically-cohesive groups. This application provides testable hypotheses for additional studies.

Specimens from the following institutions were used in this study: American Museum of Natural History, New York (AMNH); Natural History Museum [formerly British Museum (Natural History)], London (BM); Field Museum, Chicago (FMNH); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN); University of Kansas Natural History Museum, Lawrence (KU); Museum of Comparative Zoology, Cambridge (MCZ); Museo de la Universidad de Antioquia, Medellín (MUA); Royal Ontario Museum, Toronto (ROM); National Museum of Natural History, Washington (USNM).

Systematic Biology

Cryptotis brachyonyx, new species
Figs. 1A, 1B, 2, 4A, 5A, 6A

Blarina thomasi Merriam, 1897:227 (in part).

[*Blarina* (*Cryptotis*)] *thomasi*: Trouessart, 1904:138 (in part; name combination).

Cryptotis thomasi: O. Thomas, 1921:354 (in part; name combination).

Cryptotis avia: Tate, 1932:226 (in part; not *Cryptotis avia* G. M. Allen, 1923).

Cryptotis thomasi thomasi: Cabrera, 1958: 48 (in part; name combination).

Cryptotis colombiana: Woodman, 1996:417 (in part; not *Cryptotis colombiana* Woodman & Timm, 1993).

Holotype.—Dried skin (Fig. 1) and skull (Fig. 2) of adult male, BM number 99.10.3.2, collected by an unnamed worker for George O. Child of Bogotá, Colombia, on 19 October 1895; purchased from G. O. Child and presented to the British Museum (Natural History) by Oldfield Thomas. Skin in fair to good condition: all fur present, faded; 2 small holes near right cheek; left hind foot sewn on; other feet loosely attached. Skull in good condition: slight damage to orbital areas; small crack running dorsally from foramen magnum; mandibles separate; both angular processes intact. Of standard external field measurements, only length of hind foot (= 12 mm) was recorded on the skin tag, and this measurement probably was taken from the dried skin.

Type locality.—COLOMBIA: *Department of Cundinamarca*: "La Selva, near Bogotá." La Selva was the name of George O. Child's estate on the Plains of Bogotá, the altitude of which he estimated as approximately 8900 feet (G. O. Child, in litt.

Table 1.—Measurements of selected *Cryptotis* from Colombia. Statistics are mean ± *SD*, and range. Measurements follow Woodman & Timm (1993).

	C. mera	*C. colombiana*	*C. brachyonyx*	*C. thomasi*
External measurements:				
	n = 7	*n* = 4	*n* = 0	*n* = 12
Head-and-body length (HB)				
	69 ± 2	65 ± 7	—	87 ± 6
	66–73	60–76		74–96
Tail length (TL)				
	27 ± 2	30 ± 3	—	24 ± 2
	24–31	27–34		20–27
Skull measurements:				
	n = 6[a]	*n* = 6[a]	*n* = 4[a]	*n* = 17[a]
Condylobasal length (CBL)				
	18.3 ± 0.4	19.6 ± 0.3	20.4 ± 0.1	21.7 ± 0.5
	17.7–18.7	19.4–20.1	20.3–20.4	20.7–22.6
	(*n* = 5)		(*n* = 3)	
Cranial breadth (CB)				
	9.4 ± 0.3	9.7 ± 0.4	9.7	10.5 ± 0.2
	9.1–9.8	9.2–10.0		10.2–10.9
			(*n* = 1)	(*n* = 13)
Breath of zygomatic plate (ZP)				
	2.0 ± 0.1	2.0 ± 0.1	1.9 ± 0.1	2.0 ± 0.2
	1.9–2.2	1.8–2.1	1.7–2.0	1.7–2.4
Interorbital breadth (IO)				
	4.5 ± 0.2	4.8 ± 0.1	4.9 ± 0.2	5.0 ± 0.2
	4.3–4.7	4.7–4.9	4.6–5.0	4.6–5.2
Breadth across first unicuspids (U1B)				
	2.5 ± 0.1	2.7 ± 0.05	2.6 ± 0.1	2.7 ± 0.1
	2.4–2.6	2.6–2.7	2.5–2.6	2.6–2.9
			(*n* = 3)	
Breadth across third unicuspids (U3B)				
	2.9 ± 0.1	3.1 ± 0.1	3.0 ± 0.05	3.1 ± 0.1
	2.7–3.0	2.9–3.2	2.9–3.0	2.9–3.2
Breadth across second molars (M2B)				
	5.6 ± 0.1	6.2 ± 0.2	5.8 ± 0.1	6.2 ± 0.2
	5.5–5.8	6.0–6.4	5.7–5.9	5.8–6.5
Palatal length (PL)				
	7.8 ± 0.1	8.7 ± 0.3	8.6 ± 0.2	9.4 ± 0.2
	7.6–7.8	8.1–9.0	8.3–8.8	8.8–9.8
Length of upper toothrow (TR)				
	7.1 ± 0.1	7.6 ± 0.2	7.6 ± 0.3	8.2 ± 0.3
	6.9–7.2	7.3–7.8	7.3–7.9	7.7–8.7
Length of unicuspid toothrow (UTR)				
	2.4 ± 0.1	2.5 ± 0.1	2.5 ± 0.1	2.8 ± 0.2
	2.3–2.5	2.4–2.6	2.4–2.5	2.4–3.0
Length of molariform toothrow (MTR)				
	5.1 ± 0.1	5.5 ± 0.2	5.5 ± 0.2	5.8 ± 0.1
	5.1–5.2	5.3–5.8	5.3–5.7	5.5–6.0

Table 1.—Continued.

C. mera	*C. colombiana*	*C. brachyonyx*	*C. thomasi*
Posterior width of first upper molar (M1W)			
1.8 ± 0.05	2.0 ± 0.1	1.8 ± 0.5	1.9 ± 0.1
1.8–1.9	1.9–2.0	1.8–1.9	1.8–2.1
Length of mandible (ML)			
5.9 ± 0.4	6.7 ± 0.2	6.8 ± 0.3	7.0 ± 0.2
5.2–6.2	6.3–7.0	6.4–7.0	6.6–7.4
Height of coronoid process (HCP)			
4.5 ± 0.1	4.6 ± 0.2	4.6 ± 0.1	4.7 ± 0.1
4.3–4.6	4.3–4.7	4.5–4.7	4.5–4.9
Height of coronoid valley (HCV)			
2.7 ± 0.1	2.8 ± 0.2	2.8 ± 0.05	3.1 ± 0.1
2.6–2.8	2.5–3.0	2.8–2.9	2.9–3.3
Height of articular condyle (HAC)			
3.8 ± 0.1	3.8 ± 0.2	3.9 ± 0.1	4.3 ± 0.1
3.6–3.8	3.6–4.2	3.8–4.1	4.1–4.6
Breadth of articular condyle (BAC)			
3.0 ± 0.1	3.2 ± 0.2	3.1 ± 0.2	3.6 ± 0.2
2.9–3.1	3.0–3.4	3.0–3.4	3.4–4.1
Articular condyle to m3 (AC3)			
4.4 ± 0.1	4.9 ± 0.1	5.0 ± 0.1	5.7 ± 0.3
4.3–4.6	4.6–5.0	4.9–5.1	5.0–6.0
Length of lower toothrow (TRM)			
5.5 ± 0.1	5.9 ± 0.2	6.0 ± 0.2	6.4 ± 0.2
5.4–5.7	5.6–6.3	5.7–6.2	6.1–6.7
Length of lower toothrow (M13)			
4.3 ± 0.1	4.6 ± 0.1	4.5 ± 0.1	4.7 ± 0.2
4.1–4.4	4.5–4.8	4.3–4.5	4.2–5.1
	(*n* = 4)		(*n* = 17)
Length of first lower molar (Lm1)			
1.8 ± 0.1	1.9 ± 0.1	1.8 ± 0.1	1.9 ± 0.1
1.7–1.8	1.8–1.9	1.7–1.8	1.7–2.0
Weight (g):			
—	—	—	10, 10
			(*n* = 2)

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[a] Except as noted.

13 July 1895). Merriam (1897) gave the elevation of La Selva as 9000 ft. This slightly higher elevation probably was based on information in a letter to him from Thomas (quoted below).

Paratypes (2).—COLOMBIA: *Cundinamarca*: Plains of Bogotá (USNM 80905; "topotype" [of *C. thomasi*] written on tag); La Selva, near Bogotá (BMNH 99.10.3.3).

Referred specimen (1).—COLOMBIA: *Cundinamarca*: San Juan de Ríoseco (AMNH 70597).

Etymology.—Greek: *brachys* (short) + *onyx* (claw), hence "short claw;" a noun in apposition.

Distribution.—Presumably Premontane Moist Forest, Premontane Wet Forest, Lower Montane Moist Forest, Montane Moist

Table 2.—Characters of selected Colombian *Cryptotis*.

	C. mera (*n* = 7)[a]	*C. colombiana* (*n* = 7)[a]	*C. brachyonyx* (*n* = 4)	*C. thomasi* (*n* = 39)[a]
Foramen of sinus canal present				
	0%	0%	0%	8% (minute)
		(*n* = 5)		(*n* = 38)
Foramen dorsal to dorsal articular facet present				
	71% two	43% two	25% two	3% two
	14% one	14% one	50% one	15% one
	14% none	43% none	25% none	82% none
Two dorsal foramina present				
	71%	86%	100%	79%
Petromastoid foramen present one or both petromastoids				
	14% (med–lg)	100%	100%	100%
		(*n* = 5)		(*n* = 35)
Postero-lingual cuspules on cingulae of U1–3				
	17% absent			16% absent
	83% minute		100% minute	62% minute
		100% obvious		22% obvious
	(*n* = 6)	(*n* = 4)		(*n* = 32)
Size of U4 (% of U3)				
	54 ± 10.0%	42 ± 13%	40 ± 7%	48 ± 9%
	40–66	32–61	31–48	22–64
	(*n* = 6)	(*n* = 5)		(*n* = 35)
Emargination of posterior borders of P4, M1				
	v. slight to slight	v. slight to slight	v. slight to slight	v. slight to mod. deep
Complexity of M3				
	100% simple	86% simple		50% simple
		14% complex	100% complex	50% complex
				(*n* = 28)
Lower sigmoid notch				
	v. shallow to shallow	shallow	v. shallow to mod. deep	v. shallow to mod. deep
Entoconid of m3 present				
				11% obvious
	29% minute		100% minute	32% minute
	71% absent	100% absent		57% absent
				(*n* = 28)
Mensural characters:				
	n = 6[a]	*n* = 6[a]	*n* = 4[a]	*n* = 17[a]
Relative tail length (TL/HB × 100)				
	39 ± 4	47 ± 9	—	28 ± 3
	34–46	36–57		21–36
	(*n* = 7)	(*n* = 4)		(*n* = 22)
Relative length of rostrum (PL/CBL × 100)				
	42.2 ± 1.1	43.8 ± 1.5	42.9 ± 0.6	43.2 ± 0.5
	41.3–44.1)	41.8–46.2	42.2–43.4	42.4–44.0
	(*n* = 5)		(*n* = 3)	
Relative breadth of zygomatic plate (ZP/PL × 100)				
	26.0 ± 1.3	22.7 ± 0.8	21.7 ± 1.1	21.2 ± 1.5
	24.7–28.2	22.1–24.1	20.5–23.3	18.7–24.7

Table 2.—Continued.

C. mera (*n* = 7)[a]	*C. colombiana* (*n* = 7)[a]	*C. brachyonyx* (*n* = 4)	*C. thomasi* (*n* = 39)[a]
Relative breadth of zygomatic plate (ZP/CBL × 100)			
11.0 ± 0.7	9.9 ± 0.5	9.5 ± 0.3	9.2 ± 0.6
10.3–12.1	9.3–10.5	9.3–9.8	7.8–10.6
(*n* = 5)		(*n* = 3)	
Breadth of interorbital area (IO/CBL)			
24.8 ± 0.6	24.5 ± 0.4	24.4 ± 0.3	23.1 ± 0.8
24.3–25.8	23.9–25.1	24.0–24.6	21.0–24.6
(*n* = 5)		(*n* = 3)	
Relative length of unicuspid toothrow (UTR/CBL × 100)			
13.3 ± 0.4	12.7 ± 0.4	12.1 ± 0.3	13.0 ± 0.6
12.6–13.6	12.0–13.2	11.8–12.3	11.6–14.0
(*n* = 5)		(*n* = 3)	
Relative palatal breadth (M2B/PL × 100)			
72.7 ± 2.2	71.2 ± 2.2	67.0 ± 2.0	66.6 ± 2.6
70.5–76.3	69.0–75.3	64.8–68.7	60.8–70.5
Relative height of coronoid process (HCP/ML × 100)			
76.3 ± 4.8	68.3 ± 1.9	67.8 ± 2.6	66.1 ± 1.9
71.0–82.7	65.7–71.2	64.3–70.3	63.4–70.6
Relative length of posterior portion of the mandible (AC3/ML × 100)			
75.5 ± 5.7	73.1 ± 2.0	74.1 ± 2.2	81.0 ± 3.4
68.4–82.7	70.0–75.8	71.4–76.6	71.4–86.8
Relative length of posterior portion of the mandible (AC3/HCP × 100)			
98.9 ± 2.3	107.0 ± 2.7	109.3 ± 1.2	122.5 ± 4.7
95.7–102.2	104.3–111.4	108.5–111.1	111.1–128.9

[a] Except as noted.

Forest, and Montane Wet Forest life zones on the Cordillera Oriental in central and eastern Cundinamarca Dept., Colombia (Fig. 3); known elevational distribution, ca. 1300–2715 m.

Diagnosis.—A small- to medium-sized *Cryptotis* with a moderately long tail, long dorsal pelage, small forepaws, and short foreclaws. Typically two large dorsal foramina; no lateral branch of the sinus canal or associated foramen; a large foramen on postero-medial edge of tympanic process of each petromastoid. Interorbital area broad; rostrum, zygomatic plate, and palate of moderate breadth. Dentition bulbous; U4 large, but not visible in lateral view; teeth moderately pigmented, with distinct color in protoconal basins (and occasionally pale pigmentation in hypoconal basin) of P4 and M1–2; posterior borders of P4 and M1–2 only slightly recessed; anterior and posterior elements of ectoloph of M1 about equal; M3 complex. Coronoid process moderately high, joins horizontal ramus at a high angle; posterior mandible short; articular process low and broad; inferior sigmoid notch variably shallow; p3 short and high; minute entoconid on m3.

Description.—A small- to medium-sized *Cryptotis*. Tail moderately long (Fig. 1; there are no external measurements, except length of hind foot, recorded for any of the four specimens). Forepaws and foreclaws small (Fig. 4), similar in proportions to those of *C. nigrescens* and other members of the *C. nigrescens*-group. Dorsal fur typically 5–6 mm long, individual hairs up to 7 mm. Dorsal pelage of the four available

Table 3.—Factor loadings for the first three factor axes from principal components analysis (PCA) of 18 cranial measurements from *Cryptotis colombiana, C. mera, C. brachyonyx,* and *C. thomasi.* Variables are listed in descending order by their loadings on the second axis. Abbreviations of measurements are explained in Table 1.

	Correlations		
Variable	PC1	PC2	PC3
ZP	−0.060	0.210	−0.610
IO	−0.238	0.202	−0.081
M2B	−0.245	0.406	0.079
PL	−0.298	−0.088	0.058
TR	−0.298	−0.077	0.082
UTR	−0.264	−0.133	0.070
MTR	−0.293	0.128	0.073
M1W	−0.136	0.647	−0.107
LM	−0.277	−0.015	−0.037
HCP	−0.197	−0.068	−0.057
HCV	−0.276	−0.174	−0.156
HAC	−0.265	−0.288	−0.022
AC3	−0.291	−0.224	−0.014
TRM	−0.291	−0.009	0.158
Lml	−0.161	0.303	0.443
BAC	−0.265	−0.153	0.106
Eigenvalue:	10.183	1.308	1.143
Proportion of variation explained:	0.636	0.082	0.071

specimens Chestnut Brown to Prout's Brown to Mummy Brown; venter Olive Brown to Buffy Brown to Hair Brown; dorsal and ventral hairs 2-banded, with gray base and mid-section and ca. 1 mm brownish distal tip. [Pelage of these skins is faded; live *C. brachyonyx* probably have a darker pelage, possibly similar to that of *C. colombiana* (see *Comparisons,* below).]

Two obvious dorsal foramina present along the suture between the frontals (100%; Table 2); generally about equal in size (75%). Typically lacking lateral branch of sinus canal and associated foramen (see Woodman & Timm 1999) posterior to the dorsal articular facet (100%). A minute foramen often present dorsal to one (50%) or both (25%) dorsal articular facets. Large, obvious foramen on the postero-medial edge of the tympanic process of both petro-

Table 4.—Factor loadings for the first three factor axes from principal components analysis (PCA) of 8 cranial measurements from *Cryptotis colombiana* and *C. brachyonyx.* Variables are listed in descending order by their loadings on the second axis. Abbreviations of measurements are explained in Table 1.

	Correlations		
Variable	PC1	PC2	PC3
U3B	−0.246	0.533	0.075
UTR	−0.140	0.506	−0.695
M1W	−0.231	0.478	0.526
ZP	−0.404	−0.006	0.347
PL	−0.449	−0.034	−0.1.08
MTR	−0.429	−0.093	−0.059
TR	−0.417	−0.242	−0.310
IO	−0.379	−0.404	0.054
Eigenvalue:	4.1890	1.3537	0.9006
Proportion of variation explained:	0.524	0.169	0.113

Fig. 1. Dried skins of *C. brachyonyx* (A: BM 99.10.3.2—holotype; B: USNM 80905) and *C. thomasi* (C: USNM 80904; D: USNM 80903). The smaller body size and shorter length of tail in *C. brachyonyx* are perceptible despite the irregular preparation.

mastoids (100%); foramen not as large as in *C. thomasi* or *C. colombiana*; positioned more medially than in either of those species. Rostrum of moderate length (PL/CBL = 42.9%). Interorbital area broad (IO/CBL = 24.4%). Zygomatic plate of moderate breadth in proportion to CBL (9.5%) and PL (21.7%); anterior border of zygomatic plate at posterior mesostyle-metastyle valley to metastyle of M1; posterior border from parastyle to posterior half of M3, and from posterior one-half to posterior edge of maxillary process. Palate of moderate breadth for the genus (M2B/PL = 67.0%). Anterior process of petromastoid variable in size.

Dentition bulbous. Teeth moderately pigmented: medium red to dark red on tips of cones, styles, and cristae; pale to medium pigment typically extends into protoconal basins of M1 and M2; very pale pigment only occasionally in hypoconal basins. Short, somewhat crowded unicuspid toothrow (UTR/CBL = 12.1%); U4 mostly obscured by U3 and P4 in lateral view of skull (100%; Fig. 5). U1–3 broad in lateral view and straight to convex on posteroventral margin. Cuspules on posterolingual cingulum of U1–3 typically absent to minute; this region of these unicuspids typically pigmented. U4 large, averaging ca. 40% of the surface area of U3 (Fig. 6). Posterior borders

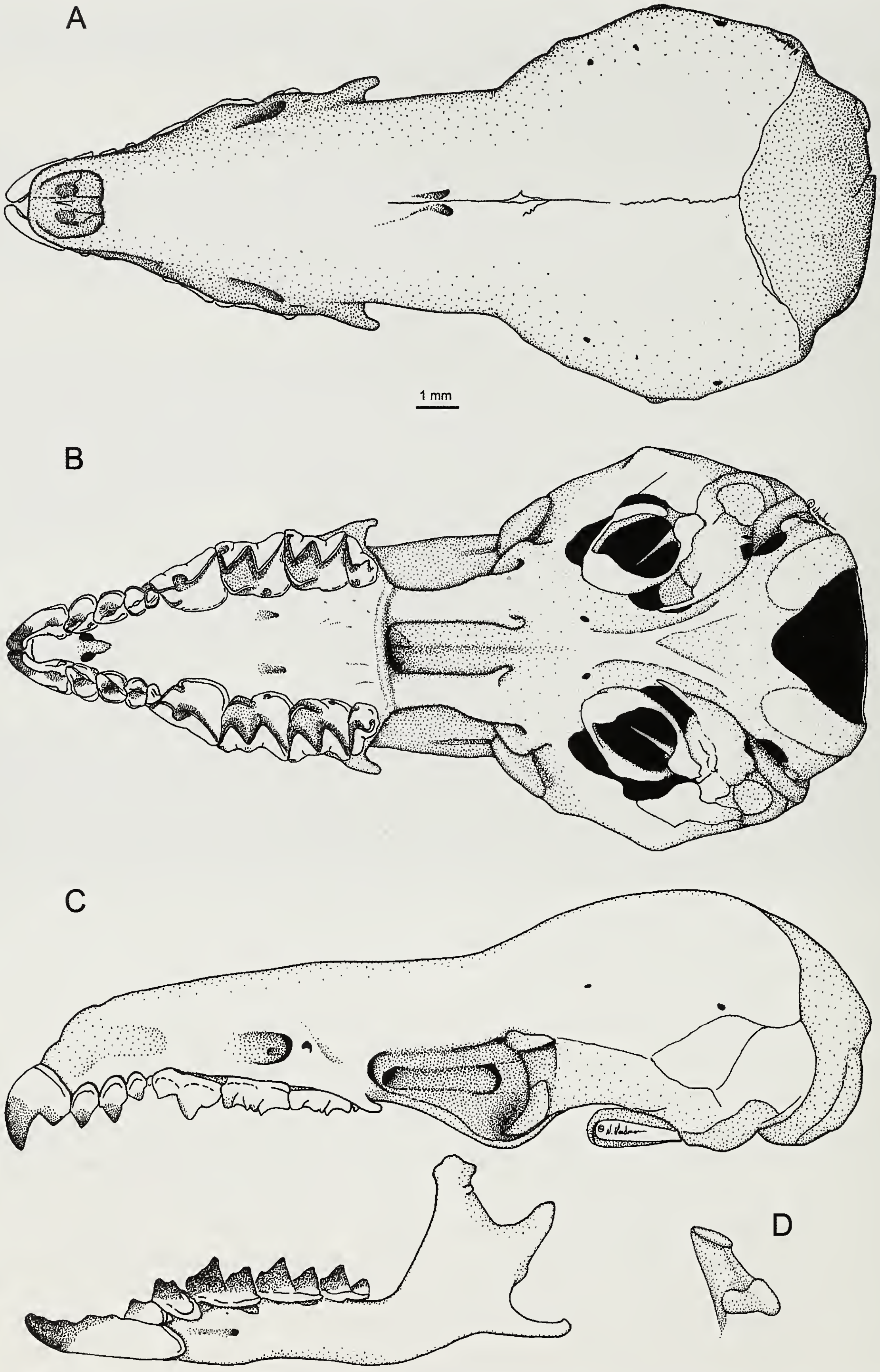

Fig. 2. Skull of the holotype of *Cryptotis brachyonyx* (BM 99.10.3.2): (A) dorsal view of cranium; (B) ventral view of cranium; (C) lateral view of cranium and mandible; and (D) posterior view of articular process of the mandible.

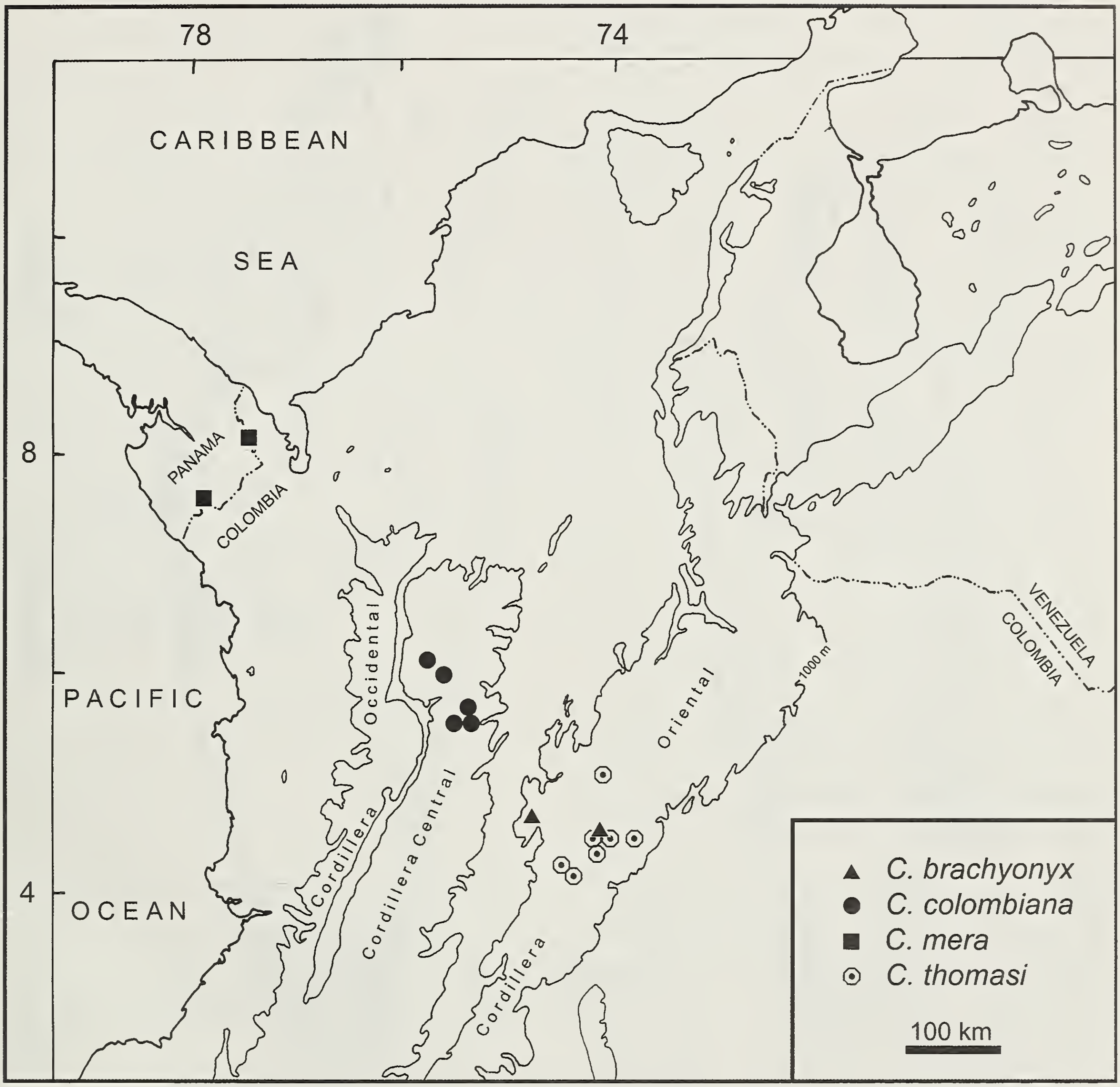

Fig. 3. Map of the northern Andes showing the distributions of *Cryptotis brachyonyx, C. colombiana, C. mera,* and *C. thomasi.* The 1000 m contour is shown.

of P4, M1, M2 only slightly recessed. Anterior element of ectoloph of M1 approximately equal in length to posterior element; protoconal basin of M1 about equal in size to hypoconal basin. M3 appears moderately complex, partly resulting from the presence of a small, but distinct hypocone that squares off the labial border of the tooth and from the relatively extensive pigmentation; parastyle, paracrista, paracone, and precentrocrista well-developed and pigmented; mesostyle, postcentrocrista, and metacone reduced, but pigmented and obvious; protocone pigmented and obvious; hypocone present, but reduced and unpigmented.

Anterior border of coronoid process of mandible joins horizontal ramus at a relatively high angle; coronoid process moderately high (HCP/LM = 67.8%). Inferior sigmoid notch variably shallow to moderately deep. Posterior mandible behind m3 short (AC3/ML = 74.1%). Articular process relatively low and broad. Third lower premolar nearly as high as it is long. Minute, uncolored, but distinct entoconid present (100%) on talonid of m3.

Fig. 4. Ventral views of left forepaws of (A) *Cryptotis brachyonyx* (BM 99.10.3.2) and (B) *C. thomasi* (BM 99.10.3.4), both from La Selva, Colombia.

Postcranial skeleton unknown.

Comparisons.—Cryptotis colombiana: Externally, *C. brachyonyx* and *C. colombiana* may be difficult to distinguish. Based on cranial dimensions, *C. brachyonyx* is generally close in size to *C. colombiana* (e.g., see *Multivariate Analyses,* below), both appear to have a moderately-long tail, and both may have dark pelage. The original description of the pelage of *C. colombiana* (dorsum Olive Brown to Fuscous; ventrum Buffy Brown to Hair Brown—Woodman & Timm 1993) was based solely on the faded holotype. Study of a more recently-collected specimen (MUA 62) indicates that the pelage is closer to Sooty Black to Chaetura Black dorsally, with a Dark Olive Gray to Chaetura Black venter. Dorsal and ventral hairs have a medium-gray base and middle, with a ca. 1 mm dark-brown to black tip. However, the two species are easily distinguished cranially: *C. brachyonyx* has a smaller and more medially located foramen on the tympanic process of the petromastoid; relatively and absolutely narrower palate; darker, more extensively pigmented dentition, with pigment more completely coloring protoconal basins of M1–2 and hypocone of M1; narrower upper dentition; larger and more complex M3, resulting from more strongly pigmented protocone, better developed (but uncolored) hypocone, and better developed and pigmented postcentrocrista and metastyle; minute entoconid in talonid of m3.

Cryptotis mera: *Cryptotis brachyonyx* is absolutely larger in many cranial dimensions, and it possesses a large, obvious foramen on the tympanic process of the petromastoid; relatively shorter zygomatic plate (Table 2); relatively narrower palate; more extensively pigmented dentition, with darker pigment more completely filling protoconal basins of M1–2 and coloring hypocone of M1; relatively shorter unicuspid toothrow; smaller average U4; more complex M3 possessing a small hypocone, strongly pigmented protocone, and more distinct postcentrocrista and metastyle; relatively lower coronoid process; minute entoconid more commonly present in talonid of m3.

Cryptotis thomasi-group: Like other members of the *C. nigrescens*-group, *C. brachyonyx* has noticeably smaller forefeet and shorter foreclaws; U1–3 typically are relatively broad and conical in lateral view of the skull, with a straight or convex posteroventral margin (Fig. 5); the anterior element of ectoloph of M1 is approximately equal in size to the posterior element; the anterior border of the coronoid process of the mandible joins the horizontal ramus at a relatively high angle; the articular process is relatively low and broad.

Cryptotis thomasi: This is the only species of shrew with which *C. brachyonyx* may be sympatric. In addition to the characters that separate it from members of the *C. thomasi*-group in general, *Cryptotis brachyonyx* can be separated by its smaller body size and longer tail. Cranially, *C. brachyonyx* has a smaller and more medially located foramen on the tympanic process of the petromastoid; smaller average

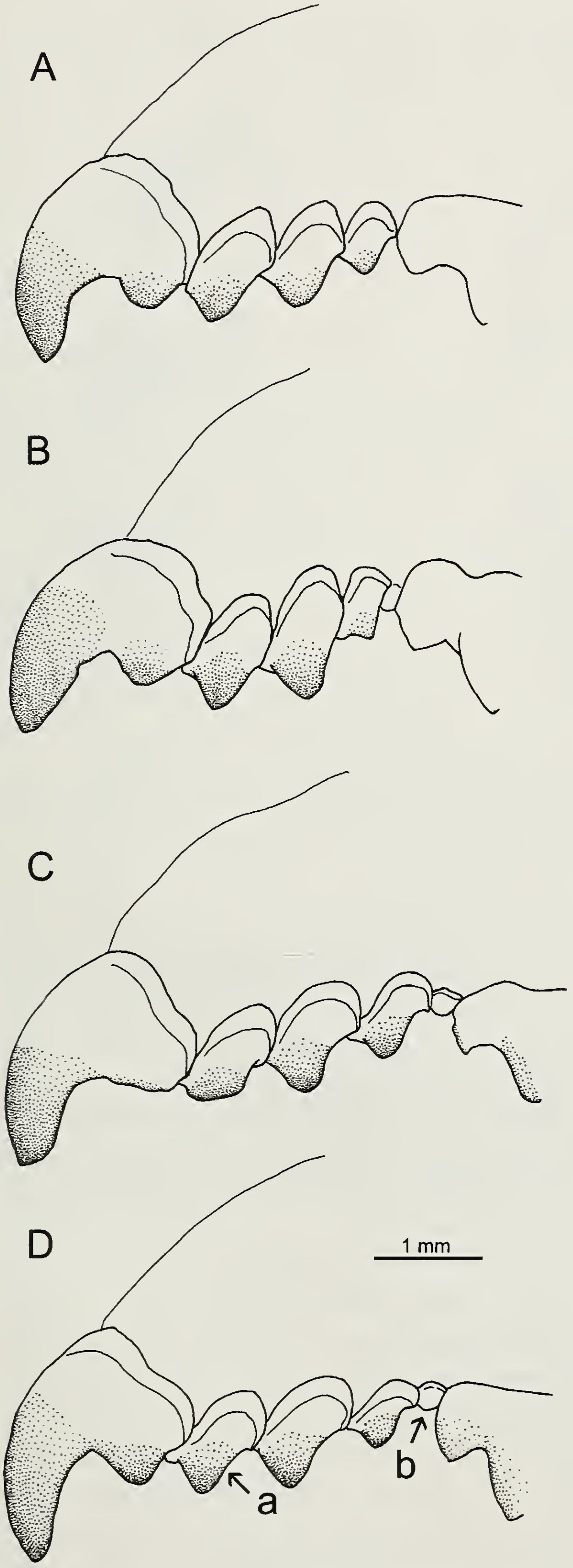

Fig. 5. Lateral view of upper first incisor and unicuspids: (A) *C. brachyonyx* (USNM 80905); (B) *C. colombiana* (MUA 62); (C, D) *Cryptotis thomasi* (KU 157765, FMNH 71030). Arrows point to (a) curvature of posteroventral margin of U1 and (b) visible U4.

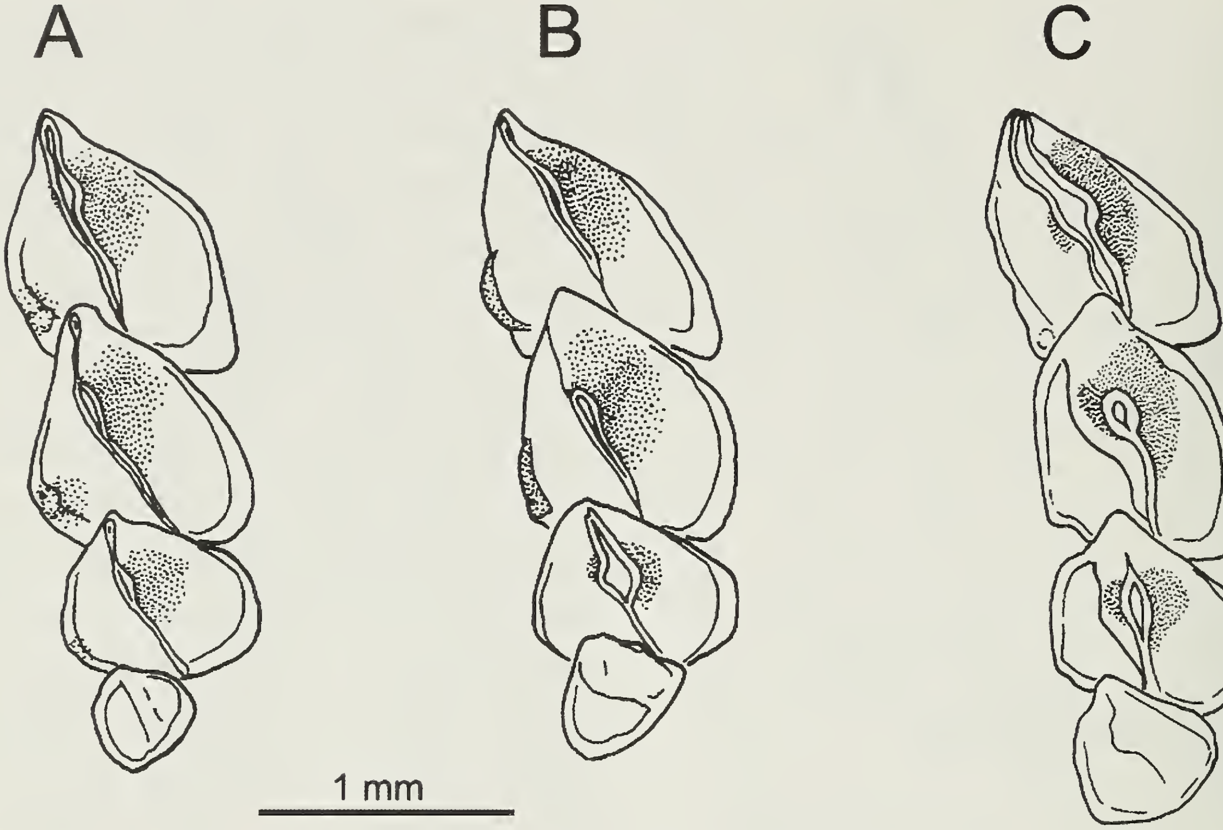

Fig. 6. Occlusal view of upper unicuspids: (A) *C. brachyonyx* (USNM 80905); (B) *C. colombiana* (MUA 62); and (C) *Cryptotis thomasi* (USNM 80906).

U4; less emarginate posterior borders of P4, M1, and M2; relatively shorter posterior portion of the mandible (AC3); minute entoconid more commonly present on talonid of m3.

Results of multivariate analysis.—Principal components analyses (PCA) of craniomandibular variables measured from *C. brachyonyx, C. colombiana, C. mera,* and *C. thomasi* strongly support the distinctiveness of *C. brachyonyx.* The first analysis, which incorporated all four species, showed greatest separation among groups on factor axes 1 and 2. When factor scores on these two axes are plotted, individuals of the four species form four distinct groups of points (Fig. 7). Along the first factor axis, interpreted as size (Table 3), the species separated into three size groupings with minimal overlap. Specimens of *C. thomasi* comprise the largest individuals, and those of *C. mera* the smallest. Individuals of *C. brachyonyx* and *C. colombiana,* which overlap nearly completely along this axis, form a single group of intermediate size. The largest *C. colombiana* and the smallest *C. thomasi* also overlap along this axis. Along the second factor axis, which is interpreted as representing width of palate (M2B) and width of dentition (WM1—see Table 3), the groupings of individuals of *C. colombiana* and *C. brachyonyx* separate without overlap.

A second PCA incorporating cranial variables from just *C. colombiana* and *C. brachyonyx* (Fig. 8) again shows nearly complete overlap along the first factor axis, interpreted as overall size of the cranium (Table 4). However, the two species segregate completely along the second factor axis, which represents the combined effects of variables that include IO, U3B, UTR, and WM1 (Table 4). The variable M2B was specifically excluded from this analysis to assess whether the two species could be separated using other variables. The lack of intersection between the scatters defined by the two samples is notable, because over-

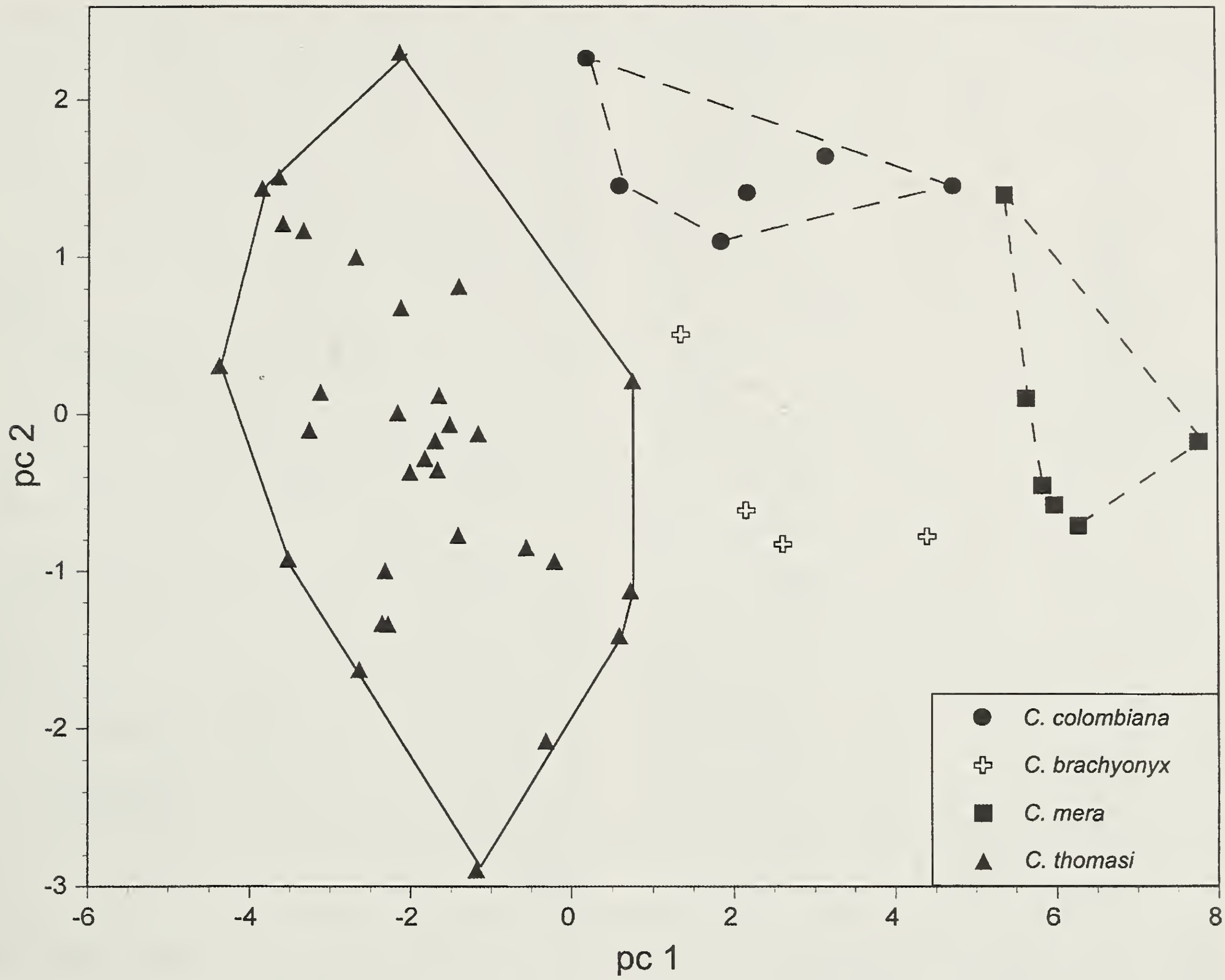

Fig. 7. Plot of scores on factor axes 1 and 2 from PCA of 18 craniomandibular measurements (Table 3) from *Cryptotis brachyonyx, C. colombiana, C. mera,* and *C. thomasi.*

laps in multivariate space are common among species within the *Cryptotis nigrescens*-group, even those that are geographical neighbors (Woodman & Timm 1993, Woodman 2000).

Discussion

The histories of the original specimens of *C. brachyonyx* and *C. thomasi* are closely associated. At least one of the specimens that Merriam (1897) used to name *C. thomasi* is now known to be of *C. brachyonyx,* indicating that since its original description, *C. thomasi* has been polytypic in content. This seeming oversight partly reflects an understandable ignorance at that time of the quality and extent of variation within and among species of small-eared shrews. It also can be attributed to the poor quality of preparation of the specimens, a point noted by Thomas in a letter to Merriam (see below).

In his paper naming *C. thomasi,* Merriam (1897:227) wrote: "For the opportunity to describe this very interesting shrew I am indebted to Mr. Oldfield Thomas, Curator of Mammals in the British Museum, who sent me seven specimens from the type locality. Heretofore the genus *Blarina* has not been recorded from any point south of Costa Rica; hence the discovery of the present species in South America is of unusual interest." The seven specimens sent to Merriam were from a collection of shrews that eventually numbered at least ten skins (eight with accompanying skulls) collected at or near La Selva for George O. Child in 1895 and purchased by Oldfield Thomas for the BM (Table 5). Six of these specimens, including the holotype of *C. thomasi,* cur-

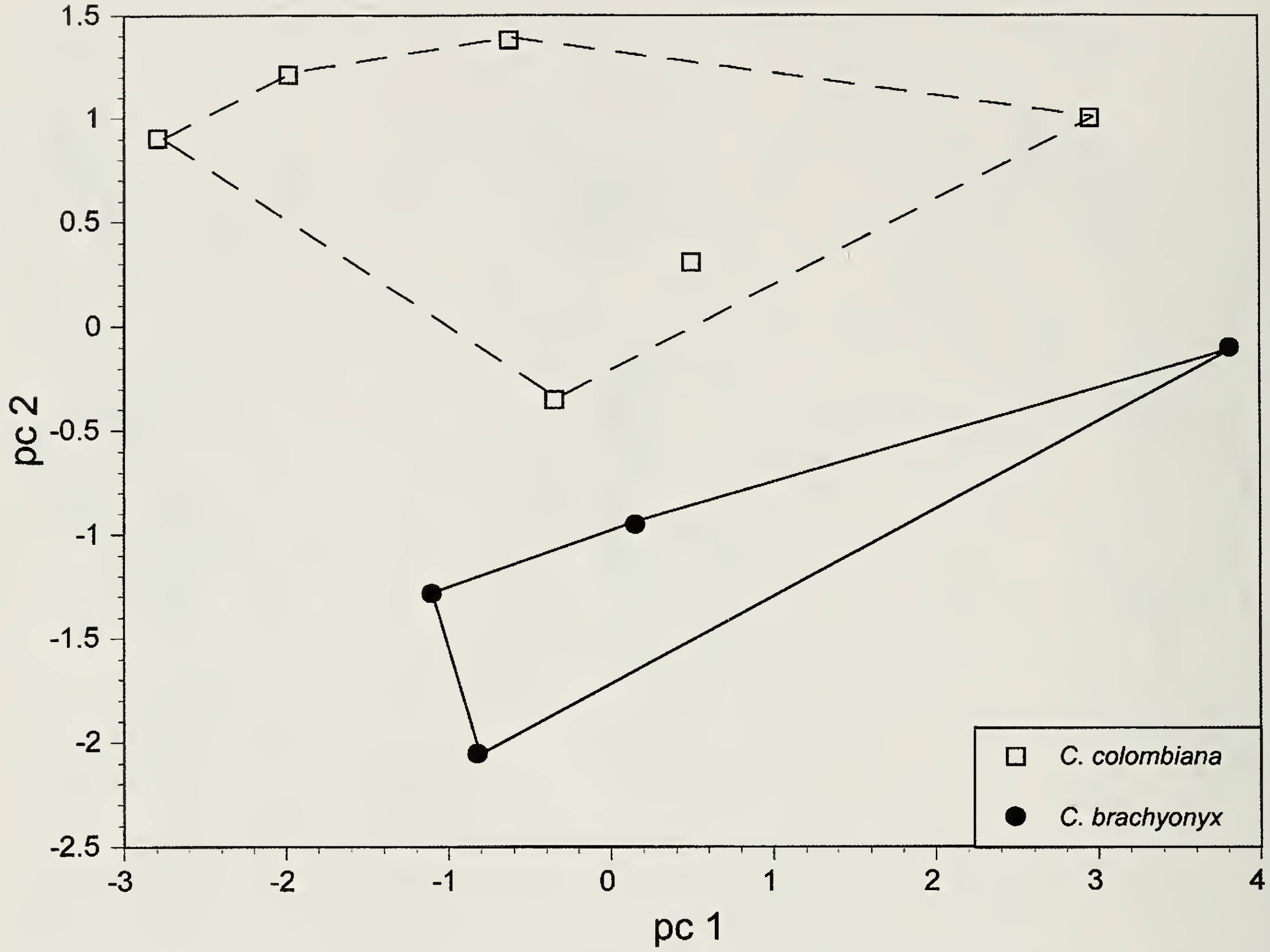

Fig. 8. Plot of scores on factor axes 1 and 2 from PCA of 8 craniomandibular measurements (Table 4) from *Cryptotis brachyonyx* and *C. colombiana.*

rently are in BM and four are in the USNM, the result of an ongoing exchange of specimens between Thomas and Merriam. In his letter to Merriam regarding these specimens, Thomas (in litt. 25 December 1895) wrote:

> I am sending you 6 or 7 Blarinas from Bogotá, a long way south of any locality that I expect you know of. We have had an odd specimen from there since about 1845 but it has never been named, & this lot have just come in to me personally. It is sad that they are such awful skins, but they are made by natives, & one must be thankful for the perfect

Table 5.—Specimens of shrews collected for G. O. Child from near the type locality of *C. brachyonyx* and *C. thomasi.* Specimens are listed in order by date. All specimens with dates were collected in the year 1895. Abbreviations and symbols: SS—skin and skull; SO—skin only; *—holotype.

Museum number	Species	Tag locality	Date	Preparation
USNM 80904	*C. thomasi*	Plains of Bogota	5 April	SO
USNM 80905	*C. brachyonyx*	Plains of Bogota	5 April	SS
USNM 80906	*C. thomasi*	La Selva	6 Aug.	SS
USNM 80903	*C. thomasi*	La Selva	9 Aug.	SS
BM 99.10.3.3	*C. brachyonyx*	Le Selva, near Bogota	10 Aug.	SS
BM 97.5.21.2*	*C. thomasi*	G. Child's Estate, Plains of Bogota	14 Sept.	SS
BM 99.10.31	*C. thomasi*	Boqueron, near Bogota	24 Sept.	SS
BM 99.10.3.2*	*C. brachyonyx*	La Selva, near Bogota	10 Oct.	SS
BM 99.10.3.4	*C. thomasi*	La Selva, near Bogota	1 Nov.	SS
BM no number (GDC #311)	*C. thomasi*	Bogota (Child)	no date	SO

> skulls & exact localities. A dozen more are likely to come to me, so I will give you all these except one, the best, which you shall select for me, & return with your determination upon it, of course if new, & you would kindly describe it I would ask you to make that one the type.
>
> "Plains of Bogota" means an estate some few miles out of the town, at an altitude of about 9000 feet. The other places are all about the Bogotá district.
>
> The material is so poor compared to what you are accustomed to that you may despise it, & not care to work it out. I have kept then back some here hoping to get your paper on the genus, but I am now going away for a long holiday on account of my health, & prefer to send them you before I go.

There is a discrepancy between the numbers of specimens noted by both Thomas and Merriam and the current number of specimens available. Although Thomas clearly noted sending Merriam up to seven specimens (with permission to keep all but one), and, based on Merriam's (1897) report all seven arrived, only four specimens ever were catalogued in the collection of the USNM. The difference does not result from counting skins and skulls separately, because the four USNM specimens and the holotype in the BM include five skins and four skulls, which would yield nine specimens. There is no evidence that any specimens from Child were exchanged by either BM or USNM with any other collections in North America or Europe. One possibility is that Merriam returned to Thomas two specimens in addition to the holotype, in which case, the remaining specimens may be among those in the BM. Unfortunately, I have yet to find correspondence that mentions the return of the holotype to Thomas. Alternatively, some of specimens may have been lost or discarded prior to cataloging in either collection.

That there may at one time have been even more specimens is suggested by Thomas in his letter to Merriam, when he noted, "a dozen more are likely to come to me. . . ." This statement probably was based on a letter from Child to Thomas (in litt. 7 Nov. 1895), in which Child wrote, "I have got already some 12 shrews ready for you and some 20 bats." What happened to all of these specimens is not known. I have been able to trace only the 10 specimens now in the BM and USNM (Table 5).

The AMNH specimen of *C. brachyonyx* and one of the AMNH specimens of *C. thomasi* at one time were identified as the only other known specimens of *Cryptotis avia* G. M. Allen, 1923 (Tate 1932). *Cryptotis avia* originally was described on the basis of a single specimen, a dried skin with skull (MCZ 20091), collected by Nicéforo María at El Verjón on the Cordillera Oriental in 1922. Although the holotype is a small individual based on both the external measurements from the dried skin reported by G. M. Allen (1923) and my cranial measurements, in my opinion it is conspecific with specimens of *C. thomasi* (AMNH 62789, 62790; MCZ 19995) taken by the same collector from the type locality of *C. avia* in March and October 1922 and with specimens of *C. thomasi* from elsewhere (Woodman 1996). The name *C. avia* is therefore a junior synonym of *C. thomasi* and not applicable to *C. brachyonyx*. The previous confusion of the AMNH specimen of *C. brachyonyx* with *C. avia* is understandable, because the crania of both specimens are incomplete (Woodman 1996) and because, for some time, the mandibles of the two specimens had been interchanged. Both conditions served to obscure some of the characteristics important for distinguishing the two taxa.

As noted by Merriam (1897), *C. thomasi* was the first species of that genus (at that time a subgenus of *Blarina*) described from south of Costa Rica. It also represents the first valid species of the family Soricidae or of the order (Insectivora *or* Soricomorpha) from South America. Several species previously had been interpreted as South American shrews, although all were determined eventually to be otherwise. These erroneous soricids included *Mus araneus* Marggraf, 1648, and *Musaraneus brasiliensis* Brisson, 1762, both based on specimens of the didelphid marsupial *Monodelphis* from Brazil [In any case, Marggraf's names are pre-Linnaean, and Brisson's names generally are considered unavailable (Hopwood 1947)]. Two species from Surinam, *Sorex surinamensis* Gmelin, 1789 and *Blarina pyrrhonota* Jentinck, 1910 (first mentioned, but not described, by Jentinck 1888), were based on specimens of European *Sorex araneus* mistakenly purported to hail from South America (Husson 1963, Hutterer 1993).

It is reasonable to presume that the specimens collected for George Child in 1895 may have been the first specimens of true shrews collected in South America. However, as noted by Thomas in his correspondence to Merriam, there is one other specimen in the BM (number 54.1.11.4)—a skull of *C. thomasi* without skin from "New Grenada" that had been "purchased of Mr. S. Stevens." Based on the catalog number, this specimen must have been collected in 1854 or earlier, and Thomas (in litt. 25 Dec. 1895) noted that it had been in the possession of the BM "since about 1845," making it the first verifiable specimen of a shrew from South America.

My inspection of 54 specimens of shrews from the Cordillera Oriental in Cundinamarca Department, Colombia, that are available in systematic collections has yielded only four specimens of *C. brachyonyx,* all of which were collected either in 1895 or in 1925. The remainder are all *C. thomasi. Cryptotis brachyonyx* represents 30% of the ten existing specimens collected from near La Selva in 1895. The four specimens of *C. brachyonyx* comprise 13% of 26 shrews collected in this region through 1931. Among 24 specimens collected since 1950, all are *C. thomasi*; there are no specimens of *C. brachyonyx.* The overall scarcity of *C. brachyonyx* and its absence in later collections may reflect a species restricted to habitats that have not been adequately sampled since the 1920s and that have shrunken dramatically in size or disappeared in the region surrounding the type locality as a result of agriculture and urban development. Alternatively, it is possible that the species may be extinct, but previous experience with the history of collecting *C. colombiana* (Woodman et al. 2003) suggests that this is unlikely and new specimens will begin to be collected. However, intensive surveys in the Cordillera Oriental using appropriate methods will be required to elucidate the modern geographic and ecological distributions of *C. brachyonyx.*

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Literature Cited

Allen, G. M. 1923. A new shrew from Colombia.—Proceedings of the New England Zoölogical Club 8:37–38.

Brisson, M. J. 1762. Regnum animale in classes ix. Distributum, sive synopsis methodica sistens generalem Animalium distributionem in classes ix, & duarem primarium classium, Quadrupedum scilicet & Cetaceorum, particularem divisionem in ordines, sectiones, genera & species. Theodurom Haak, Lugduni Batavorum.

Cabrera, A. 1958. Catálogo de los mamíferos de América del Sur.—Revista del Museo Argentino de Ciencias Naturales "Bernadino Rivadavia" 4 (1):i–iv, 1–307.

Choate, J. R. 1970. Systematics and zoogeography of

Middle American shrews of the genus *Cryptotis*.—University of Kansas Publications, Museum of Natural History 19:195–317.

Espinal T., L. S., and E. Montenegro M. 1963. Formaciones vegetales de Colombia. Memoria explicativa sobre el mapa ecológico. Instituto Geográfico "Agustín Cocazzi," Departamento Agrológico, Bogotá, 201 pp.

Frost, D. R., & D. M. Hillis. 1990. Species in concept and practice: herpetological applications.—Herpetologia 46:87–104.

Gmelin, J. F. 1789. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species; cum characteribus, differentiis, synonymis, locis, 13th edition. Volume I. J. B. Delamollierre, Lugdunum.

Hopwood, A. T. 1947. The generic names of the mandrill and baboons, with notes on some of the genera of Brisson, 1762.—Proceedings of the Zoological Society of London 117:533–536.

Husson, A. M. 1963. On *Blarina pyrrhonota* and *Echimys macrourus*: two mammals incorrectly assigned to the Suriname fauna.—Studies on the Fauna of Suriname and Other Guyanas, 13:34–41, pl. 1–2.

Hutterer, R. 1993. Order Insectivora. Pp. 69–130 *in* D. E. Wilson and D. M. Reeder, eds., Mammal species of the world. Smithsonian Institution Press, Washington, 1206 pp.

IGAC. 1988. Suelos y bosques de Colombia. Instituto Geográfico Agustín Codazzi, Santafé de Bogotá. 135 pp.

Jentinck, F. A. 1888. Catalogue systematique des mammiferes (rongeurs, insectivores, cheiropteres, edentes et marsupiaux). E. J. Brill, Leiden.

———. 1910. Description of a shrew from Surinam.—Notes from the Leyden Museum, 32:167–168.

Marggraf, G. 1648. Historiae rerum naturalium, liber sextus, qui agit quadrupedibus, & serpentibus. Pp. 221–236, 243–244 *in* W. Piso and G. Marggraf, Historia Naturalis Brasiliae. F. Hackium, Lugdunum Batavorum.

Merriam, C. H. 1897. Descriptions of five new shrews from Mexico, Guatemala, and Colombia.—Proceedings of the Biological Society of Washington 11:227–230.

Paynter, R. A., Jr., & M. A. Traylor. 1981. Ornithological gazetteer of Colombia. Bird Department, Museum of Comparative Zoology, Harvard University, Cambridge, 311 pp.

Ridgway, R. 1912. Color standards and color nomenclature. Published privately, Washington, 43 pp., 53 pl.

Tate, G. H. H. 1932. Distribution of the South American shrews.—Journal of Mammalogy 13:223–228.

Thomas, O. 1921. New *Cryptotis, Thomasomys*, and *Oryzomys* from Colombia.—Annals and Magazine of Natural History, Series 9, 8:354–357.

Trouessart, É.-L. 1904. Catalogus mammalium tam viventium quam fossilium. Quinquennale Supplementum Anno 1904. Fasciculus 1, pp. 1–288. R. Friedländer and Sohn, Berolini.

USBGN [U.S. Board on Geographical Names]. 1988. Gazetteer of Colombia, 3rd edition. Defense Mapping Agency, Washington, D.C., 859 pp.

Wiley, E. O. 1978. The evolutionary species concept reconsidered.—Systematic Zoology 27:17–26.

———, & R. L. Mayden. 2000. The evolutionary species concept. Pp. 70–89 *in* Q. D. Wheeler and & R. Meier, eds., Species concepts and phylogenetic theory. A debate. Columbia University Press, New York, xiv + 230 pp.

Woodman, N. 1996. Taxonomic status of the enigmatic *Cryptotis avia* (Mammalia: Insectivora: Soricidae), with comments on the distribution of the Colombian small-eared shrew, *Cryptotis colombiana*.—Proceedings of the Biological Society of Washington 109:409–418.

———. 2000. *Cryptotis merriami* Choate in Costa Rica: syntopy with *Cryptotis nigrescens* (Allen) and possible character displacement.—Caribbean Journal of Science 36:289–299.

———. 2002. A new species of small-eared shrew from Colombia and Venezuela (Mammalia: Soricomorpha: Soricidae: genus *Cryptotis*).—Proceedings of the Biological Society of Washington 115:249–272.

———, & R. M. Timm. 1993. Intraspecific and interspecific variation in the *Cryptotis nigrescens* species complex of small-eared shrews (Insectivora: Soricidae), with the description of a new species from Colombia.—Fieldiana: Zoology, New Series 1452:1–30.

———, & ———. 1999. Geographic variation and evolutionary relationships among broad-clawed shrews of the *Cryptotis goldmani*-group (Mammalia: Insectivora: Soricidae).—Fieldiana: Zoology, New Series 1497:1–35.

———, & ———. 2000. Taxonomy and evolutionary relationships of Phillips' small-eared shrew, *Cryptotis phillipsii* (Schaldach, 1966), from Oaxaca, Mexico (Mammalia: Insectivora: Soricidae).—Proceedings of the Biological Society of Washington 113:339–355.

———, C. A. Cuartas-Calle, and C. A. Delgado-V. 2003. The humerus of *Cryptotis colombiana* and its bearing on the phylogenetic relationships of the species (Soricomorpha: Soricidae).—Journal of Mammalogy 84:832–839.

Appendix: Specimens Examined

Specimens marked with an asterisk (*) in the following listings are cranial remains recovered from owl pellets. Specimens marked with an asterisk and in brackets are mandibles from owl pellets.

Cryptotis brachyonyx (4).—COLOMBIA: *Cundinamarca*: San Juan de Ríoseco (AMNH 70597); La Selva, near Bogotá (BM 99.10.3.2—holotype, 99.10.3.3); Plains of Bogotá (USNM 80905).

Cryptotis colombiana (14).—COLOMBIA: *Antioquia*: Corregimiento San Antonio de Prado, 2100–2800 m (MUA 060, 062); Finca Campiño, Alto de San Miguel, 2000 m (KU 157761); Reserva Ecológica Alto de San Miguel, 2150 m (MUA 12009, 12010*, 12011* [MUA 12012*, 12013*]); Vereda San Francisco, 2750 m (KU 157762*, MUA 12005* [MUA 12007*, 12008*]); Río Negrito, 15 km E of Sonsón, 1750 m (FMNH 69816—holotype); Finca Los Sauces, 2150 m (MUA 12001).

Cryptotis mera (7).—PANAMA: *Darien*: Cerro Tacarcuna, 4800 ft (USNM 337967–337969); Cerro Malí, 4700 ft (USNM 337966); Mount Pirri [Cerro Pirre], E slope near head of Río Limón, 4500–5000 ft (USNM 178974–178976—including holotype).

Cryptotis thomasi (50).—COLOMBIA: [no specific locality] (BM 54.1.11.4; MCZ 27596). *Cundinamarca*: Represa del Neusa (ICN 9659); Bogotá (AMNH 34605); Plains of Bogotá (USNM 80904); Páramo de Bogotá, 2900 m (AMNH 37381; MNHN 1962-1068); La Selva [G. O. Child's Estate], near Bogotá, (BM 97.5.21.2—holotype, 99.10.3.4, BM no number [GDC #311]; USNM 80903, 80906); Boquerón, near Bogotá (BM 99.10.3.1); Páramo de Monserrate, 3200–3300 m (ICN 9649, 9650, 9652, 9658; ROM 51870); San Francisco, 3000–3500 m (AMNH 71354, 71355; FMNH 71023, 71024, 71025, 71026, 71027, 71028, 71029, 71035); San Cristóbal, 2800–2900 m (FMNH 71030, 71031, 71032, 71033, 71034, 71036, 71037); Reserva Biológica Carpanta, 3000 m (ICN 10995, KU 157765); Páramo de Choachí, 3000 m, (AMNH 38405, MCZ 19885, 20090, 20092, 27597, 27598); Páramo el Verjón (AMNH 62789, 62790, MCZ 19995, 20091—holotype of *C. avia*); Chipaque (USNM 251960); Fusagasugá (MCZ 27599); Páramo de Chisacá, 3100 m (ICN 5223).

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A new species of the catfish genus *Ituglanis* from French Guyana (Osteichthyes: Siluriformes: Trichomycteridae)

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Abstract.—*Ituglanis nebulosus* is described from the Aprouague basin in French Guiana. It differs from all other species of *Ituglanis* by a color pattern composed of large, round spots irregularly distributed on body and not coalesced into longitudinal stripes. It is also diagnosable from most congeners by the round caudal fin and the reduced number of vertebrae (35 or 36). The new species shares all synapomorphies so far proposed for the genus *Ituglanis,* as well as other characteristics supporting the placement of the genus within trichomycterids.

The neotropical catfish family Trichomycteridae is known mostly for the semiparasitic (hematophagous and lepidophagous) habits of some of its members in the subfamilies Stegophilinae and Vandelliinae, popularly called "candirus". However, most species in the family are free-living generalized predators of aquatic invertebrates, usually inhabiting fast-flowing, clear-water streams. The majority of those are included in the subfamily Trichomycterinae, a vast non-monophyletic assemblage (de Pinna 1989) comprising over 100 described species (cf. Eigenmann 1918, Tchernavin 1944) plus many others undescribed (de Pinna 1998).

One consequence of the non-monophyly of the Trichomycterinae is that some forms included in the group are expected to be more closely related to other subfamilies than to remaining trichomycterines (de Pinna 1989, 1998). Costa & Bockmann (1993) recognized a small monophyletic group of species formerly included in *Trichomycterus,* which they removed to a separate genus, *Ituglanis.* Costa & Bockmann proposed that *Ituglanis,* rather than forming a clade with other species of *Trichomycterus,* is instead the sister group to a large clade comprising the subfamilies Tridentinae, Stegophilinae, Vandelliinae, Sarcoglanidinae, and Glanapteryginae. That hypothesis implies that *Ituglanis,* though superficially similar to *Trichomycterus* and other members of the subfamily Trichomycterinae, is a key taxon in understanding the evolution of the pronounced morphological and behavioral specializations found in more distal trichomycterids, including the parasitic forms.

The genus *Ituglanis,* as defined by Costa & Bockmann (1993), currently comprises ten species, namely *I. amazonicus* (Steindachner), *I. eichorniarum* (Miranda Ribeiro), *I. gracilior* (Eigenmann), *I. herberti* (Miranda Ribeiro), *I. laticeps* (Kner), *I. metae* (Eigenmann), *I. parahybae* (eigenmann), *I. parkoi* (Miranda Ribeiro), *I. passensis* Fernández & Bichuette, and *I. proops* (Miranda Ribeiro). The distribution of species assignable to the genus, several of which remain undescribed, covers much of cis-Andean South America, from the Guyanas in the north to Uruguay in the south.

In this paper, we describe a distinctive new species of *Ituglanis,* representing the first species of the genus described from French Guyana.

Material and methods.—Meristics and morphometrics are taken according to de Pinna (1992). Skeletal observations are mostly based on a single paratype, cleared and counterstained for bone and cartilage according to a procedure combined and modified from the methods of Taylor & Van Dyke (1985) and Song & Parenti (1995). Data on vertebral number and pleural ribs were taken from the cleared and stained paratype and from radiographs of the holotype and alcoholic paratype. Radiographs were made with a digital x-ray system at the National Museum of Natural History, Smithsonian Institution. Vertebral counts do not include those in the Weberian complex, and the compound caudal centrum (PU1+U1) is counted as one. Number of branchiostegal rays and odontodes are based on the single cleared and stained paratype.

Comparative material examined.—*Ituglanis amazonicus,* MZUSP 30449 (1 ex c&s); *I. eichorniarum,* MZUSP 40792 (13 ex, 2 c&s), 59387 (2 ex); *I. gracilior,* FMNH 53264, x-ray of holotype, MZUSP 65415 (1 ex); *I. herberti,* MZUSP 22186 (1 ex), 2209 (1 ex); *I. parahybae,* MZUSP 79810 (2 ex, 1 c&s), MZUSP 71852 (3 ex); *I. metae,* MZUSP 26030 (2 ex); *I. parkoi,* MNRJ 3849 (holotype), MZUSP 23368 (1 ex); *I. passensis,* MZUSP 80097 (3 ex), 80098 (3 ex), 80099 (2 ex); *I. proops,* MZUSP uncat (5 ex c&s); *Ituglanis* sp. 1, MCP 10420 (1 ex c&s, from Uruguay); *Ituglanis* sp. 2 MZUSP 24128 (2 ex c&s, from the Amazon); *Ituglanis* sp. 3 MNRJ 11489 (5 ex c&s, from Tocantins basin). The unidentified species listed above (sp. 1, sp. 2, etc.) refer to undescribed species which are comparatively relevant for this paper. They will be described in separate publications. Material of *I. laticeps* was not available for examination, and data on that species were obtained from Eigenmann (1918). Additional comparative material of other trichomycterids and other catfishes is listed in de Pinna (1992).

***Ituglanis nebulosus,* new species**

Figs. 1 and 2

Ituglanis sp.; Le Bail, Keith & Planquette, 2000:164, 165 (brief description and color photograph)

Holotype.—MNHN 2001-1128, 36.6 mm SL, French Guiana, Arataye river (tributary of Approuague river), near the natural preserve "Reserve naturelle des Nouragues", (04°00′22″N, 52°36′34″W), col. P. Planquette & et al., Sep 1985.

Paratypes.—Two specimens, both collected with holotype. MNHN 2001-1129, 31.1 mm SL; MZUSP 69574, 35.1 mm SL (specimen cleared and stained).

Diagnosis.—*Ituglanis nebulosus* is distinguished from all other species of *Ituglanis* by a color pattern composed of large dark blotches (larger than twice eye diameter), which often contact each other at their borders but do not coalesce. Dark spots in all other *Ituglanis* species, when present, are either very fine and irregular or regularly spaced and round, no larger than eye, or irregular and coalescent forming roughly-defined longitudinal stripes. *Ituglanis parahybae* has the color pattern most similar to that of *I. nebulosus,* but its dark markings are mostly irregular (vs. round) and partly coalesce as two or three longitudinal series. The differences in color pattern between the two species are well demonstrated in color photographs of fresh or live specimens included in fig. 1 of Costa & Bockmann (1993) and page 165 of Le Bail et al. (2000). The round caudal fin distinguishes *I. nebulosus* from all of its congeners except *I. metae.* In all other species of *Ituglanis,* the caudal fin is either truncate or truncate with rounded dorsal and ventral corners and a gently convex posterior margin (see Discussion). The new species is further diagnosable from *I. gracilior,* geographically its closest congener, by the

Table 1.—Morphometric data for *Ituglanis nebulosus.* A—holotype, B and C—paratypes, D—mean. Measurements 2–13 expressed as % of SL, 14–27 as proportions of HL.

	A	B	C	D
1—Standard length (mm)	36.6	31.1	35.1	34.3
2—Total length	120.8	121.9	118.2	120.3
3—Body depth	16.1	14.5	15.1	15.2
4—Caudal peduncle length	18.0	17.4	18.5	18.0
5—Caudal peduncle depth	11.5	11.6	11.4	11.5
6—Predorsal length	72.4	73.0	70.4	71.9
7—Preanal length	75.4	74.6	77.2	75.7
8—Prepelvic length	62.6	62.7	63.5	62.9
9—Antevent distance	68.9	68.5	69.8	69.0
10—Dorsal-fin base length	7.7	7.4	7.7	7.6
11—Anal-fin base length	6.3	6.4	6.3	6.3
12—Pelvic-fin length	8.7	8.4	8.3	8.5
13—Head length	18.6	19.3	18.8	18.9
14—Head width	88.2	90.0	89.4	89.2
15—Head depth	51.5	45.0	39.4	45.3
16—Interorbital	26.5	30.0	27.3	27.9
17—Eye diameter	10.3	8.3	6.1	8.2
18—Snout length	36.8	38.3	39.4	38.2
19—Mouth width	50.0	48.3	40.9	48.4
20—Length of interopercular patch of odontodes	25.0	26.7	25.8	25.8
21—Length of opercular patch of odontodes	13.2	13.3	10.6	12.4
22—Posterior internarial width	19.1	20.0	18.2	19.1
23—Anterior internarial width	22.1	21.7	19.7	21.1
24—Posterior internarial diameter	5.9	5.0	6.1	5.6
25—Anterior internarial diameter	5.9	5.0	4.5	5.1
26—Pectoral-fin length	58.8	55.0	57.6	57.1
27—Length of pectoral-fin filament	29.4	31.7	37.9	33.0

shorter maxillary barbel (reaching posteriorly slightly beyond posterior margin of pectoral-fin base; vs. minimally to midlength of pectoral fin exclusive of filament). The presence of only three pleural ribs distinguishes *I. nebulosus* from all congeners except *I. amazonicus* and *I. gracilior.* However, rib number is not known in all species of *Ituglanis.* The reduced number of vertebrae in *I. nebulosus,* 35 or 36, is also unusual in the genus, where vertebral counts normally range otherwise from 39 to 41 (41 in *I. gracilior,* 39 in *I. eichorniarum* and *I. parahybae,* 40–41 in *I. proops*). The only other species with 36 vertebrae is *I. passensis,* a cave species easily distinguished from all other *Ituglanis* species by the reduction of eyes and of integumentary pigmentation.

Description.—Morphometric data for the holotype and paratypes are provided in Table I. Cross-section of body round or slightly depressed at pectoral-fin insertion, becoming increasingly compressed posterior to midlength of trunk. Caudal peduncle tapering gradually to caudal fin in dorsal view. Dorsal profile of body straight from head to origin of dorsal fin, sometimes slightly convex at posterior half of trunk. Dorsal profile of head continuous with that of dorsum (Fig. 1). Caudal peduncle evenly deep, nearly as much as remainder of body, expanded posteriorly by procurrent rays. Ventral profile of body gently convex along abdomen, then practically straight from origin of pelvic fins to origin of caudal fin. Myotomes obscured by thick integument but visible by relief on caudal peduncle and dorsal part of posterior half of trunk. Region of longitudinal skeletogenous septum visible as a shallow wide depression, probably in part due to post-mortem shrinkage. Axillary gland inconspicuous on surface of

Fig. 1. *Ituglanis nebulosus,* holotype, MNHN 2001-1128, 36.7 mm SL, lateral view.

body, apparenly located dorsoposteriorly to base of pectoral fin, as inferred from slightly different texture of integument. Its small slit-like pore located shortly dorsoposteriorly to first pectoral-fin ray, slightly anteroventral to first lateral-line pore.

Head depressed, parabolic in dorsal view (nearly round excluding snout), slightly longer than wide. Snout differentiated from rest of head by deep concavity on each side in dorsal view (Fig. 2). Jaw muscles hypertrophied laterally, resulting in swollen cheeks. Eyes small, without free orbital rim, located dorsally on head but directed dorsolaterally. Skin covering eyes thin and transparent. Eyes located entirely on anterior half of HL. Interorbital nearly four times eye diameter. Eye lens well-formed and visible. Anterior nostril located slightly closer to margin of snout than to anterior margin of eye, surrounded by membrane of integument forming short tube, continuous laterally or posterolaterally with nasal barbel. Anterior nares separated by space slightly smaller than interorbital. Posterior nostrils slightly smaller than eye, located slightly closer to anterior nares than to eye, partly closed by thin cup-like flap of integument along their anterior margin (no corresponding flap posteriorly). Posterior internarial width slightly smaller than anterior one.

Fig. 2. *Ituglanis nebulosus,* holotype, MNHN 2001-1128, dorsal view of head.

Opercular patch of odontodes small, dorsolaterally located on head, its posterior end reaching vertical through posterior margin of base of first pectoral-fin ray or to middle of fin-base. Approximately 12 opercular odontodes underlain by small, well-differentiated oval fold of integument. Interopercular patch of odontodes located ventrolaterally on head, anteroventral to and approximately twice size of opercular patch. Opercular and interopercular odontode patches close to each other, almost juxtaposed in some specimens (Fig. 1). Approximately 17 interopercular odontodes, underlain by short flap of integument. Posterior odontodes largest.

Mouth subterminal, its corners only slightly curved posteriorly. Upper lip almost straight, covered with large papillae. Premaxillary teeth arranged in two well-defined regular rows. Outer row teeth fine and conical, inner row teeth more robust, somewhat blunt at tip. Lower lip thin, poorly-differentiated from remainder of ventral surface of head, covered with papillae smaller than those on upper lip. Flat, thin integumentary outgrowth at corner of mouth, adjacent to posterior margin of rictal barbel base. Branchiostegal membranes thick, narrowly joined to isthmus medially and forming large free fold. Six branchiostegal rays. Branchial openings broad, unconstricted. All barbels large (Fig. 2). Maxillary barbel longest and broadest, reaching posteriorly slightly beyond posterior margin of pectoral-fin base. Rictal barbel smaller than maxillary one, extending to posterior margin of interopercular patch of odontodes or to anterior margin of pectoral-fin base. Nasal barbel approximately as long and wide as rictal one, extending posteriorly to perpendicular through posterior margin of opercular patch of odontodes, or slightly beyond.

Lateral line reduced to short tube immediately posterior to head, its terminal pore slightly posterior to vertical through posterior margin of pectoral-fin base. Single additional pore anterior to it, located close to posterior margin of opercular patch of odontodes. Pectoral fin narrow, distally convex, with i+5 rays. Rays progressively shorter posteriorly. First pectoral-fin ray preceded by broad anterior margin of integument, forming anterior edge of fin. First ray longer and thicker than others, prolonged into filament representing approximately one-third the total length of ray. Length of pectoral fin (filament included) approximately equal to HL. Pelvic-fin i+4; first unbranched ray shorter than second and third. Origin of fin well anterior to that of dorsal fin. Large pelvic splint present. Posterior margin of pelvic fin slightly convex, covering anal and urogenital openings but not reaching origin of anal fin. Dorsal fin small, with broadly round distal margin, its origin anterior to vertical through origin of anal fin. Dorsal-fin rays ii+6 plus one accessory anteriorly. Anal fin similar to caudal in size but deeper in shape, with ii+5 rays plus one accessory anteriorly. Caudal fin round, approximately twice as long as deep, continuous with caudal peduncle, with 6+6 principal rays. Procurrent caudal-fin rays difficult to discern in alcohol-preserved specimens, 12 dorsally and 10 ventrally in cleared and stained paratype.

Vertebrae 35 (MNHN paratype) or 36 (holotype and MZUSP paratype). Pleural ribs three. Branchiostegal rays seven.

Pigmentation.—A color photograph of a freshly-collected specimen is provided in Le Bail et al. (2000:165). In preservative, whole of dorsum and sides of body covered with irregularly-distributed, roundish dark markings (Fig. 1). Most individual marks larger than twice eye diameter, often partly coalescent, with those on ventral part of sides smaller than rest and those on dorsum less conspicuous due to darker background. Thin, dendritic, white threads evident on close examination, probably representing superficial blood vessels, sometimes outlining limits between myotomes. Hypural plate outlined by large, dark, triangular spot. Dorsal part of head as dark as dorsum, but marbled tan, with spots less clearly defined. Area around eyes and nares markedly darker than rest, especially on region immediately lateral to nares (Fig. 2). Cheeks with well-defined spots smaller than those on body. Area of opercular odotodes nearly or totally white, but surrounding integument rim very darkly-pigmented, forming narrow round black edge around odontode patch (Fig. 1, 2). Interopercular patch of odontodes white, except for dark area at base. Ventral surface of head mostly white, except for faint fields of dark chromatophores on anterior part of mental region, lower jaw and lower lip. Part of cheek chromatophores also visible in ventral view. Nasal barbel and dorsal surface of maxillary barbels covered with irregular fields of dark chromatophores along their basal three-fourths. Rictal barbel lacking dark integument pigmentation. All barbels with clearly visible reddish-tan cores (cf. nasal barbels in Fig. 2). Caudal fin, except for its hyaline distal third, covered with spots similar to those on body. Dorsal fin with elongate dark fields on its proximal half. Anal fin with sparse, dark fields along base. Pectoral fin with small, elongate dark field along bases of one or two anterior rays. Pelvic fin lacking dark pigment. Abdomen white.

Etymology.—From the Latin *nebulosus,* meaning cloudy, misty, in reference to the integumentary pigmentation pattern of this species.

Ecological notes.—All material of the new species was collected at a slow-flowing section of the river, about 3 meters wide, 20–50 cm deep, and densely shaded by tropical rain forest (gallery forest). The bottom was sandy, covered with leaf litter. Water was clear, slightly tea-stained. The exact microhabitat of the specimens could not be determined, because collecting was done with rotenone. Eight species were found together with *Ituglanis nebulosus*: *Dysichthys coracoideus, Helogenes marmoratus, Bryconops affinis, Hoplias aimara, Gasteropelecus sternicla, Copella carsevennensis, Astyanax meunieri,* and *Poptella brevispina.* Stomach contents seen by transparency in the cleared and stained paratype of *I. nebulosus* show numerous arthropod remains.

Distribution.—So far known only from type locality, in Approuague basin, French Guyana (Fig. 3).

Comments on the taxonomy of Ituglanis.—The genus *Ituglanis* seems monophyletic as presently constituted and of particular importance in being the sister-group to a large subclade of trichomycterids, including highly specialized parasitic forms (see section below). However, the limits of most of its species remain poorly-known, and there are, additionally, several yet undescribed species assignable to the genus. The systematics of the genus, therefore, is clearly in need of detailed revisionary studies.

Fig. 3. Type locality (square mark) of *Ituglanis nebulosus* in French Guiana.

In the course of this study, some comparative data were encountered that may be useful in elucidating the taxonomy of *Ituglanis.* The shape of the caudal fin was found to be of systematic value. In most species of *Ituglanis,* as in most of *Trichomycterus,* the caudal fin is vertically truncate with round corners, with the posterior margin gently convex or straight. The shape of the fin seems to vary little intraspecifically, even in the largest samples examined (over 100 specimens of *I. proops*). In a few species, the caudal fin is round, as in the new species herein described. Miranda Ribeiro (1908) and Eigenmann (1918) reported the caudal fin as round in *I. proops,* but this seems to be mistaken, since it is truncate in all specimens examined of the species. Illustrations in Miranda Ribeiro (1908, 1912) clearly show a specimen preserved with a collapsed caudal fin, which partly obscures its truncate shape. Although the description in Eigenmann (1918) repeats the information on the round caudal fin, the illustration in his pl. 51 fig. 2 more accurately represents the actual truncate condition. The caudal fin has also been erroneously reported as round in *I. eichorniarum* by Eigenmann (1918), even though the original description (Miranda Ribeiro 1912) reports it as truncate, a shape confirmed in specimens examined. The shape of the caudal fin indicates that the form described by Dahl (1960) as *Pygidium metae guayaberensis* (actually an *Ituglanis*), with a truncate fin, probably represents a separate species, and should be referred to as *I. guayaberensis.* The fin in *I. metae* is round.

The species geographically closest to *I. nebulosus* is *I. gracilior,* from the lower Potaro River in Guyana. The two species are evidently distinct, as demonstrated by the characters already discussed and listed in the diagnosis and by a few other, less obvious, traits which could not be confirmed in the holotype of *I. gracilior,* such as the more numerous procurrent caudal-fin rays (15/12). However, diagnosis of *I. gracilior* is problematic. It seems like the original description in Eigenmann (1912), based on a single, very small specimen, may in part be misleading. The only statement about pigmentation pattern is "all upper parts obscurely spotted". The subsequent illustration in Eigenmann (1918) shows a uniform coloration. We suspect that *I. gracilior* is actually strongly spotted, and corresponds to the form illustrated in Le Bail et al. (2000) as *I. amazonicus.* The very long barbels reported in the holotype of *I. gracilior* are seen in some specimens from French Guyana here identified as that species, although that character is subject to some degree of intraspecific variation and the condition illustrated by Eigenmann is one extreme.

The superficial similarity in color patterns in *I. nebulosus* and *I. parahybae* is not reflected in other morphological characters. The two species differ markedly in the number of vertebrae (cf. Diagnosis above), ribs (3 in *I. nebulosus* and 6 in *I. parahybae*), and branchiostegal rays (7 vs. 8). *Ituglanis parahybae* also has the fewest pectoral- and pelvic-fin rays in the genus (5 and 4, respectively, with a vestigial fifth pelvic-fin ray sometimes present). The reduction in pelvic fin-ray number may be part of a trend to reduce the pelvic fins, since some specimens of that species have been reported to lack those fins entirely (Costa & Bockmann, 1993). *Ituglanis nebulosus* has 6 pectoral- and 5 pelvic-fin rays, values that are plesiomorphic for *Ituglanis.* The vertebral count (35 or 36) in *I. nebulosus* is one of the lowest among *Ituglanis.* The only other species with a similar value is *I. passensis,* reported to have 36 vertebrae by Fernández & Bichuette (2002: 276). So far as known, all other *Ituglanis* have at least 39 vertebrae. Samples examined of multiple cleared and stained specimens of *I. proops* and *Ituglanis* sp. 3 show that vertebral number is subject to only minor variation (±2 vertebra), and that the value observed for *I. nebulosus* is therefore taxonomically significant, despite being based on only three specimens. Costa & Bockmann (1993:44) reported 34–38 total vertebrae in the generic diagnosis of *Ituglanis,* but their method of counting vertebrae was not specified and comparisons are therefore difficult. *Ituglanis gracilior* is the species described from nearest to the type locality of *I. nebulosus* and it has 41 (value for holotype) to 43 vertebrae.

Ituglanis proops, from the Rio Ribeira basin, and *I. eichorniarum,* from the Paraguay basin, are similar in external aspect and pigmentation. However, there are additional differences that indicate that they are not conspecific. The most conspicuous differences are found in the interopercular patch of odontodes. *Ituglanis proops* has the largest interopercular patch of odontodes in the genus. Most of that enlargement occurs dorsolaterally, so that the dorsoposterior margin of the interopercular patch closely approaches the ventral margin of the opercular one. The integumentary folds of the opercular and interopercular patches contact each other in preserved specimens. In all other species of *Ituglanis*, the two patches are clearly separated by a broad band of normal head integument. The condition in *I. proops* seems to be autapomorphic, and clearly diagnoses it from all other species of *Ituglanis*, including *I. eichorniarum.*

Ituglanis herberti may be a synonym of *I. eichorniarum.* The two come from the Paraguay basin. The original description of *I. herberti* by P. de Miranda Ribeiro (1940) considered the species as "evidently alied to *Trichomycterus proops*" [= *I. proops*], but fails to mention *I. eichorniarum,* from the same basin as *I. herberti.* The original description reports the color pattern of *I. herberti* as a series of vertical stripes along the sides of the trunk. This characteristic is unique in *Ituglanis* and, if confirmed, would provide evidence of specific distinctiveness. However, the original description also notes that the vertical striped pattern was not evident in the live fish. It seems likely that the dark vertical stripes were artifactual, resulting from folds of integument following preservation and shrinkage. This is common in large trichomycterids with thick integument, where deep ridges of the folds forming after preservation may be mistaken for darkly-pigmented stripes. We have seen this effect clearly in one specimen referable to *I. herberti* (MZUSP 2209), which is an old specimen where dark pigment is entirely faded. No additional taxonomically relevant data were found to justify separation of *I. herberti* and *I. eichorniarum.*

Phylogenetic relationships.—The placement of the new species in *Ituglanis* is unproblematical. The three synapomorphies for the genus provided in Costa & Bockmann (1993) are present in *I. nebulosus.* The first is the vestigial condition of the posterior fontanel, reduced to a small round orifice on the posterior half of the supraoccipital (Fig. 4). The second is a deep notch on the mesial margin of the palatine. The condition in *I. nebulosus* is not as extreme as that illustrated for *I. parahybae* by Costa & Bockmann (1993, fig. 6), but is still clearly present. The third synapomorphy *I. nebulosus* shares with its congeners is an anteriorly-directed anterior portion of the sphenotic (Fig. 4).

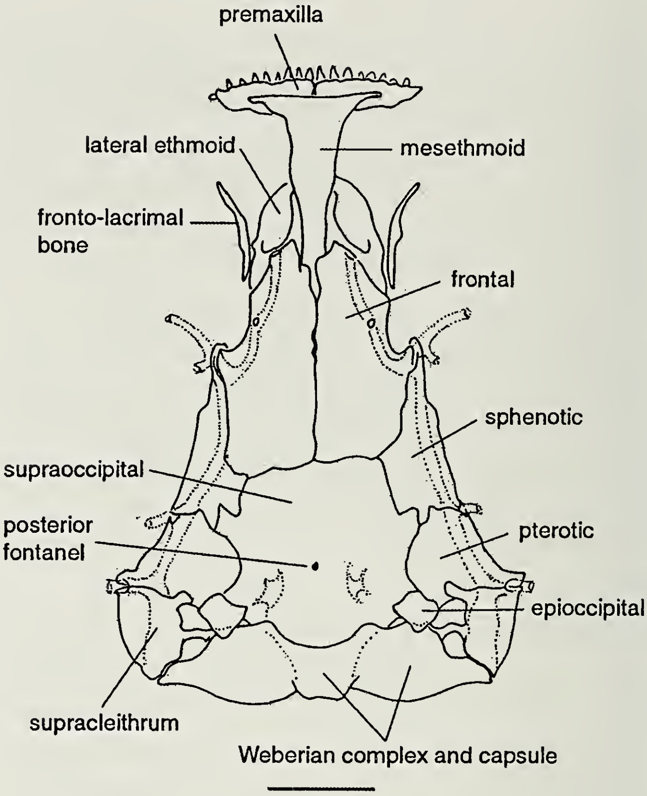

Fig. 4. *Ituglanis nebulosus,* paratype, MZUSP 69574, dorsal view of neurocranium. Scale bar = 1 mm.

Elucidation of the relationships of *I. nebulosus* within *Ituglanis* requires a phylogenetic analysis, preferably associated with a species-level revision, and is beyond the scope of this paper. However, characters found in the course of this study support preliminary inferences about relationships.

Among the species of *Ituglanis* available for skeletal examination, *Ituglanis* sp. 2 has the fewest pleural ribs, with only 2 pairs. The next lowest value, 3 pairs, is seen in *I. nebulosus, I. amazonicus* and *I. gracilior.* Remaining species for which data are available, *I. eichorniarum, I. parahybae, I. proops, I. passensis, Ituglanis* sp. 1 and *Ituglanis* sp. 3 have between 5 and 7 pairs. Reduction in rib number is considered derived because basal trichomycterids have nine or more ribs. A reduction in rib number (seven or fewer) has been considered synapomorphic for *Ituglanis* plus a large subset of Trichomycteridae (see below). A more extreme reduction (three or fewer) is a state synapomorphic for a subset of the genus, including *I. nebulosus, I. amazonicus, I. gracilior* and *Ituglanis* sp. 2. Such rib reduction is homoplastically seen, in similar or more extreme degrees, also in the highly especilized subfamilies which constitute the sister group to *Ituglanis* (see below).

A smaller clade including only *I. nebulosus, I. amazonicus,* and *Ituglanis* sp. 2. further shares a peculiar widening of the mesethmoid shaft. In those species, the width of the mesethmoid shaft equals or surpasses the length of one of the mesethmoid cornua. This condition is markedly distinct from that in other species of *Ituglanis* and remaining species of the subfamily Trichomycterinae, where the mesethmoid shaft is narrow, its width being markedly smaller than the length of each mesethmoid cornua.

Another subgroup of *Ituglanis,* including *I. eichorniarum, I. parahybae, I. proops, Ituglanis* sp. 1 and *Ituglanis* sp. 3, share a peculiar lateral, or posterolateral, process on the anterior third of the antorbital (fronto-lacrimal tendon bone of some authors). In *I. proops,* some specimens have the process on one side only. The presence of this process is a derived condition, because the antorbital is a simple rod in all other relevant trichomycterine taxa.

The characters discussed indicate that *Ituglanis* seems to comprise two main monophyletic groups. One includes northern South American species from the Amazon and the Guyanas. The other includes southern forms from the Paraná/Paraguai, Ribeira de Iguape, Paraíba do Sul and Southeastern drainages in Brazil and Uruguay, plus *I. eichorniarum* and *Ituglanis* sp. 3, which also occur in Southern Amazonian tributaries. This idea is just a first approximation to an understanding of *Ituglanis* phylogeny. Further study, on the basis of additional characters and broader taxonomic sampling, is necessary to formulate a detailed hypothesis on the relationships among species of the genus.

Costa & Bockmann (1993) hypothesized *Ituglanis* as the sister group to a large clade including the subfamilies Tridentinae, Stegophilinae, Vandelliinae, Sarcoglanidinae and Glanapteryginae. This group shares a synapomorphic reduction in the number of pleural ribs (2 to 6 pairs). *Ituglanis nebulosus,* with 3 pleural ribs, conforms to the condition of this character in the clade. The same happens with a more inclusive group, including the multi-subfamilial clade and *Ituglanis,* plus the genus *Scleronema.* This clade relies on two characters: a reduction in size of the interopercular patch of odontodes and the fine, elongated lateral arms of the urohyal. Again, both derived conditions are present in *I. nebulosus.* Thus, the discovery of the new species does not bring in any new character state conflicting with current understanding of the relationships of *Ituglanis* within Trichomycteridae.

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Literature Cited

Costa, W. J. E. M., & F. A. Bockmann. 1993. Un noveau genre néotropical de la famille des Trichomycteridae (Siluriformes: Loricarioidei).—Revue Française d'Aquariologie 20:43–46.

Eigenmann, C. H. 1918. The Pygidiidae, a family of South American catfishes.—Memoirs of the Carnegie Museum 7:259–398.

Fernández, L., & M. E. Bichuette. 2002. A new cave dwelling species of *Ituglanis* from the São Domingos karst, Central Brazil (Siluriformes: Trichomycteridae).—Ichthyological Explorations of Freshwaters 13:273–278.

Le Bail, P. Y., P. Keith, & P. Planquette. 2000. Atlas des poissons d'eau douce de Guyane. Tome 2, fascicule II: Siluriformes. Patrimoines Naturels (M.N.H.N./S.P.N.) 43(II): 307 pp.

de Pinna, M. C. C. 1989. A new sarcoglanidine catfish, phylogeny of its subfamily, and an appraisal of the phyletic status of the Trichomycterinae (Teleostei, Trichomycteridae).—American Museum Novitates 2950:1–39.

———. 1992. A new subfamily of Trichomycteridae (Teleostei, Siluriformes), lower loricarioid relationships and a discussion on the impact of additional taxa for phylogenetic analysis.—Zoological Journal of the Linnean Society 106:175–229.

———. 1998. Phylogenetic relationships of neotropical Siluriformes (Teleostei: Ostariophysi): historical overview and synthesis of hypotheses. Pp. 279–300 *in* L. Malabarba, R. E. Reis, R. P. Vari, Z. M. Lucena, and C.A.S. Lucena, eds., Phylogeny and classification of neotropical fishes. Porto Alegre, Edipucrs.

Song, J., & L. R. Parenti. 1995. Clearing and staining whole fish specimens for simultaneous demonstration of bone, cartilage and nerves.—Copeia 1995:114–118.

Taylor, W. R., & G. C. Van Dyke. 1985. Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study.—Cybium 9:107–109.

Tchernavin, V. 1944. A revision of some Trichomycterinae based on material preserved in the British Museum (Natural History).—Proceedings of the Zoological Society of London 114:234–275.

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116(4):883–891. 2003.

A new species of the hatchetfish genus *Argyripnus* (Stomiiformes: Sternoptychidae) from the Indo-Pacific

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Abstract.—The sternoptychid species *Argyripnus brocki* Struhsaker, originally described from the Hawaiian Islands, has been reported in the literature from various Indo-Pacific localities and to the west off east Africa. We have made univariate and multivariate comparisons, using sheared principal components analysis, of specimens from this broad area and found there to be evidence of two distinct species: *Argyripnus brocki,* endemic to the Hawaiian Islands and vicinity, and *A. pharos* n. sp., occurring in all other investigated areas. These two species are distinguished from the other four in the genus by their relatively low numbers of gill rakers, vertebrae, and certain photophores. *Argyripnus pharos* is distinguished from *A. brocki* by several features but most clearly by its VAV + ACA photophore cluster, which is dorsally inflected in an arch-like form and reaches a higher elevation on the flank.

Fishes of the order Stomiiformes are mainly meso- and bathypelagic fishes, found in all oceans but more diverse at tropical and subtropical latitudes. The relationships and composition of the order have been examined in a series of papers by Weitzman (1974), Ahlstrom et al. (1984), Harold and Weitzman (1996), and Harold (1998). Four families are currently recognized in the order: Gonostomatidae, Photichthyidae (also spelled Phosichthyidae), Stomiidae, and Sternoptychidae. The last comprise the hatchetfishes, to which *Argyripnus* belongs. Unlike the deep-bodied hatchetfish genera, *Argyropelecus, Polyipnus* and *Sternoptyx* (see Baird, 1971, and Harold, 1994), *Argyripnus* species are quite shallow-bodied and overall rather similar to gonostomatids (bristlemouthes). Unlike the many pelagic stomiiforms, *Argyripnus* species are considered to be benthopelagic (Badcock and Merritt 1972), living in association with the benthic community and geographically restricted to the continental slope and other features of positive topographic relief.

Grey (1961, 1964) recognized three *Argyripnus* species: *A. atlanticus* Maul 1952, *A. ephippiatus* Gilbert and Cramer 1897, and *A. iridescens* McCulloch 1926. *Argyripnus brocki* Struhsaker 1973 and *A. electronus* Parin 1992 were added subsequently, bringing the total in the genus to five. Struhsaker (1973) reviewed species occurring in the Indo-Pacific region and described *A. brocki* from off the Hawaiian Islands. Low gill-raker counts and other features in combination were used to distinguish it from the most similar congeneric species, *A. ephippiatus* and *A. iridescens.* Strusaker (1973:835) examined several non-Hawaiian specimens, some of which he tentatively ascribed to *A. brocki,* stating that the geographic range of the species "may extend from Hawaii to the Indian Ocean." We report on additional collections of "low count" *Argyripnus* from the Philippines and other areas of the Pacific and Indian oceans and describe the non-Hawaiian specimens as a new species, *Argyripnus pharos.* In making comparisons with *A. brocki* we rely on standard morphometric and meristic tabular and graphical presentations, as well as a sheared principal components analysis (PCA) (sensu Humphries et al. 1981, Bookstein et al. 1985) of a subset of the morphometric characters.

Materials and Methods

Specimen length is standard length (SL) in mm. Morphometric, meristic, photophore and other characters were determined following the methods and terminology of Weitzman (1986) and Harold (1994). Terminology of the photophores is repeated here for convenience, and to describe and illustrate certain photophore characters not covered by previously published works. The abbreviation for each photophore or photophore series ("cluster," in cases where associated photophores joined in a common organ) and its anatomical location, as defined by Weitzman (1986), and with modifications of the AC series terminology according to Harold (1994), are as follows: ACB (cluster dorsal to central portion of anal fin), ACC (cluster along ventral surface of caudal peduncle), BR (cluster on branchiostegal membranes), IP (cluster on isthmus), OP 1 (single photophore associated with anterior base of preopercle), OP 2 (single photophore near anterodorsal margin of opercle, posterior to center of eye), OP 3 (single very large photophore associated with subopercle), ORB (single photophore anteroventral to eye), OV (dorsal abdominal series/cluster posterior to pectoral fin base), PV (ventral abdominal cluster between bases of pectoral and pelvic fins), and VAV + ACA (combined VAV and ACA clusters of other sternoptychids in a long organ extending from above pelvic-fin base to vertical through about seventh to tenth anal-fin ray; VAV/AC_1 of Badcock and Merrett, 1972:fig.1). Counts of fin rays and numbers of photophores in clusters are the total number of elements in all cases. Elevation of the VAV + ACA photophore cluster is a character developed specifically for this study, determined by taking the distance from the dark pigment border of the dorsalmost VAV + ACA photophore to the base of the immediately ventral anal-fin ray.

A sheared principal components analysis was performed on a subset of morphometric characters for which the greatest number of specimens had values for all characters. Humphries et al. (1981) discussed computational aspects of the procedure. The program "Shear," written by N. MacLeod, was used for the analysis (McLeod 1990); this software was published as part of the Proceedings of the Michigan Morphometrics Workshop (Rohlf & Bookstein 1990).

One of the difficulties with systematic study of deep-sea fishes is their delicate nature and the resultant poor condition of trawl-captured material. Specimens may lack structures, rendering them of little value for analyses such as PCA, in which a complete set of data for each is specimen is desirable. Damaged specimens were adequate for making counts and some measurements included in the description but were excluded from multivariate analysis. A complete truss network was not utilized, but instead selected homologous point-to-point measurements were used that provide critical shape comparisons.

Sources of material for this project are listed as institutional acronyms and associated catalog numbers for *A. pharos* in the account and for other *Argyripnus* species in Appendix I. Institutional abbreviations are as listed in Leviton et al. (1985).

Argyripnus pharos new species

Fig. 1

Argyripnus sp.—Grey, 1961:470–474, tables 1, 2, 3 (USNM 135402, Philippines).—Grey, 1964:207 (off northern Mindinao, Philippines; Key to Species).—Bourret, 1985:57–58 (USNM 135402).

Argyripnus brocki.—Struhsaker, 1973:835 (part, USNM 207984, Indian Ocean).—Parin, 1992:136 (part, northwestern Australia, northwestern Madagascar).—Har-

Fig. 1. *Argyripnus pharos*, holotype, BMNH 1986.9.22.41, 78.9 mm SL.

old, 1999:1901 (part, western Central Pacific). [not *Argyripnus brocki* Struhsaker, 1973]

Holotype.—BMNH 1986.9.22:41, (1, 78.9 mm), Saleh Bay, South Java, approx. 8°30′S, 118°00′E, field no. TGT 1676, coll. T. Gloerfelt-Tarp (no other data available).

Paratypes.—AMS I.24338002 (2, 55.7–79.3 mm), Saleh Bay, South Java, 8°30′S, 117°46′E, 150–280 m, coll. T. Gloerfelt-Tarp, Jul 1981. BMNH 1986.9.22:42–45 (4, 59.4–76.6 mm), collected with holotype.

Non-type material.—AMS I.31174005 (11, 58.6–72.3 mm), Shark Bay, Western Australia, 26°42.3–42.1′S, 112°38.4–38.5′E, (0–) 285 m, coll. J. Paxton, 30 Jan 1991. CSIRO H2169-01 (1, 57.8 mm), E of Fraser Island, Queensland, Australia, 24°44.2–47.7′S, 154°12.5–14.8′E, (0–) 492 m, R/V Soela, Sta. S00685/7, 17 Nov 1985. IOAN uncataloged (2, ~45–51.4 mm), western Indian Ocean, 12°31′S, 48°17′E, (0–) 380 m, R/V Vityaz, Cr. 17, Sta. 2603, 12 Nov 1988. MNHN 1979–98 (1, 67.9 mm), Philippines, 13°49′N, 120°04′E, (0–) 200 m, R/V MUSORSTOM I, Sta. 51CP4, Mar 1976. MNHN 1979–99 (1, 62.4 mm), Philippines, 14°00′N, 120°16′E, (0–) 195 m, R/V MUSORSTOM I, Sta. 64CP4, Mar 1976. USNM 135402 (1, 78.4 mm), N of Mindinao, Philippines, 8°48.5′N, 123°35.5E, (0–) 366 m, R/V Albatross, Sta. D5542, 20 Aug 1909. USNM 207984 (1, 47.8 mm), Indian Ocean, 06°51′S, 39°54′E, (0–) 100 m, R/V Anton Bruun, Cr. 9, Sta. 422, 19 Nov 1964. YPM 10015 (12, 52.3–80.8 mm), Albay Gulf, Philippines, 13°10′N, 124°00′E, 22 Sep 1995.

Diagnosis.—Characters that in combination serve to distinguish *Argyripnus pharos:* gill rakers 15–16, usually 16, with typically 12 on the ventral limb; VAV + ACA photophores 13–18; total number of vertebrae 42–44, usually 42 or 43; dorsal-fin rays 9–12; VAV + ACA photophore elevation 3.7–6.4% SL. No uniquely derived characters known.

Description.—Moderate-sized species, maximum observed adult body length 80.8 mm SL (Table 1; Philippines, YPM 10015) with shallow body profile, body depth 24.7–31.9% SL. Head large (up to 35.1% SL), lateral profile forming a slightly rounded angle of about 90 degrees, with its apex at dentary symphysis. Mouth large, oblique. Scales deciduous, none remaining in any specimens examined; based upon observations of scale pockets, scales quite large and dorsoventrally elongate. Adipose fin present. Maximum body depth located at vertical through occiput, body nearly as deep at dorsal-fin origin. Dorsal-fin origin approximately at vertical through base of most lateral pelvic-fin ray, and located at about mid-body (predorsal length 47.0–55.2% SL, prepelvic length 44.1–53.5% SL). Body profile gently tapered posterior to dorsal-fin origin to shallowest point at about middle of caudal peduncle; caudal peduncle slightly flared posteriorly.

Orbit circular to slightly dorsoventrally elongate, and large, up to 47.1% of head

Table 1.—Morphometric characters expressed as percentages of head length (orbit diameter and snout length) or standard length (all others) and meristic character values for *Argyripnus pharos* holotype (BMNH 1986.9.22: 41), and other material, and *Argyripnus brocki* holotype (USNM 207653), and other material combined.

	Argyripnus pharos				*Argyripnus brocki*			
	Holotype	Other	Mean	N	Holotype	Other	Mean	N
Standard length	78.9	47.8–80.8	65.8	35	81.5	48.8–89.0	69.6	80
Orbit diameter	37.7	37.7–47.1	41.1	33	39.8	38.6–46.8	42.2	64
Snout length	21.0	21.6–26.0	23.7	32	21.9	21.1–29.0	24.2	65
Head length	32.6	29.0–35.1	32.1	33	30.8	27.9–33.8	30.8	68
Body depth	27.6	24.7–31.9	28.9	35	27.7	25.3-31.6	28.3	73
Caudal peduncle length	16.2	12.8–18.1	14.2	34	13.0	12.2–17.4	14.7	67
Caudal peduncle depth	8.3	8.1–11.3	9.4	34	8.2	7.7–11.6	9.2	72
Dorsal fin length	13.1	12.1–18.3	14.1	35	13.5	12.0–17.1	14.3	71
Anal fin length	25.3	23.7–35.1	29.3	26	27.6	25.1–33.3	28.4	65
Preanal length	61.3	52.2–62.4	58.2	31	57.5	53.6–62.8	58.4	65
Predorsal length	48.9	47.0–55.2	49.4	32	49.4	44.4–52.4	48.7	65
Prepelvic length	51.0	44.1–53.5	48.2	30	49.5	45.2–54.6	49.4	58
Postdorsal length	54.5	52.8–62.5	55.5	33	53.7	52.0–60.0	56.3	60
Postanal length	42.9	39.1–47.6	43.5	33	40.4	41.0–47.8	43.9	63
Dorsal-pelvic length	28.2	24.4–30.6	28.4	33	27.4	24.3–34.6	28.3	66
OP 3 height	3.0	1.8–3.9	2.8	32	4.3	2.9–6.0	4.7	53
VAV + ACA elevation	5.6	3.7–6.4	5.2	34	3.6	2.8–4.9	3.8	56
VAV + ACA − ACB length	3.7	1.8–8.0	4.3	34	4.4	2.9–7.4	5.0	56
ACB − ACC length	6.1	6.4–11.2	8.8	34	9.0	7.8–14.3	10.0	67
ACC length	9.6	4.7–8.7	7.0	33	10.1	8.6–12.7	10.6	64
Dorsal-fin rays	11	9–12	10.9	35	11	10–13	11.1	75
Anal-fin rays	21	20–24	22.1	32	21	18–24	21.2	75
Pectoral-fin rays	15	14–17	15.6	33	16	14–16	14.9	77
Pelvic-fin rays	7	6–7	6.9	32	7	6–7	6.9	66
Dorsal gill rakers	4	3–4	4.0	29	4	3–4	3.9	14
Ventral gill rakers	12	11–12	11.7	29	12	12–13	12.1	14
Total gill rakers	16	15–16	15.7	29	16	15–17	16.0	14
Total vertebrae	42	42–44	42.8	21	41	41–43	41.9	40
VAV + ACA photophores	15	13–18	15.3	34	15	13–18	15.4	54
ACB photophores	5	5	5.0	35	5	5	5.0	76
ACC photophores	11	9–12	10.2	32	10	8–12	10.1	66

length. No spines or serrae present in association with elements of the head skeleton or elsewhere. Premaxillary teeth uniserial, differing in size and shape, ranging from, medially, three widely spaced conical to recurved large teeth (about 1 mm in length in 78.9 mm SL holotype) interspersed with much shorter teeth; laterally, a short comb-like patch of minute teeth (each about one tenth the length of the largest premaxillary teeth) along extremity of alveolar process. Maxillary teeth uniserial, subequal, conical to recurved, up to about one half the length of the largest premaxillary teeth, variable in number: 17 in series in 59.4 mm SL paratype, and 29 in 78.9 mm SL holotype. Dentary teeth biserial, inner row comprising numerous (more than 20) minute, recurved teeth increasing in length toward the jaw angle, outer row three or four widely-spaced larged recurved teeth similar in size and shape to largest teeth of premaxilla. One or two large, recurved vomerine teeth located laterally on extremity of each anterior wing-like process; no teeth present on posterior shaft. Four or five minute, conical palatine teeth in a longitudinal row. Mesopterygoid teeth absent. Pseudobranch present and well-developed.

Photophore counts as for genus (Ahlstrom et al. 1984), except VAV + ACA and ACC: AC group combined with VAV, from anterior to posterior, VAV + ACA (13–18), forming a distinctive arch in central portion of cluster directly dorsal to third or fourth anal-fin ray. ACB (5). ACC (9–12), beginning adjacent to second or third last anal-fin ray and continuing posteriorly to near anteriormost ventral procurrent caudal-fin ray. BR (6). IP (6). OP 3. ORB 1. OV (6) + 1. PV (10).

Color in preservative.—Dark brown chromatophores on head in association with iris, photophores (BR, IP, OP, and ORB), posterior portion of cranium, areas immediately dorsal, ventral, and posterior to orbit including dorsal portion of opercle, symphysial portions of premaxilla and dentary, anterior margin of medial one half of maxilla, and entire medial one half of posterior supramaxilla. Reflective guanine pigment associated with photophores, iris, and most of gill cover. Dorsal portion of body above lateral septum pigmented with dark brown chromatophores, with greatest concentration between pectoral girdle and dorsal-fin origin, in a patch on caudal peduncle, delineating myosepta, and forming predorsal stripe between occiput and dorsal-fin origin. Other areas of concentration include patches of dark pigment at bases of dorsal- and procurrent-caudal rays, and covering main body of all photophores. Reflective guanine pigment on body on lateral surface of pectoral-fin base associated with posterior IP photophore reflector; guanine pigment also associated with other photophores, especially ventrolateral area of the abdomen lining OV and PV organs and region of body wall between these clusters. Fin rays largely unpigmented. Pectoral fins with lines of small dark brown chromatophores along basal portions of fin rays and widely separated spots of dark pigment distally. Longest three or four rays of both lobes of caudal fin darkly pigmented along approximately one quarter to one third of their lengths.

Etymology.—The specific name *pharos* is based on the feminine Greek noun pharos, meaning lighthouse or beacon, with reference to the dorsally displaced elements of the VAV + ACA photophore cluster.

Distribution.—West Pacific, from Philippines southward through Indonesian Archipelago and Coral Sea, and western Indian Ocean off Africa.

Ecology.—In almost all cases *Argyripnus* species, including *A. pharos,* have been captured at mesopelagic depths (100–492 maximum depth of capture for *A. pharos*) but near the sea floor. Captures have most typically been made by bottom trawl, although Badcock and Merrett (1972) reported collections of *A. atlanticus* made by a rectangular midwater trawl (RMT8/5) when it was towed near (within 40 m) or on the bottom. The specimens caught were juveniles and subadults (26.0–53.0 mm SL), suggesting the existence of a population of *A. atlanticus* near the sea floor. Available collection data for *A. pharos* indicate that this species likely occurs typically in this near-bottom, benthopelagic habitat. Certain other sternoptychids, such as *Sonoda* and *Polyipnus,* are also reported to have such affinity with the sea floor.

Remarks.—A multivariate statistical approach, sheared principal components analysis, was used to quantify aspects of shape variation in the complex of forms here recognized as *A. brocki* and the new species *A. pharos.* Characters used in the analysis are listed in Table 2. The principal components analysis extracted three components, with their eigenvalue and total variance, respectively, as follows: PC 1 (0.049, 62.262), PC 2 (0.020, 23.604), and PC 3 (0.005, 5.964). The cumulative percent of variance accounted for by these principal components is 91.831. The size vector, PC 1, is not important in addressing the issue of interspecific discrimination in this problem. Variable loadings for PC 1 and two sheared principal components (PC 2 and PC 3), the shape components, for each specimen are reported in Table 2, with the five most important variables in terms of variance explained indicated. Analyzed speci-

Table 2.—Sheared principal component loadings for eighteen morphometric characters from analysis of *Argyripnus pharos* and *A. brocki,* 27 and 39 specimens, respectively. Five highest loadings for each principal component followed by *.

Character	PC 1 (size)	PC 2 (sheared)	PC 3 (sheared)
1 Standard length	0.251959	−0.026222	0.064297
2 Head length	0.240692	0.015219	−0.027908
3 Orbit diameter	0.233235	−0.045382	0.010296
4 Snout length	0.255381*	−0.008259	0.010706
5 Caudal-peduncle length	0.223821	0.017732	0.216135*
6 Caudal-peduncle depth	0.205857	−0.097824	−0.035673
7 Dorsal-fin length	0.253762	−0.112102*	0.033499
8 Anal-fin length	0.191146	−0.129438*	−0.051035
9 Preanal length	0.293429*	−0.020121	0.062156
10 Predorsal length	0.262491*	0.009478	0.054128
11 Prepelvic length	0.293861*	−0.000413	0.084425
12 Postdorsal length	0.232723	−0.058346	0.078760
13 Postanal length	0.215870	−0.088821	0.027782
14 Dorsal-fin origin to pelvic-fin origin	0.260888*	−0.000512	0.083734
15 ACC photophore cluster length	0.242147	0.064465	0.219743*
16 Posterior ACB to anterior ACC photophore	0.183837	−0.331822*	0.267798*
17 Posterior VAV + ACA to anterior ACB photophore	0.112730	−0.782794*	−0.509556*
18 VAV + ACA photophore cluster elevation	0.224150	0.445263*	−0.740109*

mens are plotted with respect to sheared PC 2 and PC 3 scores in Fig. 2. The character VAV + ACA photophore elevation was found to be an important discriminating feature in PC space and is therefore plotted separately as a bivariate with standard length (Fig. 3).

Argyripnus pharos shares with the other five species in the genus a united series of VAV + ACA photophores (18–32 photophores overall for the genus), dorsal fin with 10 to 14 rays and originating near or anterior of vertical through anal-fin origin (Weitzman 1974, 1986). The six species are separated into two main groups of morphologically similar species (see key to species, Grey 1964:207): (1) those with the dorsal fin originating nearly directly above the origin of the anal fin and with numerous (28–32) VAV + ACA photophores (*A. atlanticus* and *A. electronus*), and (2) those with the dorsal fin originating well anterior of a vertical through the anal-fin origin, and fewer (13–21) VAV + ACA photophores (*A. brocki, A. ephippiatus, A. iridescens,* and *A. pharos*). The new species, *A. pharos,* and *A. brocki* are clearly most similar, based upon the presence of relatively few gill rakers (15–17, usually 16, as compared with 18–22 overall in *A. ephippiatus* and *A. iridescens*), fewer VAV + ACA photophores (13–18, as compared with 19–21), and low vertebral counts (41–44 total vertebrae, as compared with 44–53). Meristic features that, in part, distinguish *A. pharos* from *A. brocki* include the presence of slightly more vertebrae (42–44 in *A. pharos,* as compared with 41–43 in *A. brocki*), and fewer dorsal-fin rays (9–12, as compared with 10–13, respectively). In terms of morphometric features, *A. pharos* compared with *A. brocki* has more highly elevated VAV + ACA photophores (elevation 3.7–6.4% SL, as compared with 2.8–5.9, respectively, a larger head (head length 29.0–35.1% SL, as compared with 27.9–33.8), and the dorsal-fin origin located slightly posteriorly (predorsal length 47.0–55.2% SL, as compared with 44.4–52.4).

Grey (1961) reported on an *Argyripnus* specimen (USNM 135402) from off Mindinao, Philippines, that she was unable to place to species level, and consequently referred to *Argyripnus* sp. The specimen, with

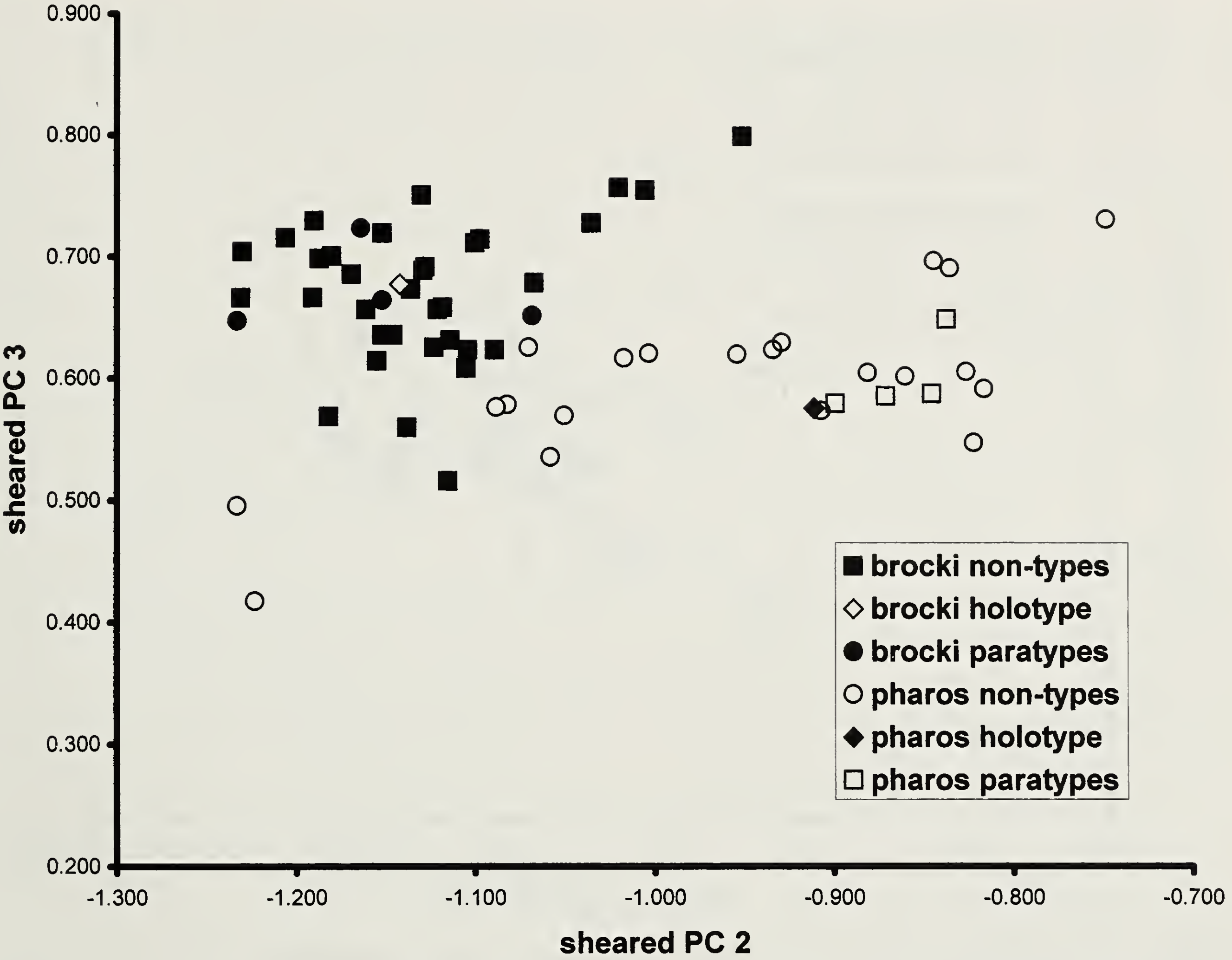

Fig. 2. Plot of principal component scores for *Argyripnus pharos* and *A. brocki* with respect to the first two sheared (shape) principal components, PC 2 and PC 3. The size axis, PC 1, is not illustrated.

that same designation, was later incorporated into a Key to Species (Grey 1964); lack of additional material apparently prevented Grey from describing what was evidently a representative of an undescribed *Argyripnus* species. Neither was Struhsaker (1973) able to assign USNM 135402 to a species, although the single specimen was reported to be very similar to his new species, *A. brocki,* from the Hawaiian Islands. He did, however, assign another geographically removed specimen (USNM 207984, western Indian Ocean) to *A. brocki.* These specimens were examined and placed herein well within the ranges of variation of *A. pharos.* Other Indian Ocean material examined, from off the east coast of Africa (IOAN uncataloged, 12°31S, 48°17E) is assigned to *A. pharos.*

In conclusion, *A. brocki* is an endemic of the Hawaiian Islands vicinity. The similar, and likely phylogenetically related species, *A. pharos,* occurs in the Indo-Australian region, from the Coral Sea northwards to the Philippines, and in the western Indian Ocean off Africa. There are, however, no records of *A. pharos* from the central Indian Ocean. This situation could be due to a paucity of slope habitat at appropriate latitude and, concomitantly, collections of benthopelagic fishes in the region, although it is possible the species has disjunct western and eastern populations.

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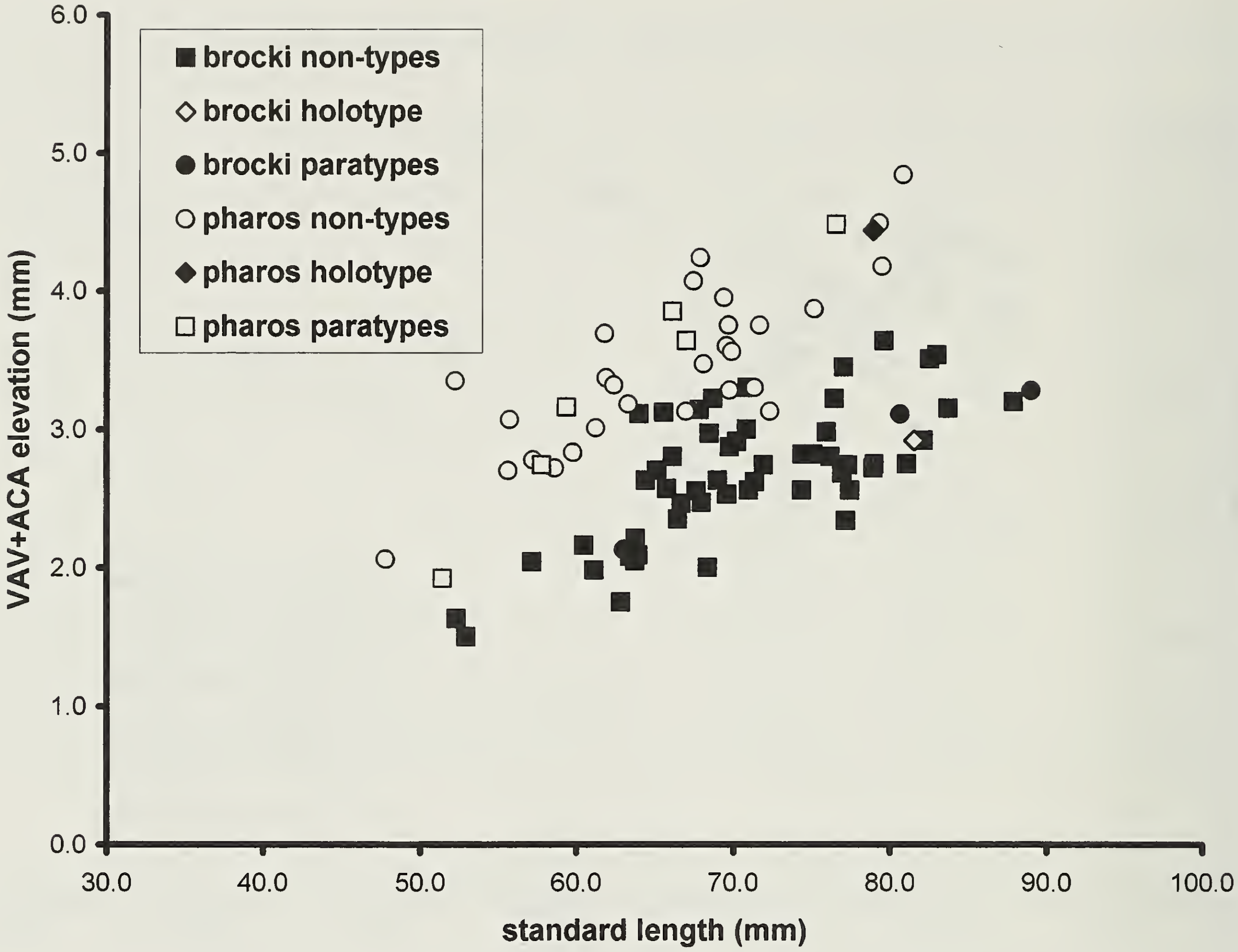

Fig. 3. Bivariate plot of VAV + ACA photophore elevation (mm) versus standard length (mm) for *Argyripnus pharos* and *A. brocki.*

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Literature Cited

Ahlstrom, E. H., W. J. Richards, & S. H. Weitzman. 1984. Families Gonostomatidae, Sternoptychidae, and associated stomiiform groups: development and relationships. Pp. 184–198 *in* H. G. Moser, W. J. Richards, D. M. Cohen, M. P. Fahay, A. W. Kendall, Jr. & S. L. Richardson, eds., Ontogeny and systematics of fishes.—American Society of Ichthyologists and Herpetologists, Special Publication Number 1:1–760.

Badcock, J. R., & N. R. Merrett. 1972. On *Argyripnus atlanticus,* Maul 1952 (Pisces, Stomiatoidei), with a description of post-larval forms.—Journal of Fish Biology 4:277–287.

Baird, R. C. 1971. The systematics, distribution, and zoogeography of the marine hatchetfishes (Family Sternoptychidae).—Bulletin of the Museum of Comparative Zoology, Harvard University 142:1–128.

Bookstein, F. L., B. Chernoff, R. L. Elder, J. M. Humphries, Jr., G. R. Smith, & R. E. Strauss. 1985. Morphometrics in evolutionary biology. Academy of Natural Sciences of Philadelphia, Special Publication 15, 277 pp.

Bourret, P. 1985. Poissons téléostéen: Gonostomatidae, Sternoptychidae, et Myctophidae (MUSORSTOM II). Muséum National d' Histoire Naturelle, Mémoirs, Séries A, Zoologie 133:55–82.

Gilbert, C. H., & F. Cramer. 1897. Report on the fishes dredged in deep water near the Hawaiian Islands, with descriptions and figures of twenty-three new species. Proceedings of the United States National Museum 19 (1114):403–435, (pls. 36–48).

Grey, M. 1961. Fishes killed by the 1950 eruption of Mauna Loa, Part V Gonostomatidae.—Pacific Science 15:462–476.

———. 1964. Family Gonostomatidae. Pages 78–240 *in* H. B. Bigelow, ed., Fishes of the western North Atlantic.—Memoir Sears Foundation for Marine Research Number 1 (Part 4), 599 pp.

Harold, A. S. 1994. A taxonomic revision of the sternoptychid genus *Polyipnus* (Teleostei: Stomiiformes), with an analysis of phylogenetic relationships.—Bulletin of Marine Science 54: 428–534.

———. 1998. Phylogenetic relationships of the Gonostomatidae (Teleostei: Stomiiformes).—Bulletin of Marine Science 62:715–741.

———. 1999. Sternoptychidae. Pp. 1900–1902 *in* K. Carpenter & V. H. Niem (eds.), Western central Pacific identification guide for fishery purposes. FAO Species Identification and Data Programme, Volume 3, 2067 pp. (pls. 1–4).

———, & S. H. Weitzman. 1996. Interrelationships of stomiiform fishes. Pp. 333–353 *in* M. L. J. Stiassny, L. R. Parenti, & G. D. Johnson, eds., The interrelationships of fishes. Academic Press, London, 496 pp.

Humphries, J. M., Jr., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder, & S. G. Poss. 1981. Multivariate discrimination by shape in relation to size.—Systematic Zoology 30:291–308.

Leviton, A. E., R. H. Gibbs, Jr., H. Heal, & C. E. Dawson. 1985. Standards in ichthyology and herpetology: part I. Standard symbolic codes for institutional resource collections in herpetology and ichthyology.—Copeia 1985:802–832.

McLeod, N. 1990. SHEAR. Computer software published with F. J. Rohlf & F. L. Bookstein, eds., Proceedings of the Michigan Morphometrics Workshop. University of Michigan Museum of Zoology, Special Publication Number 2, 380 pp.

Maul, G. E. 1952. Additions to previously revised families.—Boletim do Museu Municipal do Funchal Number 6 (Article 16):51–62.

McCulloch, A. R. 1926. Report on some fishes obtained by the F. I. S. "Endeavour" on the coasts of Queensland, New South Wales, Victoria, Tasmania, South and South-Western Australia. Part V. Biological Results "Endeavour" 5 (Part 4): 157–216 (pls. 43–56).

Parin, N. V. 1992. *Argyripnus electronus*, a new sternoptychid fish from the Sala y Gomez Submarine Ridge.—Japanese Journal of Ichthyology 39:135–137.

Rohlf, F. J., & F. L. Bookstein (eds.). 1990. Proceedings of the Michigan Morphometrics Workshop. University of Michigan Museum of Zoology, Special Publication Number 2, 380 pp.

Struhsaker, P. 1973. *Argyripnus brocki*, a new species of stomiatoid fish from Hawaii, with observations on *A. ephippiatus* and *A. iridescens*.—Fishery Bulletin 71:827–836.

Weitzman, S. H. 1974. Osteology and evolutionary relationships of the Sternoptychidae, with a new classification of stomiatoid families.—Bulletin of the American Museum of Natural History 53: 327–478.

———. 1986. Family No. 75: Sternoptychidae. Pp. 253–254 *in* M. M. Smith, & P. C. Heemstra, eds., Smith's sea fishes. MacMillan South Africa, Johannesburg, 1047 pp.

Appendix I
Comparative Material Examined

Lots are listed alphabetically by species, general geographical area, and then by catalog number. Numbers in parentheses indicate number of specimens in a lot.

Argyripnus atlanticus.—Western North Atlantic: FMNH 64551 (1), 65693 (1), 65694 (1), 71018 (2), 71587 (1), 71600 (4), 71735 (2), USNM 324583 (1).

Argyripnus brocki.—Hawaiian Islands: BPBM 23979 (30), 23995 (35), USNM 207653 (holotype), 207658 (4 paratypes), 204739 (11).

Argyripnus ephippiatus.—Hawaiian Islands: BPBM 24965 (21), 24962 (2), 24968 (21), USNM 47708 (holotype), 126079 (2), 207663 (12), 207664 (3).

Argyripnus electronus.—Sala y Gomez Ridge, eastern Pacific: AMS I.28181001 (3 paratypes), IOAN uncataloged, R/V Professor Shtokman, Cr. 18, Sta. 1976 (8), Cr. 19, Sta. 1977 (1).

Argyripnus iridescens.—Great Australian Bight: CSIRO H 2604-06 (6), T 999 (7), T 1068 (8), T 1129 (10).

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New findings and an overview of the oligochaetous Clitellata (Annelida) of the North Atlantic deep sea

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Abstract.—Six species of Tubificidae are reported from abyssal depths (over 2600 m) off New York/New Jersey in the Northwest Atlantic Ocean. Two members of the subfamily Phallodrilinae, *Bathydrilus medius* Erséus, 1983 and *B. sandersi* Erséus, 1983, previously known only from deep-sea localities in the Northeast Atlantic, are described. The known depth distributions of all deep-sea oligochaetes known to occur in the North Atlantic (38 species of Tubificidae, three species of Enchytraeidae) are analysed, and their pattern suggests that, while abyssal species tend to be distributed on both sides of the ocean, the bathyal taxa are largely endemic to either the American or the European continental slopes.

In the course of a study of rates and magnitude of trace metal redistributions following the end of sludge dumping at the 106-Mile Dumpsite on the continental rise off New York/New Jersey (Dr. J. Frederick Grassle, Principal Investigator), new material of deep-sea clitellates (families Enchytraeidae and Tubificidae) was collected and placed at our disposal.

The tubificids from this collection are reported in the present paper. Two of them, *Bathydrilus medius* Erséus, 1983a and *B. sandersi* Erséus, 1983a, were first described from similar depths off Ireland in the Northeast Atlantic (Erséus 1983a), and the new records are thus a considerable range extension. As there is limited access to collections of oligochaetous Clitellata from the deep sea, the new American specimens of these two species are described in this paper. One new deep-sea species of enchytraeid, *Grania papillinasus,* found during the dumpsite study as well as on the European side of the North Atlantic, was recently described by Rota & Erséus (2003). The distributional pattern of all known North Atlantic deep-sea oligochaetes is analyzed herein.

Material and Methods

The worms studied originate from nine dives with the submersible "*Alvin,*" undertaken in June 1996 during the "Atlantic II" cruise #133 at the 106-Mile Dumpsite area off New York/New Jersey. The actual dumpsite (38.8°N, 72.1°W) is located about 106 miles SE off New York City, i.e., east of the mouth of Delaware Bay, where dumping of sewage sludge was done between 1989 and 1992. All dives were made to similar depths but at various distances from the dumpsite, including two reference dives at about 39.3°N, 70.7°W (S of Massachusetts) (J. Frederick Grassle, personal information).

The specimens were fixed in formalin, stained with Rose Bengal, and stored in 70% ethanol. They were later stained with alcoholic paracarmine and mounted whole in Canada balsam. The measurements in the descriptions refer to this whole-mounted material, examined by a light microscope. The material is deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., and the Swedish Museum of Natural History (SMNH), Stockholm.

Taxonomy

Class Clitellata
Family Tubificidae
Subfamily Phallodrilinae
Genus *Bathydrilus* Cook, 1970

Bathydrilus medius Erséus, 1983

Fig. 1A–B

Bathydrilus medius Erséus, 1983a:140–142, fig. 9.

New material examined.—USNM (1018636), sexually mature specimen in two parts (on two slides), from continental slope S of Massachusetts, U.S.A., 39.33°N, 70.66°W, 2610 m (*Alvin* dive # 3076); 8 Jun 1996. USNM (1018637), immature specimen in two parts (on two slides), from same dive.

Description of new, sexually mature specimen.—Length 6.4 mm, 37 segments. Width at clitellum 0.33 mm, but this region much flattened by coverslip; preclitellar and postclitellar parts of body only 0.08–0.14 mm wide. Prostomium damaged. Clitellum well developed, extending over 1/2X–XII. Chaetae (Fig. 1A) bifid, with diverging, subequal teeth; upper tooth slightly thinner than lower. Bifids 55–65 μm long, 2–2.5 μm thick, three to four per bundle in preclitellar segments, two per bundle in midbody, mostly three per bundle in posterior part of body. Ventral chaetae of segment XI absent. Male pores paired, in line with ventral chaetae, in middle of XI; each pore as a small copulatory sac covered by a papilla formed by a fold of body wall. Spermathecal pores paired, in anteriormost part of X; pores appear dorso-lateral, but exact position not established.

Pharyngeal glands poorly developed. Male genitalia (Fig. 1B) paired. Vas deferens about 7 μm wide, thin-walled, not observed in its whole length, but entering ectal part of atrium. Atrium cylindrical, sigmoid, totally about 270 μm long, with entalmost part about 50 μm wide, tapering to about 25 μm wide at ectal, duct-like part. Most of atrium heavily muscular, with muscle layer up to about 7 μm thick; ectal duct less muscular. Atrium opening into small copulatory sac. Ental, apical end of atrium in posterior end of segment XI. Anterior prostate gland communicating with ectal part of atrium, near entrance of vas deferens. Posterior prostate located near ental, apical end of atrium, and extending into XII, but actual entrance into atrium not observed. Spermathecae elongated oval, about 135 μm long, about 70 μm wide, but exact outline not clear in specimen; ducts inconspicuous, ampullae with large globules of secretion (in walls?) and irregular lumen containing loose sperm.

Remarks.—The second specimen is immature, but its somatic features conform to those of the sexually mature worm.

Bathydrilus medius was originally described on the basis of two specimens from a locality at about 3350 m depth, southwest of Ireland (Erséus 1983a). The present mature specimen has more sigmoid atria than those reported for the type material, but this may be merely a result of muscular contraction (i.e., shortening) of its body. More noteworthy is that its spermathecal pores appear to be dorso-lateral, rather than lateral as was clearly observed for the Northeast Atlantic material (Erséus 1983a:141); we did not find it necessary to re-examine the type specimens. However, even if this difference is real (i.e., if the present worm indeed has dorso-lateral pores), it could be interpreted as intra-specific, considering the great geographical distance between the two populations of *B. medius* studied.

Distribution and habitat.—South of Massachusetts (U.S.A.) in Northwest Atlantic (new record), and off Ireland/France in Northeast Atlantic. Deep-sea sediment, 2610–3356 m depth.

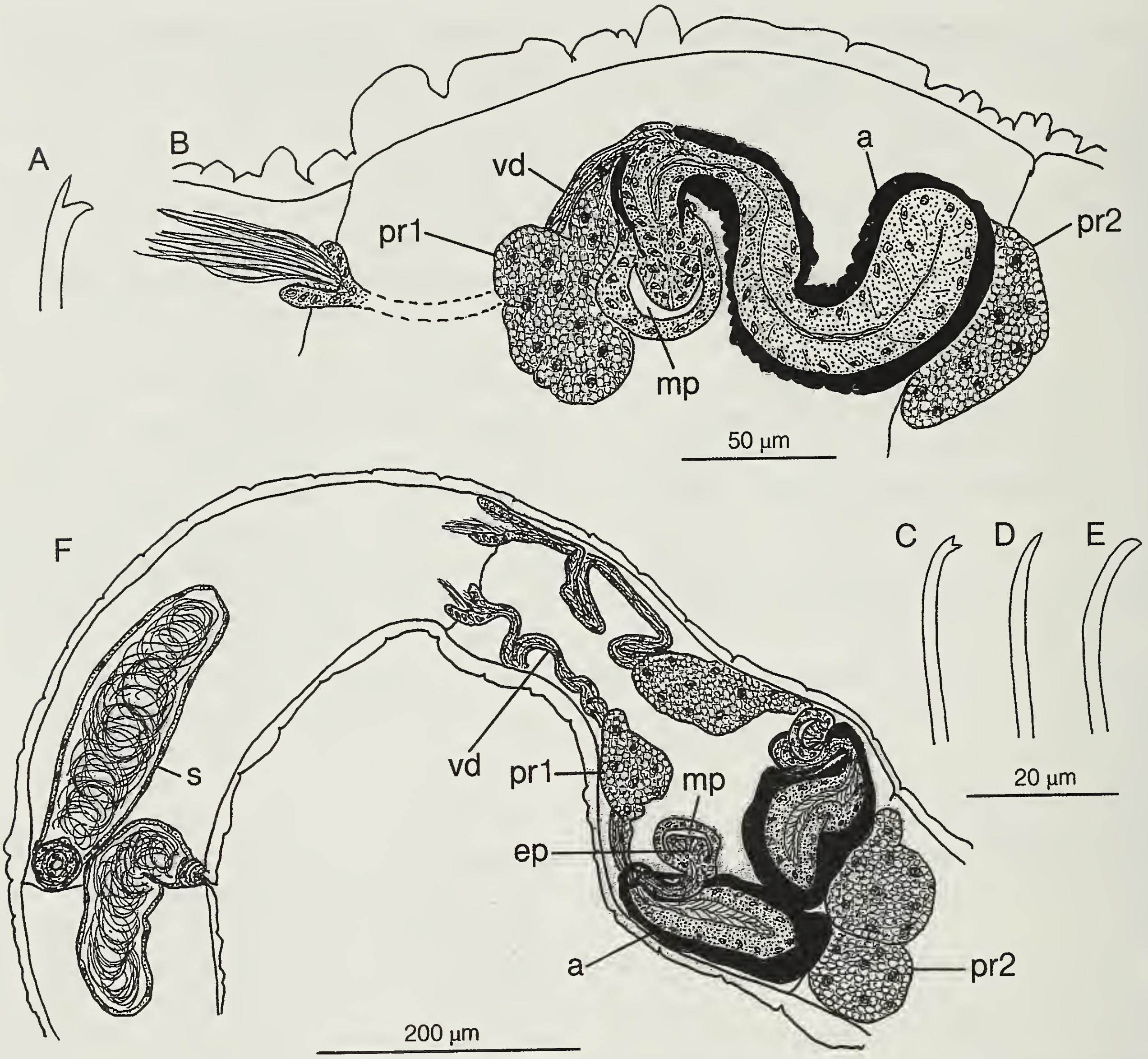

Fig. 1. A, B: *Bathydrilus medius* Erséus. A, Free-hand drawing of chaeta (ectal portion). B, Ventral view of male genitalia in segment XI. C–F: *Bathydrilus sandersi* Erséus. C, Ectal portion of chaeta from segment III. D, Ectal portion of chaeta from segment IV. E, Ectal portion of chaeta from posterior end of worm. F, Ventral view of male genitalia and spermathecae in segments X–XI. Abbreviations: a, atrium; ep, epidermal papilla; mp, male pore; pr1, anterior prostate gland; pr2, posterior prostate gland; s, spermatheca; vd, vas deferens.

Bathydrilus sandersi Erséus, 1983
Fig. 1C–F

Bathydrilus sandersi Erséus, 1983a:139–140, fig. 8.

New material.—USNM (1018638–1018639), two specimens (one complete, sexually mature; the other a posterior end only) from continental slope E of Delaware, U.S.A., 38.57°N, 72.50°W, 2625 m (*Alvin* dive # 3078); 10 Jun 1996. SMNH Main Coll. 46160–46161, two sexually mature specimens from same site, but 2630 m (dive # 3077); 9 Jun 1996.

Description.—Length of single complete specimen 10.5 mm, with 43 segments. Width at segment XI, 0.19–0.24 mm. Prostomium pointed, triangular, rather muscular, and with more or less demarcated apical papilla. Anus somewhat subterminal on pygidium. Clitellum poorly developed. In segments II–III, chaetae bifid with upper tooth slightly smaller than lower (Fig. 1C) or single-pointed (Fig. 1D); these chaetae about 50 µm long, about 2 µm thick, generally one or two (occasionally three or zero) per bundle. From IV onwards, chaetae sharply single-pointed (Fig. 1E), 55–70 µm long, 2–3 μm thick, two to four (occasionally one) per bundle; those of postclitellar segments seldom more than two per bundle. Chaetae absent from segment bearing male pores; no modified genital chaetae present. Male pores paired, in line with ventral chaetae, located posterior to middle of segment X (one specimen) or XI (two specimens). Spermathecal pores paired, located dorsal to lateral lines, almost in line with dorsal chaetae, in anteriormost part of segment immediately preceding the male pore segment.

Pharynx wide, conspicuous. Pharyngeal glands poorly developed. Male genitalia (Fig. 1F) paired. Vas deferens about 10–13 μm wide, thin-walled, somewhat coiled, entering (together with stalk of anterior prostate gland) ectal end of atrial ampulla; i.e., approximately where atrium narrows abruptly to form its ectal duct (see below). Atrium consisting of oval-to-spindle-shaped (generally somewhat twisted) ampulla, 135–160 μm long, 60–100 μm wide, with 10-20 μm thick muscular layer and somewhat granulated and ciliated inner epithelium, and ectal muscular duct; latter shorter and distinctly narrower than ampulla and leading to copulatory organ. This organ an epidermal papilla (Fig. 1F, ep) inside a small copulatory sac. Spermathecae (Fig. 1F, s) consisting of narrow, short, but distinctly muscularized ducts, and thin-walled, oblong ampullae; latter 160–240 μm long, 70–90 μm wide, lacking muscular layer, but containing dense masses of sperm.

Remarks.—This species was originally described on the basis of three specimens from abyssal depths SW of Ireland, in the Northeast Atlantic (Erséus 1983a). The new material conforms well to the original description, even in terms of dimensions of the chaetae and various genital structures. It is particularly noteworthy that the genitalia are located in segments IX–X in one of the new specimens from the Northwest Atlantic, while genitalia normally are in X–XI in tubificids; the genitalia were in such a forward position (in either VIII–IX, or IX–X) also in the three Northeast Atlantic specimens.

The presence of an epidermal papilla inside each copulatory sac was noted as a possibility in the original description (Erséus 1983a:140: "..atrial duct opening into a deep vagination, the wall of which is thickened at inner end (possibly a papilla is present here, as in *B. meridianus* Erséus (1979a, fig. 6); but this is not quite clear in available material)"; see also Erséus (1983a, fig. 8C), where the thickening is depicted, albeit partly hidden by the atrial duct). The papillar nature of the structure is confirmed by the new material of *B. sandersi* (Fig. 1F, ep).

This study has also shown that *Bathydrilus sandersi* has a somewhat muscular prostomium equipped with a small apical papilla, a feature shared by three other deep-sea species of *Bathydrilus, B. asymmetricus* Cook, 1970a, *B. atlanticus* Erséus, 1979a, and *B. hadalis* Erséus, 1979a. It is noteworthy that two deep-sea representatives of the large genus *Grania* Southern, 1913 (family Enchytraeidae), *G. torosa* Rota & Erséus, 2003, and *G. papillinasus* Rota & Erséus, 2003, possess similar frontal papillae (see Rota & Erséus, 2003, figs. 12A, 13A). Other deep-sea Tubificidae (e.g., *Atlantidrilus hamulus* Erséus, 1992, *Mexidrilus grasslei* (Erséus, 1984), and *M. obtusus* Erséus, 1992) have triangular prostomia but with less demarcated tips, while at least two abyssal species, *Atlantidrilus rostratus* (Erséus, 1984), and *Adelodrilus fimbriatus* Erséus, 1983b, appear even further modified; their prostomium as a whole being prolonged into a conspicuous muscular "snout."

The occurrence of muscle fibers in the prostomium is reported for members of several oligochaetous families. Such musculature, which is embryologically derived from a forward extension of the anterior ends of the mesodermal bands (Dales 1963, Anderson 1973), takes either the form of parietal layers (the circular and longitudinal ones sometimes arranged in a reversed order with respect to that characteristic of the segmental body wall, e.g., in the haplotaxid *Haplotaxis ichthyophagous* Gates, 1971, Brinkhurst & McKey-Fender 1991), or of muscle strands or laminae running transversely across the lumen of the prostomium (e.g., in species of the enchytraeid genera *Achaeta* and *Oconnorella* (Vejdovsky, 1884: plate VII, fig. 1, Rota & Healy 1999), or, particularly for species with elongate prostomia, of longitudinal straps running backwards to the walls of the first two segments (e.g., in the "criodrilid" *Criodrilus lacuum* Hoffmeister, 1845 [family Almidae according to Jamieson, 1988]; Vejdovsky, 1884: plate XIV, fig. 1). By contraction of the circular parietal musculature or of transverse luminal fibers, the prostomium narrows, whereas contraction of the longitudinal fibers produces its shortening or even its retraction into the peristomium (both changes of shape are reported in the Tubificidae, e.g., in species of *Duridrilus, Limnodriloides,* and *Tectidrilus*; see Erséus 1990a, b). Such a deformable cephalic end can be used in combination with the buccal lips for food manipulation (e.g., in megadriles; Darwin 1881, Gates 1982) or as a sensitive proboscis for exploring the surroundings [as hypothesized for *Capilloventer longicapitus* Pinder & Brinkhurst, 1997 (Capilloventridae); see original description]. However, for animals dwelling in fine deep-sea sediment, heavily muscularized, movable prostomia are likely to be primarily an adaptation for burrowing, in contrast to the situation for the interstitial oligochaetous species commonly inhabiting sandy continental shelf bottoms. Until more detailed morphological studies have been made, the function of the apical papilla remains unclear, but we propose it may act as a sensory structure. At any rate, as such papillae are rare among other marine tubificid taxa, as well as among the many shallow-water *Grania* species, we can assume their independent evolution (by convergence) in at least two lineages of deep-sea oligochaetes.

Distribution and habitat.—E of Delaware (U.S.A.) in Northwest Atlantic (new record), and SW of Ireland in Northeast Atlantic. Deep-sea sediment, 2625–3356 m depth.

Other Tubificidae

The following species (all except *T. aculeatus* are members of Phallodrilinae) were also found in this study (see Table 1 for authorities).

Tubificoides aculeatus (Tubificinae) was collected during all dives (including those at the dump site, E of Delaware), at 2603–2630 m. This species is already well known from many stations, at 1330–2946 m, S of Massachusetts (Cook 1970a, b; Erséus 1984).

Mexidrilus grasslei and *Adelodrilus fimbriatus* were found at eight and four dive sites (including some at the dump site, E of Delaware), respectively, in both cases ranging 2603–2630 m. Both taxa were previously known from the continental slope S of Massachusetts, at about 1800 m (Erséus 1983b, 1984). *Mexidrilus grasslei* also occurs at 1330 m depth in the Gulf of Mexico (Erséus 1988).

Finally, a single specimen of *Atlantidrilus biparis* was encountered during dive # 3078 (E of Delaware, 2625 m). This species is already known from S of Massachusetts (at 1764 m; Erséus 1984), as well as from W of Brittany, France (at 2160–2798 m; Erséus 1983a).

Discussion

Bathydrilus medius and *B. sandersi* are new records for the Northwest Atlantic Ocean, whereas the other tubificids found in the present study were already known from this sector of the continental slope/rise off the eastern U.S.A.

Deep-sea oligochaetes were first described by Cook (1970a, b), and have subsequently been reported from all major oceans. This paper deals with the North Atlantic species, but tubificids have been obtained from great depths also in the Indian

Table 1.—Oligochaete species exclusively reported from depths greater than 200 m in the North Atlantic Ocean, ordered according to their deepest known record; data compiled from Coates & Erséus (1985), Cook (1970a, b), Erséus (1979a, b, 1982a, b, 1983a, b, 1984, 1988, 1989c, d, 1991, 1992), Erséus & Milligan (1989), and Rota & Erséus (2003). All except *Grania* spp. (Enchytraeidae) are members of Tubificidae. Species distributions are indicated for the western (''West'', Northwest Atlantic) and eastern (''East'', Northeast Atlantic) sides of the ocean.

	Distribution		
Species	West	East	Depth range (m)
Tubificoides sp. ?*	X	—	2000–4850
Bathydrilus atlanticus Erséus, 1979a	X	X	1600–4632
Abyssidrilus remus (Erséus, 1979b)	X	—	2900–3753
Abyssidrilus profundus (Cook, 1970a)	X	X	1800–3753
Atlantidrilus rostratus (Erséus, 1984)	X	—	3670–3685
Adelodrilus fimbriatus Erséus, 1983b	X	—	1839–3685
Atlantidrilus quadrisetis Erséus, 1982a	—	X	3338–3356
Bathydrilus sandersi Erséus, 1983a	X	X	2625–3356
Bathydrilus medius Erséus, 1983a	X	X	2610–3356
Abyssidrilus potens Erséus, 1992	X	—	3006–3011
Abyssidrilus opulentus Erséus, 1992	X	—	2002–3009
Tubificoides aculeatus (Cook, 1970b)	X	—	1330–2946
Bathydrilus connexus Erséus, 1988	X	—	618–2902
Grania papillinasus Rota & Erséus, 2003	X	X	2630–2885
Atlantidrilus styloatriatus (Erséus, 1979b)	—	X	2875
Bathydrilus longiatriatus Erséus, 1983a	X	—	622–2853
Bathydrilus desbruyeresi Erséus, 1983a	—	X	2730–2825
Atlantidrilus vulnus (Erséus, 1983a)	—	X	2205–2798
Atlantidrilus biparis (Erséus, 1983a)	X	X	1764–2798
Mexidrilus grasslei (Erséus, 1984)	X	—	1330–2630
Gianius cristolatus (Erséus, 1983a)	—	X	2160–2227
Pirodrilus pinguis (Erséus, 1983a)	—	X	2165–2207
Atlantidrilus hamulus Erséus, 1992	X	—	2114
Bathydrilus asymmetricus Cook, 1970a	X	—	1330–2064
Adelodrilus voraginus (Cook, 1970a)	X	—	1839–2000
Abyssidrilus altoides Erséus, 1992	X	—	1991
Bathydrilus graciliatriatus Erséus, 1979a	—	X	1491–1800
Grania torosa Rota & Erséus, 2003	—	X	1170–1800
Grania atlantica Coates & Erséus, 1985	X	X	556–1796
Phallodriloides lobatus (Erséus, 1983)	X	—	1456–1518
Limnodriloides sphaerothecus Erséus, 1982b	X	—	1000–1518
Mexidrilus constrictus (Erséus, 1988)	X	—	625–860
Mexidrilus vescus (Erséus, 1989c)	X	—	840–841
Phallodriloides pinnulatus Erséus, 1992	X	—	807
Mexidrilus obtusus Erséus, 1992	X	—	799
Olavius rallus Erséus, 1991	X	—	583
Tubificoides paracrinitus E. & Milligan, 1989	X	—	540–582
Tubificoides crinitus Erséus, 1989d	X	—	320–547
Tubificoides pequegnatae E. & Milligan, 1989	X	—	540
Limnodriloides olearius E. & Milligan, 1989	X	—	540
Tubificoides bruneli Erséus, 1989d	X	—	242

* This taxon, identified as ''?*Peloscoles gabriellae* Marcus, 1950'' by Cook (1970a), is probably one (or two?) deep-water species of *Tubificoides,* and not identical to *Tectidrilus gabriellae* (Marcus, 1950) (see Erséus, 1982b).

(Erséus 1986) and Pacific Oceans (Erséus 1979a, 1989a, b). The deepest finds so far concern two Pacific phallodrilines living in the hadal zone, *Bathydrilus hadalis* at 7298 m in the Aleutian Trench (Erséus 1979a), and *Abyssidrilus hessleri* (Erséus, 1989b) at 5916 m near the Philippine Trench.

Table 1 lists all (41) oligochaete taxa reported exclusively from depths greater than 200 m in the North Atlantic, the deepest record being from 4850 m. Thirty-three species are known from the American side of the ocean, and this includes some records from the Gulf of Mexico, and from off Surinam (north of South America), while a total of 15 species have been found in the deep sea off Europe. Seven species are reported from both sides of the ocean. Although this latter group makes up only about 17% of the total North Atlantic deep-sea oligochaete fauna known to date, a striking pattern with regard to the depth distribution emerges. Five tubificids and one enchytraeid among these seven amphi-Atlantic oligochaete taxa all extend well into the abyssal zone; i.e., they reach bottoms that are at least between 2798 and 4632 m deep, and none of them has been found shallower than 1600 m. On the other hand, among 21 species solely recorded from bottoms between 242 and 2798 m, only *G. atlantica* (Enchytraeidae) has so far been collected from both sides of the ocean. In fact, *G. atlantica* is known also from the South Atlantic Ocean (Coates & Erséus 1985). Thus, the abyssal oligochaete species, here referring to the species extending their ranges from the continental slope down towards the abyssal plain, tend to be more widely distributed in the North Atlantic than the bathyal species (i.e., those restricted to the continental slopes), which appear to be largely endemic to one or the other side of the ocean. This pattern may be explained by the more or less continuous extension of abyssal habitats across the Atlantic; i.e., although the North American Basin (in the west) is separated from the Canary and North Eastern Atlantic Basins (in the east) by the Mid-Atlantic Ridge, the latter has numerous passages that are between 3000 and 4000 m deep (see, e.g., The Times' Atlas of the World. Comprehensive ed.).

As reviewed by Wilson & Hessler (1987), there are numerous examples in the literature of deep-sea species that are said to be widespread or even cosmopolitan, but it has also been pointed out (Wilson & Hessler 1987:187) that "the perceived size of species distributions may be directly correlated with the broadness of species concepts." For the North Atlantic deep-sea oligochaetes (Table 1), however, too much lumping does not seem to be a major problem, as such a large majority (83%) of the species are so far recorded only from one side of the ocean.

Due to the scarcity of records, it would be premature to draw any detailed conclusions about the amount of endemism of oligochaetous Clitellata within different parts of the North Atlantic deep sea. The data available suggest that the abyssal species are more widely distributed than the bathyal ones, but this pattern needs to be corroborated (or refuted) by additional collections from various areas of the North Atlantic Ocean. In this context, material from the Newfoundland Basin, the Mid-Atlantic Ridge, and the continental slopes south of Greenland and off the Reykjanes Ridge, all areas from which no oligochaetes are yet recorded, would be particularly important.

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Literature Cited

Anderson, T. D. 1973. Embryology and phylogeny in annelids and arthropods.—International Series of Monographs in Pure and Applied Biology, Zoology Division, vol. 50. Pergamon Press, Oxford, 495 pp.

Brinkhurst, R. O., & D. McKey-Fender. 1991. The anatomy of the pharynx of two predatory aquatic oligochaetes.—Canadian Journal of Zoology 69:669–675.

Coates, K. A., & C. Erséus, 1985. Marine enchytraeids (Oligochaeta) of the coastal Northwest Atlantic (Northern and Mid U.S.A.).—Zoologica Scripta 14:103–116.

Cook, D. G. 1970a. Bathyal and abyssal Tubificidae (Annelida, Oligochaeta) from the Gay Head-Bermuda transect, with descriptions of new genera and species.—Deep Sea Research 17: 973–981.

———. 1970b. *Peloscolex dukei* n. sp. and *P. aculeatus* n. sp. (Oligochaeta, Tubificidae) from the North-West Atlantic, the latter being from abyssal depths.—Transactions of the American Microscopical Society 88:492–497.

Dales, R. P. 1963. Annelids. Hutchinson University Library, London, 200 pp.

Darwin, C. 1881. The formation of vegetable mould through the action of worms. Murray, London, 326 pp.

Erséus, C. 1979a. Taxonomic revision of the marine genera *Bathydrilus* Cook and *Macroseta* Erséus (Oligochaeta, Tubificidae), with descriptions of six new species and subspecies.—Zoologica Scripta 8:139–151.

———. 1979b. Taxonomic revision of the marine genus *Phallodrilus* Pierantoni (Oligochaeta, Tubificidae), with descriptions of thirteen new species.—Zoologica Scripta 8:187–208.

———. 1982a. *Atlantidrilus,* a new genus of deep-sea Tubificidae (Oligochaeta).—Sarsia 67:43–46.

———. 1982b. Taxonomic revision of the marine genus *Limnodriloides* (Oligochaeta: Tubificidae).—Verhandlungen des naturwissenschaftlichen Vereins in Hamburg (Neue Folge) 25: 207–277.

———. 1983a. Deep-sea *Phallodrilus* and *Bathydrilus* (Oligochaeta, Tubificidae) from the Atlantic Ocean, with descriptions of ten new species.—Cahiers de Biologie Marine 24:125–146.

———. 1983b. New records of *Adelodrilus* (Oligochaeta, Tubificidae), with descriptions of two new species from the Northwest Atlantic.—Hydrobiologia 106:73–83.

———. 1984. New and little-known species of deep-sea Tubificidae (Oligochaeta) from the North-West Atlantic.—Zoologica Scripta 13:101–106.

———. 1986. Two new abyssal species of *Phallodrilus* (Oligochaeta, Tubificidae) from the South Indian Ocean.—Bulletin de Muséum National d'Histoire Naturelle, Paris, 4e sér, 8 (section A, no. 3):567–572.

———. 1988. Deep-sea Tubificidae (Oligochaeta) from the Gulf of Mexico.—Proceedings of the Biological Society of Washington 101:67–71.

———. 1989a. A new bathyal species of *Atlantidrilus* (Oligochaeta, Tubificidae) from New Caledonia.—Bulletin de Muséum National d'Histoire Naturelle, Paris, 4e sér., 11 (section A, no. 1): 97–100.

———. 1989b. *Phallodrilus hessleri,* new species (Oligochaeta: Tubificidae), from abyssal depths in the western Pacific Ocean.—Proceedings of the Biological Society of Washington 102:131–133.

———. 1989c. *Phallodrilus vescus,* new species (Oligochaeta: Tubificidae) from the Gulf of Mexico.—Proceedings of the Biological Society of Washington 102:134–136.

———. 1989d. Four new West Atlantic species of *Tubificoides* (Oligochaeta, Tubificidae).—Proceedings of the Biological Society of Washington 102:878–886.

———. 1990a. Marine Oligochaeta of Hong Kong. Pp. 259–335 *in* B. Morton, ed., Proceedings of the Second International Marine Biological Workshop: the marine flora and fauna of Hong Kong and Southern China, Hong Kong, 1986 Vol. 1. Hong Kong University Press, Hong Kong, 448 pp.

———. 1990b. The marine Tubificidae and Naididae (Oligochaeta) of Southwestern Australia. Pp. 43–88 *in* F. E. Wells, D. I. Walker, H. Kirkman & R. Lethbridge, eds., Proceedings of the Third International Marine Biological Workshop: the Marine Flora and Fauna of Albany, Western Australia Vol. 1. Western Australian Museum, Perth, 438 pp.

———. 1991. Two new deep-water species of the gutless genus *Olavius* (Oligochaeta: Tubificidae) from both sides of North America.—Proceedings of the Biological Society of Washington 104:627–630.

———. 1992. A generic revision of the Phallodrilinae (Oligochaeta, Tubificidae).—Zoologica Scripta 21:5–48.

———. & M. R. Milligan. 1989. Three new species of Tubificidae (Oligochaeta) from an oil seepage area on the continental slope of the northern Gulf of Mexico.—Proceedings of the Biological Society of Washington 102:887–893.

Gates, G. E. 1971. On a new species of California earthworm, *Haplotaxis ichthyophagous* (Oligochaeta, Annelida).—Proceedings of the Biological Society of Washington 25:203–212.

———. 1982. Farewell to North American megadriles.—Megadrilogica 4:12–77.

Hoffmeister, W. 1845. Die bis jetzt bekannten Arten aus der Familie der Regenwürmer als Grundlage zu einer Monographie dieser Familie. Braunsweig, 43 pp.

Jamieson, B. G. M. 1988. On the phylogeny and higher classification of the Oligochaeta.—Cladistics 4:367–410.

Marcus, E. du Bois-Reymond. 1950. A marine tubificid from Brazil.—Comunicaciones Zoológicas del Museo de Historia Natural de Montevideo 3:1–6.

Pinder, A., & R. O. Brinkhurst. 1997. The family Capilloventridae (Annelida, Clitellata) in Australia, with descriptions of two new species of *Capilloventer.*—Zoologica Scripta 26:255–265.

Rota, E., & C. Erséus. 2003. New records of *Grania* (Clitellata, Enchytraeidae) in the Northeast Atlantic (from Tromsø to the Canary Islands), with descriptions of seven new species.—Sarsia 88: 210–243.

Rota, E., & B. Healy. 1999. A taxonomic study of some Swedish Enchytraeidae (Oligochaeta), with descriptions of four new species and notes on the genus *Fridericia.*—Journal of Natural History 33:29–64.

Southern, R. 1913. Clare Island Survey. Part 48. Oligochaeta.—Proceedings of the Royal Irish Academy 31:1–48.

Vejdovský, F. 1884. System und Morphologie der Oligochaeten. Franz Rivnac, Prague, 172 pp.

Wilson, G. D. F., & R. R. Hessler. 1987. Speciation in the deep sea.—Annual Review of Ecology and Systematics 18:185–207.

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On two new genera of pea crabs parasitic in holothurians (Crustacea: Decapoda: Brachyura: Pinnotheridae) from the Indo-West Pacific, with notes on allied genera

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Abstract.—Two new genera of pea crabs of the family Pinnotheridae, *Holotheres* and *Buergeres,* members of which are parasites of sea cucumbers, are described from the Indo-West Pacific. Species of *Holotheres* are characterized by having all the dactyli of the walking legs of females short and subequal in length, with the spatuliform dactylus of the third maxilliped inserted very near or at the base of the propodus. Species of *Buergeres* are characterized by having the last dactyli of the walking legs of females elongate and longer than those of the other legs, with the subspatuliform dactylus of the third maxilliped inserted distinctly before the base of the propodus. *Holotheres* and *Buergeres* are compared to other genera whose members are associated with holothurians, *Holothuriophilus* Nauck, 1880, and *Alain* Manning, 1998 (obligate parasites); as well as *Pinnaxodes* Heller, 1865 (facultative parasites).

In a synopsis of the Pinnotheridae, Manning (1993a: 127, 128) defined the genus *Pinnotheres* Bosc, 1802, sensu stricto as having a subhexagonal or subcircular carapace without any surface ornamentation or sculptures, a third maxilliped which has the ischium and merus completely fused (without any trace of a suture) and a three-segmented palp in which the dactylus is slender, inserted basally on the propodus; the dactyli of the first to fourth walking legs are subequal and similar, short and strongly curved, with the tips simple; and all the seven male abdominal somites are free. Manning (1993a), however, did not treat most of the species of *Pinnotheres* which live in holothurians, all of which have a third maxilliped in which the dactylus is not slender but spatuliform to subspatuliform. In addition, the third maxilliped of most of these species has the inner margin usually angular, and the carpus of the third maxilliped is distinctly shorter than the propodus that is relatively long and slender. In this combination of characters, these species are very different from almost all other taxa now classified in *Pinnotheres* sensu stricto or any of the other non-holothurian symbiotic genera recognized or described by Manning (1993a, 1993b) and other workers. Manning (1993a:128) did note briefly in his synopsis, however, that one genus parasitic in holothurians, *Holothuriophilus* Nauck, 1880, was valid, and subsequently elaborated more on this (Manning 1993b).

Currently, 16 species of pinnotherid crabs are known to be parasites of holothurians, and of these, 13 occur only in the Indo-West Pacific (see Schmitt et al. 1973, Hamel et al. 1999). The eastern Pacific spe-

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* Deceased 18 January 2000.

cies which are obligate parasites in holothurians are both members of *Holothuriophilus* Nauck, 1880, although one species of *Opisthopus* Rathbun, 1893, is occasionally found in sea cucumbers (Rathbun 1918, Schmitt et al. 1973). The 13 Indo-West Pacific species are *Alain crosnieri* Manning, 1998 (Indonesia); *Ostracotheres holothuriensis* (Baker, 1907) (South Australia); *Pinnaxodes major* (Ortmann, 1894) (Japan); *Pinnotheres deccanensis* Chopra, 1931 (southern India); *P. flavus* Nauck, 1880 (Philippines); *P. halingi* Hamel, Ng & Mercier, 1999 (Solomon Islands); *P. holothuriae* Semper, 1880 (Philippines); *P. ortmanni* Bürger, 1895 (Philippines, Peninsular Malaysia, Singapore); *P. pilumnoides* Nobili, 1905 (Red Sea, Gulf of Aden); *P. semperi* Bürger, 1895 (Java, Sumatra, Sulawesi, Singapore); *P. setnai* Chopra, 1931 (Andaman Islands); *P. tenuipes* Bürger, 1895 (Philippines); and *P. villosissimus* Doflein, 1904 (Sumatra, Andaman Islands, New Guinea) (Chopra 1931, Schmitt et al. 1973, Pregenzer 1988, Van den Spiegel & Jangoux 1989, Hamel et al. 1999).

Most of the species parasitic in holothurians now placed in *Pinnotheres* sensu lato can, however, be divided into two distinct "groups" on the basis of the dactyli of their walking legs and form of the third maxilliped (see Hamel et al. 1999). Members of one "group" (*P. semperi, P. flavus, P. villosissimus* and *P. setnai*) have all the dactyli of the female walking legs short and similar in length, and the dactylus of the palp of the third maxilliped inserted at the base of the propodus. Members of the second "group" (*P. ortmanni, P. holothuriae, P. tenuipes* and *P. deccanensis*) have the dactyli of the last female walking leg styliform and much longer than the short and hooked dactyli of the other three pairs of legs, and the dactylus of the palp of the third maxilliped inserted well before the base of the propodus.

The present paper serves to diagnose two new genera for these two "groups". The abbreviations MXP3 refers to the third maxilliped; WL1–4 refer to the first to fourth walking legs respectively; and Gl to the male first pleopod. The terminology follows Manning (1993a). Measurements are of the carapace width and length, respectively. Specimens examined are deposited in the Zoological Reference Collection of the Raffles Museum, National University of Singapore (ZRC); Senckenberg Museum, Frankfurt-am-Main (SMF); National Science Museum, Tokyo (NSMT); Zoological Museum of the University of Copenhagen (ZMUC); and National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Notes on the Material of Otto Bürger

A note on the pinnotherid material of Semper, Nauck and Bürger in the USNM is necessary. In 1906, the USNM received six lots of pinnotherid crabs on exchange from the University of Göttingen in Germany. This material was from the collections made by C. Semper and was used for several studies by Semper (1880), Nauck (1880) and Bürger (1895), all of whom were at the University of Göttingen. All of this material was reported by Bürger (1895). This shipment included: *Pinnotheres affinis* Bürger, 1895 (1 ovigerous female, 9.5 by 8.2 mm, Bohol, Philippines, USNM 32435); *Pinnotheres exiguus* Bürger, 1895 (1 ovigerous female, 5.6 by 4.6 mm, Samar, Philippines, USNM 32432); *Pinnotheres flavus* Nauck, 1880 (2 ovigerous females, 8.4 by 7.8 mm, 10.0 by 9.5 mm, Zamboanga, Philippines, USNM 32434); *Pinnotheres glaber* Bürger, 1895 (1 ovigerous female, 7.8 by 6.5 mm, Palawan Island, Palaos Islands, USNM 32431); *Pinnotheres holothuriae* Semper, 1880 (2 ovigerous females, 10.1 by 9.3 mm, 8.0 by 6.5 mm, Zamboanga, Philippines, USNM 32433); and *Xenophthalmus latifrons* Bürger, 1895 (1 ovigerous female, 9.5 by 8.1 mm, Bohol, Philippines, USNM 32436).

Mary Jane Rathbun, then Second Assistant Curator of Invertebrates at the USNM, considered these specimens to be types. Checking with various museums, including the collections in the University of Göttingen, Schmitt et al. (1973) tracked down many of the specimens of Semper, Nauck and Bürger but commented that the types of *P. exiguus, P. flavus, P. holothuriae* and *X. latifrons* were lost or unknown. Curiously, Schmitt did not check his own collections at the USNM. Apparently, sometime after 1906, at least some of Semper's material was transferred to the Zoological Museum, Berlin, where the true types of *P. affinis* and *P. glaber* are still extant (O. Coleman, in litt.). There are no types of *P. exiguus, P. flavus, P. holothuriae* and *X. latifrons* in the Berlin Museum (O. Coleman, in litt.). The surviving specimens, representing the bulk of Semper's material in the University of Göttingen, were recently transferred to the Senckenberg Museum. Michael Türkay and Andreas Allspach kindly provided a list of the extant Göttingen pinnotherid specimens now in the SMF. Of the species reported from holothurians by Semper, Nauck and Bürger, only specimens of two species are still extant, *P. flavus* and *Holothuriophilus trapeziformis*. There were also several lots in which the labels have been lost, but examination of this material by one of us (PKLN) did not uncover specimens of any pinnotherid species parasitic in holothurians. On the basis of this material, we also provide herein figures of *P. flavus* and *P. holothuriae*, each of which are transferred to one of the two new genera here recognized.

Taxonomic Account

Holotheres, new genus

Type species.—*Pinnotheres semperi* Bürger, 1895, by present designation.

Included species.—Five: *H. flavus* (Nauck, 1880), *H. halingi* (Hamel, Ng & Mercier, 1999), *H. semperi* (Bürger, 1895), *H. setnai* (Chopra, 1931), and *H. villosissimus* (Doflein, 1904).

Diagnosis.—Obligate symbionts in holothurians. Carapace circular to subcircular, often highly setose; posterior carapace margin distinctly convex. WL subequal right and left; WL3 similar in length, longer than WL4; female WL1–4 with dactyli short, similar in length and form. Ischium and merus of MXP3 completely fused, without trace of suture; dactylus of palp spatuliform, subequal in length to propodus, inserted near base of propodus. G1 simple, curved tube, tapering from base to tip, slightly recurved distally.

Etymology.—The name is derived from an arbitrary combination of the name for sea cucumbers *Holothuria,* and *Pinnotheres.* Gender masculine.

Remarks.—Among taxa wholly symbiotic with holothurians, *Holotheres* is perhaps closest to *Holothuriophilus* Nauck, 1880, sensu Manning, 1993b (type species *Holothuriophilus trapeziformis* Nauck, 1880). The dactylus and propodus of the palp of MXP3 of *Holothuriophilus* species (Fig. 7C), however, is distinctly shorter than those of *Holotheres* species (Figs. 1B, 3B). In any case, *Holothuriophilus* is known only for certain from the eastern Pacific (Manning 1993b). Takeda & Prince Masahito (2000) transferred *Pinnaxodes mutuensis* (Sakai, 1939), which is known only from bivalves, to *Holothuriophilus* but we do not agree (see "Notes on *Pinnaxodes* and *Holoturiophilus*").

Two other genera, *Pinnaxodes* Heller, 1865, and *Opisthopus* Rathbun, 1893, have some species which are facultatively found in holothurians (Rathbun 1918, Schmitt et al. 1973), and have carapaces and MXP3 similar to those of *Holotheres.* Species of *Holotheres* can be easily separated from *Pinnaxodes* in having the posterior carapace margin prominently convex (Figs. 1A, J, 2A, 3A) (versus slightly convex to almost straight, Fig. 6A, E), a proportionally longer dactylus and propodus of the MXP3 (Figs. 1B, 3B versus Fig. 6B, F), the dactylus of the MXP3 is inserted near the base of the propodus (Figs. 1B, 3B) (versus inserted ⅓ from base of propodus) (Fig. 6B,

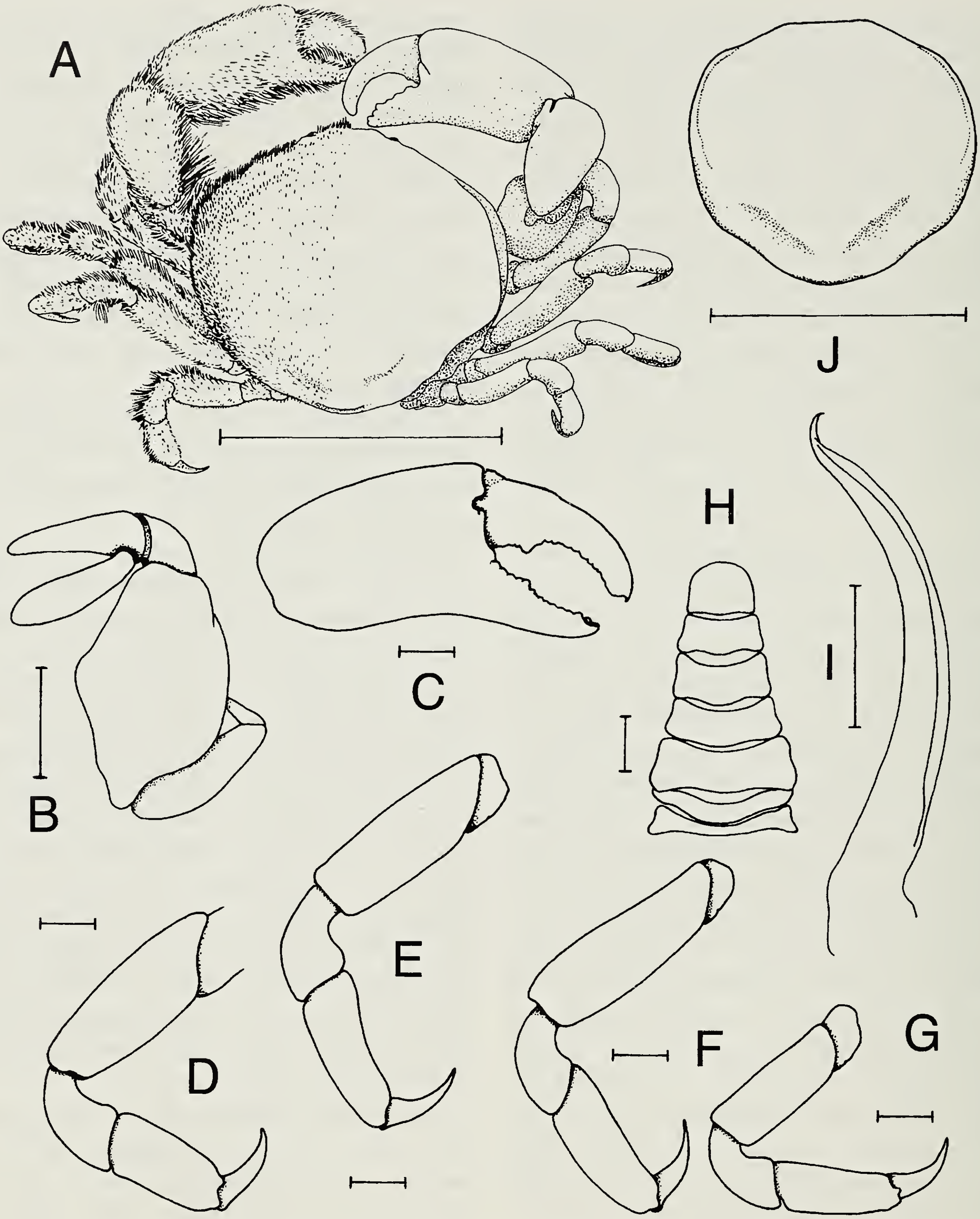

Fig. 1. *Holotheres semperi* (Bürger, 1895). A–I, neotype male (7.9 by 7.2 mm) (ZRC 1965.11.24.40); J, female (10.7 by 10.2 mm) (ZRC 1965.11.24.41). A, overall view of specimen (setae on right half of body denuded); B, left MXP3, outer view; C, right chela, outer view; D, WL1; E, WL2; F, WL3; G, WL4; H, male abdomen; I, left G1; J, carapace, dorsal view. (Except for A, all structures denuded.) Scales: A, J = 5.0 mm, B–I = 1.0 mm.

F), the ischium and merus are completely fused without any trace of a suture (Figs. 1B, 3B versus Fig. 6B, F), and the male telson is semicircular (Figs. 1H, 2G) (versus usually medially expanded laterally to form rounded to subpentagonal structure, cf. Campos et al. 1998: fig. 3A, C; Takeda & Masahito 2000: fig. 4B) (see also Campos et al. 1998, Takeda & Prince Masahito 2000). *Opisthopus* has the same male abdomen form as *Holotheres,* but can be separated by the same carapace and MXP3 characters discussed above for *Pinnaxodes* (see Campos et al. 1998, Campos & Manning 2000).

Of the five species here included in *Holotheres,* the types of two species, *H. semperi* (Bürger, 1895) and *H. flavus* (Nauck, 1880), are considered to be lost. The taxonomy of only *H. semperi* and *H. flavus* are discussed herein. *Holotheres setnai* has been well described and figured by Chopra (1931). *Holotheres halingi* has been described and figured in detail by Hamel et al. (1999). *Holotheres villosissimus* (see Doflein 1904, Van den Spiegel & Jangoux 1989) is not well known and must be redescribed when fresh specimens become available.

Holotheres semperi (Bürger, 1895)
Fig. 1

Pinnotheres semperi Bürger, 1895:382, pl. 9 fig. 28, pl. 10 fig. 27.—Lanchester, 1900:761.—Chuang, 1961:189, pl. 94.—Schmitt et al., 1973:85. (See Schmitt et al. (1973:85) for additional references).

Neotype.—Male (7.9 by 7.2 mm) (ZRC 1965.11.24.40) in respiratory tree of *Holothuria scabra,* coll. S. H. Chuang, 1950s.

Other material examined.—1 female (10.7 by 10.2 mm) (ZRC 1965.11.24.41), same data as neotype. 1 male (10.5 by 10.0 mm), 1 female (4.8 by 4.3 mm) (ZRC 1965.11.24.38–39), in cloaca of *Holothuria scabra,* coll. S. H. Chuang, 1950s. 2 males (7.7 by 6.8 mm, 7.0 by 6.6 mm), 2 females (11.2 by 9. mm, 10.7 by 9.0 mm) (all specimens badly damaged and carapace crushed in parts) (ZRC 1965.11.24.34–37), in cloaca of *Holothuria scabra,* coll. S. H. Chuang, 1950s. 1 male (8.4 by 7.9 mm) (ZRC 1965.11.24.16), 6–12 fathoms, from sea cucumber, Pulau Tekong, Singapore, coll. M. W. F. Tweedie, 1960s.

Diagnosis.—Male carapace subquadrate, width to length ratio ca. 1.1; female carapace subcircular, width length ratio 1.1–1.2; dorsal surface gently convex, covered with dense layer of short setae longer along lateral regions, completely obscuring outline and surface; intestinal region slightly depressed. Anterolateral margin of male almost straight, lateral margin gently convex, posterolateral margin gently concave; anterolateral and lateral margin of female more confluent, gently convex; sub-branchial surface densely setose. MXP3 with ischium and merus completely fused, without trace of suture, subovate, inner margin subangular submedially; exopod relatively stout, outer margin convex, with well developed setae on flagellum; palp 3-segmented, propodus elongate, conical, subequal in length to dactylus; dactylus spatuliform, articulates at base of propodus. Chelipeds subequal; surfaces of merus, carpus, palm and fingers densely covered with setae, those on inner surfaces relatively longer; palm relatively stout; fingers shorter than palm; cutting edges of dactylus and propodus each with sub-basal large tooth and numerous denticles before and after it; distalmost part of fingers excavated on inner surface. WL relatively stout, WL2 > WL3 > WL1 > WL4 in length (basis-ischium to tip of dactylus); dactyli of WL1–4 relatively long, sharply tapering, all subequal in length; dorsal and ventral margins of meri, carpi and propodi of all legs densely lined with setae of various lengths, completely obscuring margins. Male abdomen with all 6 segments distinct, freely articulating, telson semicircular; lateral margins of segments 3–6 gently concave. Female abdomen with all segments freely articulating. G1 relatively slender, gently sinuous, tip distinctly curving upwards.

Biology.—*Holotheres semperi* has been reported from inside *Holothuria fursocinerea* and *H. scabra* (see Schmitt et al. 1973).

Remarks.—The identity of *Pinnotheres semperi* Bürger, 1895, is a problem. In describing the species on the basis of one male and one female, Bürger (1895:382, pl. 9 fig. 28, pl. 10 fig. 27) described and figured a female specimen with a subhexagonal carapace highly setose over its carapace and legs, well produced triangular frontal margin, WL4 substantially shorter than the rest of the legs, and MXP3 in which the dactylus of the palp is spatuliform and as long as the propodus. A pair of specimens was subsequently reported by Lanchester (1900:761) who noted: "The specimens which Dr. Bürger has described came from the cloaca of *Hol. fusco-cinerea*; whereas the specimens we obtained from that Holothurian are, I find, referable to *P. ortmanni.* The host, from which came Dr. Bürger's example of the latter species, was, I suppose, not known, as he makes no reference to it. In both these species, the animal was found high in the respiratory tree, forming an enormous gall; whether it would be able to extricate itself from this, and move, at will, up or down the respiratory tree, I do not know, but it has the appearance of a fixture, *nolens volens*". The species was next reported by Chuang (1961:189) who noted that the species occurs in the respiratory tree of the sea cucumber, *Holothuria scabra*: "A pair of them consisting of a male and a female may occur in one single sea cucumber. The relatively thick carapace, about 1 cm in diameter, is white in colour and has a circular outline. The cylindrical legs and both chelipeds are hairy".

In their synopsis of the Pinnotheridae, Schmitt et al. (1973) stated that the male and female syntypes of *H. semperi* (museum number not stated), which were originally in the University of Göttingen, are no longer extant. The Göttingen material, as discussed earlier, was examined by one of us (PKLN), and it does not contain any specimens which can be identified with this species. A check with the Berlin Museum confirms that the types of *H. semperi* are not there (O. Coleman, in litt.). They are also not in the USNM, and are thus almost certainly lost.

Comparisons of the present series of specimens from Singapore and the description and figures of the types by Bürger (1895), however, reveal a number of discrepancies. The relatively prominently produced triangular frontal margin of the female figured by Bürger (1895: pl. 9 fig. 28a) is an important one. The females on hand all have very narrow, non-protruding front, with the margin distinctly sinuous, and the eyes are not visible in dorsal view (Fig. 1J). In contrast, males have a more produced front, appearing subtruncate when viewed dorsally (Fig. 1A). Even when a specimen is angled such that the anterior part of the carapace arches upwards, the frontal margin never appears triangular. The frontal margins of uncleaned male specimens, however, are densely lined with setae and when covered with fine sediment, the "front" does appear to be more triangular in shape, especially when observed dry and the setae clump medially. None of the examined female specimens, however, resemble the specimen figured by Bürger, even when they are not cleaned. It would thus appear that Bürger might have figured an uncleaned, undenuded male rather than a female. It is also pertinent to note that the carapace shapes of the present males agree well with Bürger's figure, although the present specimens do not appear to be as setose. The distinct pattern of setae figured by Bürger is certainly not at all apparent in the present specimens. Bürger (1895:382) noted that the male he had, measured 7.0 mm by 6.8 mm, and the female 6.5 by 6.5 mm. All the present specimens examined are broader than long. Lanchester (1900:761), however, reported that his specimens were longer than broad (male 10.5 by 11.0 mm, female 7.75 by 8.0 mm). Whether these measurements were accurate or if they were taken from cleaned specimens could not be ascertained. The very short WL4 is noteworthy, as none of the present specimens on hand (male or female) has such a short WL4 as figured by Bürger (1895: pl. 9 fig. 28a). It seems likely though, that the WL4 of Bürger's specimen appears shorter than it actually is because the leg was bent slightly upwards when it was drawn. The MXP3 figured by Bürger (1895: pl. 10 fig. 27) agrees well with those of the present specimens, although the dactylus of the palp he figured appears slightly less spatuliform, the dactylus is subequal in length to the propodus, and the outer margin of the fused ischium-merus is more rounded. The figure, however, is too schematic. The male abdomen figured by Bürger (1895: pl. 9 fig. 28b) is also too schematic to be of much use, although its general shape and proportions agree with those of the present specimens.

In describing *H. setnai* from the Andaman Islands (as *Pinnotheres setnai*), Chopra (1931:313) commented that his species differed from *H. semperi* in the carapace being more arched; the front is truncate with the anterior margin of the front depressed medially (not triangular); the large chela is more slender, with the palm proportionately longer and the fingers having well developed teeth; WL4 is very much smaller than the others; and the propodus of the palp of MXP3 is longer than the dactylus (not subequal in length). Of the above differences, as has been discussed earlier, only the proportions of the chela are really valid. On the basis of Chopra's (1931) excellent description and figures, it is clear that *H. setnai* and *H. semperi* are very close. Chopra, however, did not figure the carapace of the male. On the basis of Chopra's (1931) figures, *H. setnai* can also be separated from *H. semperi* by the relatively broader and more sinuous female frontal margin, the more slender ischio-merus of MXP3, and the carpus of the chelipeds not possessing a deep longitudinal cleft. Both species should thus be regarded as separate for the time being.

The pair of specimens figured by Chuang (1961: pl. 94: Figs. 2 and 3) is now in the ZRC (ZRC 1965.11.24.40–41), and the male, 7.9 by 7.2 mm (ZRC 1965.11.24.40), is here designated as the neotype of *Pinnotheres semperi* Bürger, 1895. The specimens are very consistent in all the characters discussed here. Other than the sexually dimorphic features of the abdomen and reproductive structures, the only major difference is in the shape of the carapace, being more ovate in the female (Fig. 1A versus Fig. 1J). The form and proportions of the chela and WL1–4 are not sexually dimorphic.

Holotheres flavus (Nauck, 1880)
Figs. 2, 3

Pinnotheres flavus Nauck, 1880:23, 66.—Bürger, 1895:383, pl. 9 fig. 29, pl. 10 fig. 29, 35.—Schmitt et al., 1973:45. (See Schmitt et al. (1973:45) for additional references).

Lectotype.—Male (8.6 by 7.9 mm) (SMF 951a), Bohol, Ubay, Philippines, coll. C. Semper, 1863–1864.

Paralectotypes.—2 males (7.9 by 7.6 mm, 8.0 by 7.6 mm), 2 females (10.3 by 10.0 mm, 8.9 by 8.0 mm) (SMF 951b), same data as lectotype. 2 ovigerous females (10.0 by 9.5 mm, 8.4 by 7.8 mm) (USNM 32434), Zamboanga, Philippines, coll. C. Semper, 1876.

Diagnosis.—Female carapace subcircular, width to length ratio ca. 1.1; female carapace subcircular, width length ratio ca. 1.1; dorsal surface gently convex, covered with short setae which obscures outline. Anterolateral margin arcuate, posterolateral margin gently convex; sub-branchial surface setose. MXP3 with ischium and merus completely fused, without trace of suture, subovate, inner margin subangular submedially; exopod relatively stout, outer margin convex, with well developed flagellal setae; palp 3-segmented, propodus elongate, subconical, subequal in length to dactylus; dactylus spatuliform, articulates at base of propodus. Chelipeds subequal; inner surfaces of merus, carpus, palm and fingers covered with setae; palm relatively stout; fingers shorter than palm; cutting edges of dactylus and propodus each with sub-basal large tooth and several denticles before it. WL relatively stout, WL2 > WL3 > WL1 > WL4 in length (basis-ischium to tip of dactylus); dactyli of WL1–4 relatively long, sharply tapering, all subequal in length; dorsal and ventral margins of meri, carpi

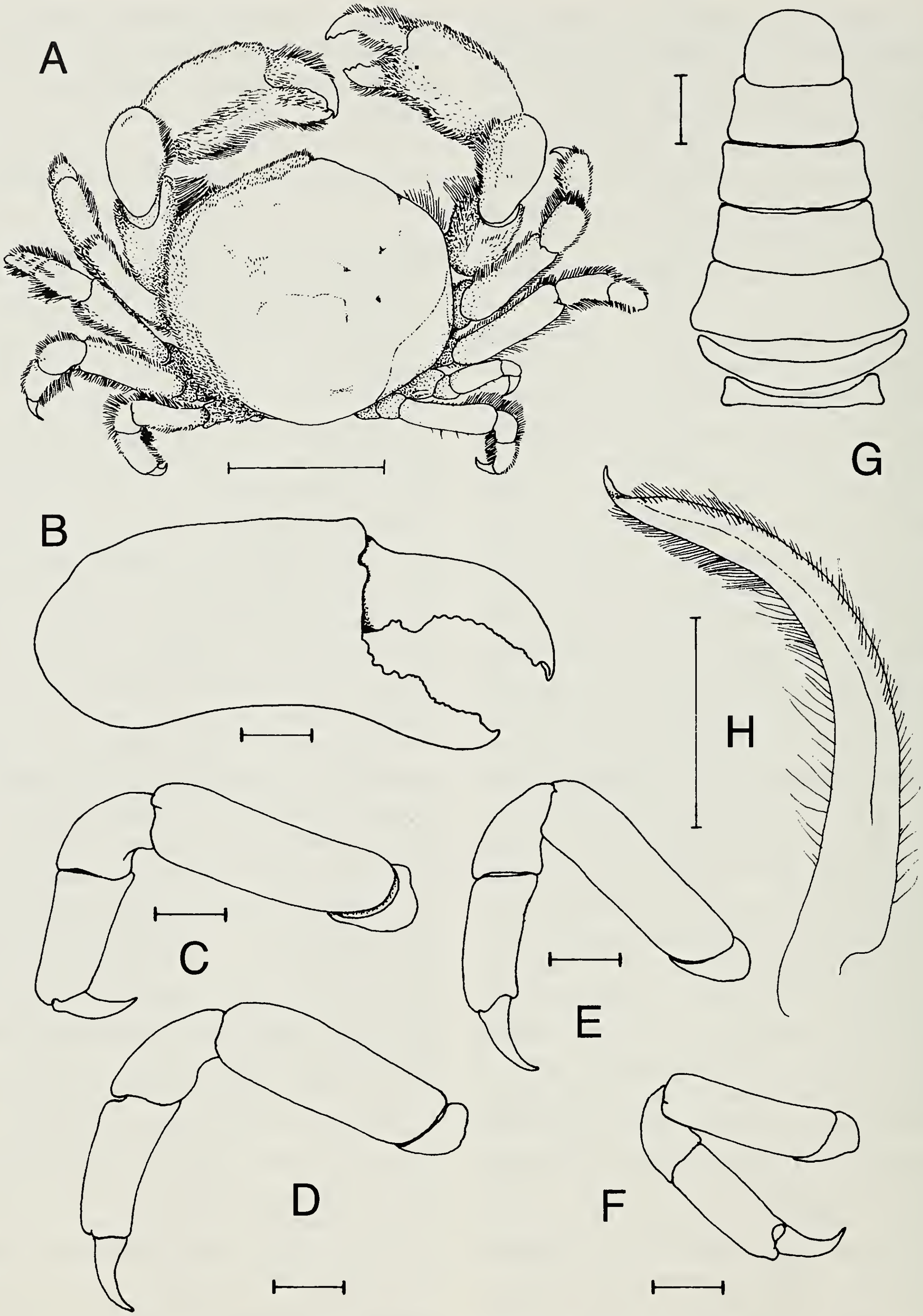

Fig. 2. *Holotheres flavus* (Nauck, 1880). Lectotype male (8.6 by 7.9 mm) (SMF 951a). A, overall view of specimen (setae on right half of body denuded); B, right chela, outer view; C–F, WL1–4 respectively; G, male abdomen; H, left G1. (Except for A, H, all other structures denuded.) Scales: A = 5.0 mm, B–H = 1.0 mm.

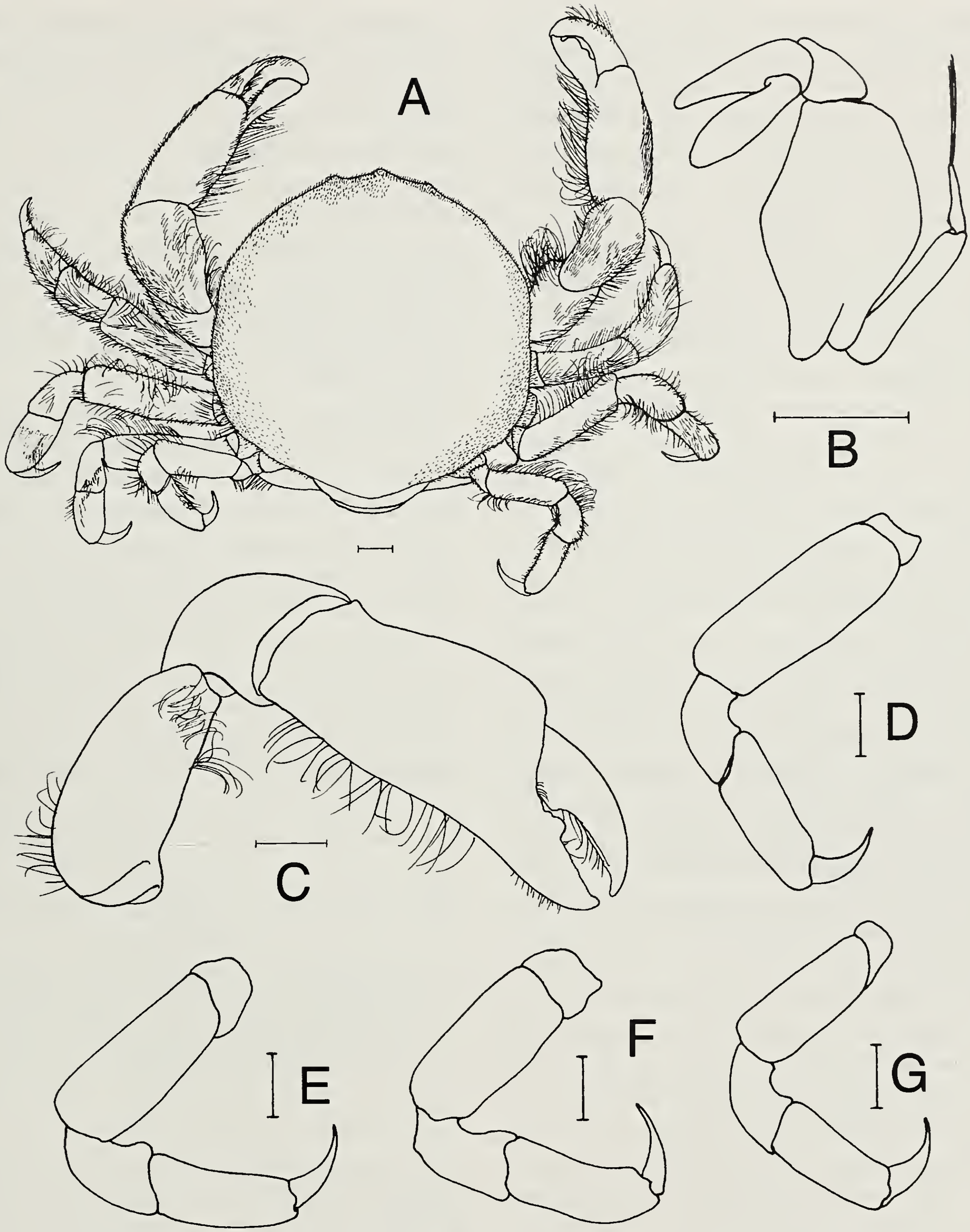

Fig. 3. *Holotheres flavus* (Nauck, 1880). Paralectotype female (10.0 by 9.5 mm) (USNM 32434). A, overall view of specimen; B, left MXP3 (denuded), outer view; C, right cheliped, outer view; D–G, WL1–4 respectively, denuded. Scales = 1.0 mm.

and propodi of all legs lined with setae of various lengths, obscures margins. Female abdomen with all segments freely articulating.

Biology.—Bürger (1895) noted that the species was collected from an unidentified holothurian. Nothing else is known.

Remarks.—*Holotheres flavus* was originally described by Nauck (1880) (as *Pinnotheres flavus*) on the basis of an unknown number of specimens from an unspecified site or sites in the Philippines, obtained from collections there by Semper (Nauck, 1880:5), although he did not explicity state so when describing the species. Bürger (1895:383) subsequently reported six males and six females collected by Semper from Zamboanga in the Philippines. De Man (1887:720, 721), who reappraised Nauck's taxa, provided measurements for only one male and one female (without specific location), suggesting he only had two specimens. Schmitt et al. (1973:45) commented that there were "2 syntypes: ZIMB 67/297 [Göttingen Museum], no longer extant; type locality: 'Philippinen'". How Schmitt et al. (1973) knew there were only two syntypes was not stated, perhaps these were the specimens used by De Man (1887). As discussed earlier, two of the females from Göttingen were actually given to the USNM, and the SMF has taken over from Göttingen three male and two female specimens of *P. flavus.* There are no specimens on this species in the Berlin Museum (O. Coleman, in litt.). Since Semper's material was used by Nauck, Bürger and De Man, it is reasonable to believe that all the material on hand are syntypes. We hereby select a male (8.6 by 7.9 mm, SMF 951a) as the lectotype of *Pinnotheres flavus* Nauck, 1880.

Holotheres flavus is similar to *H. semperi,* but can be distinguished by its more quadrate male carapace with the lateral margins straighter, appearing subparallel (Fig. 2A) (versus more rounded, Fig. 1A), the dorsal surface of the carapace covered with pubescence only along the margins (Fig. 2A) (versus uniformly all over, Fig. 1A), and most significantly, the G1 is more strongly curved, appearing distinctly C-shaped (Fig. 2H versus Fig. 1I).

Buergeres, new genus

Type species.—*Pinnotheres ortmanni* Bürger, 1895, by present designation.

Included species.—Four: *B. deccanensis* (Chopra, 1931), *B. holothuriae* (Semper, 1880), *B. ortmanni* (Bürger, 1895), and *B. tenuipes* (Bürger, 1895).

Diagnosis.—Obligate symbionts in holothurians. Carapace circular to subcircular, broader than long. WL subequal right and left; WL4 dactylus of female much longer than short, hooked dactyli of WL1–3. Ischium and merus of MXP3 completely fused, without trace of suture; dactylus of palp subspatuliform, subequal in length to propodus, inserted distal to base of propodus (⅓ to midway from base). G1 a simple tube, tapering from base to tip, slightly recurved distally.

Etymology.—The genus is named in honor of Otto Bürger, whose key paper in 1895, laid the foundation for much of what has been done recently in pinnotherid taxonomy. The genus name is derived from an arbitrary combination of Bürger's name and *Pinnotheres.* The gender is masculine.

Remarks.—The key diagnostic features of *Buergeres* are the form of the MXP3 (dactylus subspatuliform, inserted well before base of propodus), and relative length of the female WL4 (dactylus much longer than WL1–3). No other group of pinnotherids associated with holothurians has these characters. With regards to the form of the MXP3 and WL4, *Buergeres* is perhaps closest to the American *Tumidotheres* Campos, 1989, but in members of the latter genus, the carapace is less rounded with the front more distinctly produced, and the propodus and dactylus of MXP3 are proportionately shorter (see Campos 1989). *Tumidotheres* is also wholly symbiotic with various bivalves while *Buergeres* is an obligate parasite of holothurians. The relatively subspatuliform dactylus of MXP3 also allies it with Atlantic and eastern Pacific taxa like *Afropinnotheres* Manning, 1993, *Nepinnotheres* Manning, 1993, *Alainotheres* Manning, 1993, and *Raymondia* Campos, 2002 (see Manning 1993a, Campos 2002) but they are quite different in the form of the carapace and legs. Some genera of pinnotherids have adult females with the WL3 longest (e.g., *Arcotheres* Manning, 1993, see Campos & Manning 2001); or WL2 longest (e.g., the Atlantic *Zaops* Rathbun, 1900, and *Waldotheres* Manning, 1993; see Manning 1993a, 1993b; Campos and Manning 2000); but in the case of *Buergeres,* WL1–3 are more or less subequal in length, with the dactylus of WL4 longest and more prominently elongate than the rest. In any case, none of the species in these genera are associated with holothurians.

Of the four species presently referred to *Buergeres,* two, *B. holothuriae* (Semper, 1880) and *B. ortmanni* (Bürger, 1895) are treated here in detail. One of these, *B. deccanensis* (Chopra, 1931) was well described and figured by Chopra (1931) and its affinities are not in doubt. *Buergeres tenuipes* (Bürger, 1895) (type locality Ubay, Philippines) was described apparently from only one female specimen, but on the basis of Bürger's (1895:371, pl. 9 fig. 11, pl. 10 fig. 11) figures of the third maxillipeds and walking legs, we have little doubt that it belongs in this genus as well. The type of *B. tenuipes* is apparently lost (see Schmitt et al. 1973:89) and we have not been able to locate it in any of the depositories we have checked.

Buergeres ortmanni (Bürger, 1895)
Fig. 4

Pinnotheres ortmanni Bürger, 1895:384, pl. 9 fig. 30, pl. 10 fig. 28.—Schmitt et al., 1973:61. (See Schmitt et al. (1973:61) for additional references).

Neotype.—Female (11.4 by 9.5 mm) (ZRC 2003.59), in holothurian in coral reef, exposed at edge of reef, Pulau Salu, northeastern Singapore, coll. R. U. Gooding, 28 April 1967.

Other material examined.—2 females (both 12.5 by 11.8 mm) (ZRC 1965.11.24.14–15), coll. Singapore, no other data.

Diagnosis.—Female carapace almost circular, slightly wider than long, width to length ratio 1.1–1.2; dorsal surface smooth, gently convex; intestinal region slightly depressed. Lateral margins gently convex; sub-branchial surfaces densely setose. MXP3 with ischium and merus completely fused, without trace of suture, subovate, inner margin subangular at distal ⅓; exopod relatively stout, outer margin gently convex, with well developed flagellal setae; palp 3-segmented, propodus elongate, longer than dactylus; dactylus spatuliform, articulation point anterior to base of propodus. Chelipeds subequal; inner surfaces of merus, carpus, palm and fingers densely covered with relatively long setae; palm relatively stout; fingers shorter than palm; cutting edges of dactylus and propodus each with sub-basal large tooth and 1 or 2 denticles before it, rest of cutting edges smooth, almost blade-like; tips hooked. WL relatively slender, WL2 > WL1 > WL3 > WL4 in length (basis-ischium to tip of dactylus); dactyli of WL1–3 relatively short, sharply tapering; dactylus of WL4 very long, ca. 3 times as long as those of other legs; dorsal margins of meri of all legs relatively densely lined with setae of various lengths, becoming sparse or absent along distal one-quarter; ventral margins of propodus of all legs relatively densely lined with setae on distal half. Female abdomen with all 6 segments distinct, freely articulating, telson semicircular. Male unknown.

Biology.—This species had been collected from *Holothuria fursocinerea* (see Lanchester 1900). The present specimens were obtained from an unknown host.

Remarks.—Bürger (1895) described *Buergeres ortmanni* (as *Pinnotheres ortmanni*) on the basis of one ovigerous female originally obtained by Semper from "Aibukit" in the Philippines. Bürger's specimen cannot be located in the SMF, USNM or Berlin Museum, and is presumed lost, as Schmitt et al. (1973:61) had indicated. Lanchester (1900) subsequently reported the species from Singapore. No other specimens are known. The present specimens in the ZRC from Singapore agree with the type description and figures well and we are confident they are conspecific. To stabilize the taxonomy of this species (especially since it is the proposed type species of *Buergeres*), we hereby select a neotype for *Pinnotheres ortmanni* Bürger, 1895, a female specimen measuring 11.4 by 9.5 mm from Singapore (ZRC 2003.59).

Buergeres holothuriae (Semper, 1880)
Fig. 5

Pinnotheres ortmanni Semper, 1880:105.—Bürger, 1895:381, pl. 9 fig. 27, pl. 10 fig. 26.—Schmitt et al., 1973:49. (See Schmitt et al. (1973:49) for additional references).

Type material.—Lectotype: ovigerous female (10.1 by 9.3 mm) (USNM 032433a), Zamboanga, Philippines, coll. Semper, 1876. Paralectotype: 1 ovigerous female (8.0 by 6.5 mm) (USNM 032433b), same data as lectotype.

Diagnosis.—Female carapace almost circular, slightly wider than long, width length ratio 1.1–1.2; dorsal surface smooth, gently convex. Lateral margins gently convex; sub-branchial surfaces gently setose. MXP3 with ischium and merus completely fused, without trace of suture, subcircular, inner margin rounded; exopod relatively stout, outer margin gently convex, with well developed flagellal setae; palp 3-segmented, propodus elongate, longer than dactylus; dactylus spatuliform, articulation point slightly anterior to base of propodus. Chelipeds subequal; inner surfaces of merus, carpus, palm and fingers covered with relatively long setae; outer surface of chela densely covered with short pubescence; palm relatively stout; fingers shorter than palm, basal one-third covered with dense pubescence; cutting edges of dactylus and propodus each with numerous denticles except for almost unarmed distal ⅓. WL relatively slender, WL2 > WL1 > WL3 > WL4 in length (basis-ischium to tip of dactylus); dactyli of WL1–3 relatively short, distinctly hooked; dactylus of WL4 very long, ca. 5 times as long as those of other legs; dorsal and ventral margins of meri of all legs lined with setae of various lengths; ventral margins of propodus and dactylus of all legs lined with setae. Female abdomen with all 6 segments distinct, freely articulating, telson semicircular. Male unknown.

Biology.—This species has been collected from *Stichopus variegatus* (see Bürger 1895), although the record from *Holothuria scabra* by Semper may be incorrect (see Schmitt et al. 1973:44).

Remarks.—Semper (1880) described *Buergeres holothuriae* (as *Pinnotheres holothuriae*) from an unspecified number of specimens from Zamboanga on Mindanao island in the Philippines. Bürger (1895) who used Semper's specimens for his study, reported that he had three males and eight females available, all of which are regarded as syntypes. Of these, the USNM has two females. The SMF does not have any specimens. Schmitt et al. (1973:49) had incorrectly stated that the types are no longer extant. The larger female specimen (10.1 by 9.3 mm, USNM 032433a) is here designated as the lectotype of *Pinnotheres holothuriae* Semper, 1880.

Notes on Allied Taxa Symbiotic in Holothurians

The generic affinities of *Ostracotheres holothuriensis* (originally described as *Pinnotheres holothuriensis*) should be re-examined in view of recent systematic developments in the family. The species was described from South Australia and has a two-segmented palp (Baker 1907, Pregenzer 1988), but its carapace form is rather unusual. Two other species, *Pinnotheres pilumnoides* and *Ostracotheres holothuriensis,* have been reported from hosts other than holothurians (see Schmitt et al. 1973). The other species mentioned, all placed in the genus *Pinnotheres* thus far, are obligate parasites of holothurians and are not known from other hosts.

Pinnotheres pilumnoides Nobili, 1905, known only from the Red Sea and Gulf of Aden, is similar to *Holotheres,* with short WL, the last apparently not elongate (al-

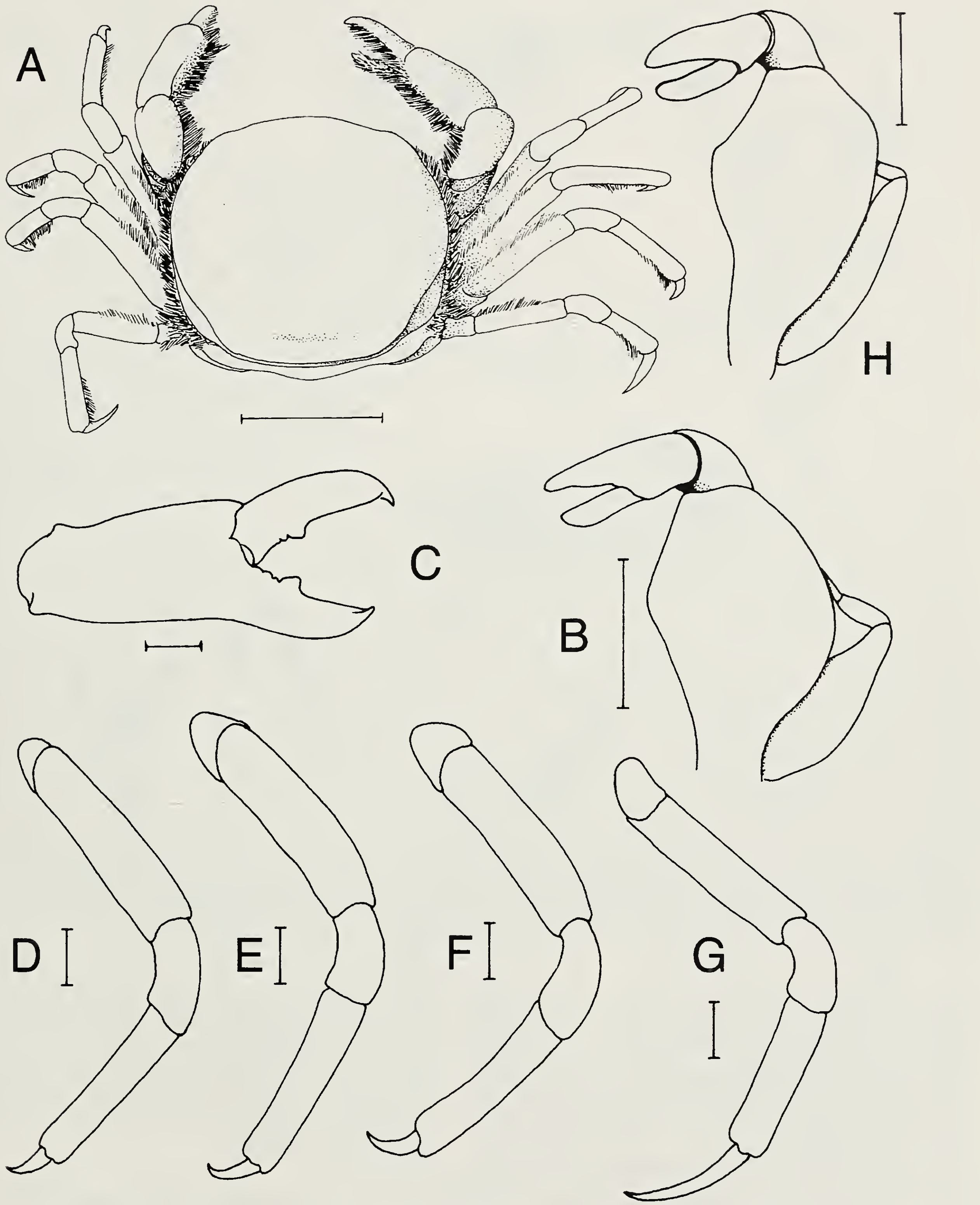

Fig. 4. *Buergeres ortmanni* (Bürger, 1895). A–G, neotype female (11.4 by 9.5 mm) (ZRC); H, female (12.5 by 11.8 mm) (ZRC 1965.11.24.14). A, overall view of specimen; B, H, left MXP3 (denuded), outer view; C, right chela (denuded), outer view; D–G, WL1–4 respectively (denuded). Scales: A = 5.0 mm, B–H = 1.0 mm.

though this is not at all clear from Nobili's (1905, 1906) descriptions, with the dactylus of MXP3 subspatuliform and inserted near the base of the propodus. The dactylus of MXP3 of *P. pilumnoides,* however, is much shorter than the propodus which is also distinctly shorter compared to other members of the group, and the inner margin of the fused ischio-merus is rounded and not angular (Nobili 1905:308, fig. 12). As such, in some ways, *P. pilumnoides* resembles members of the eastern Pacific *Holothurio-*

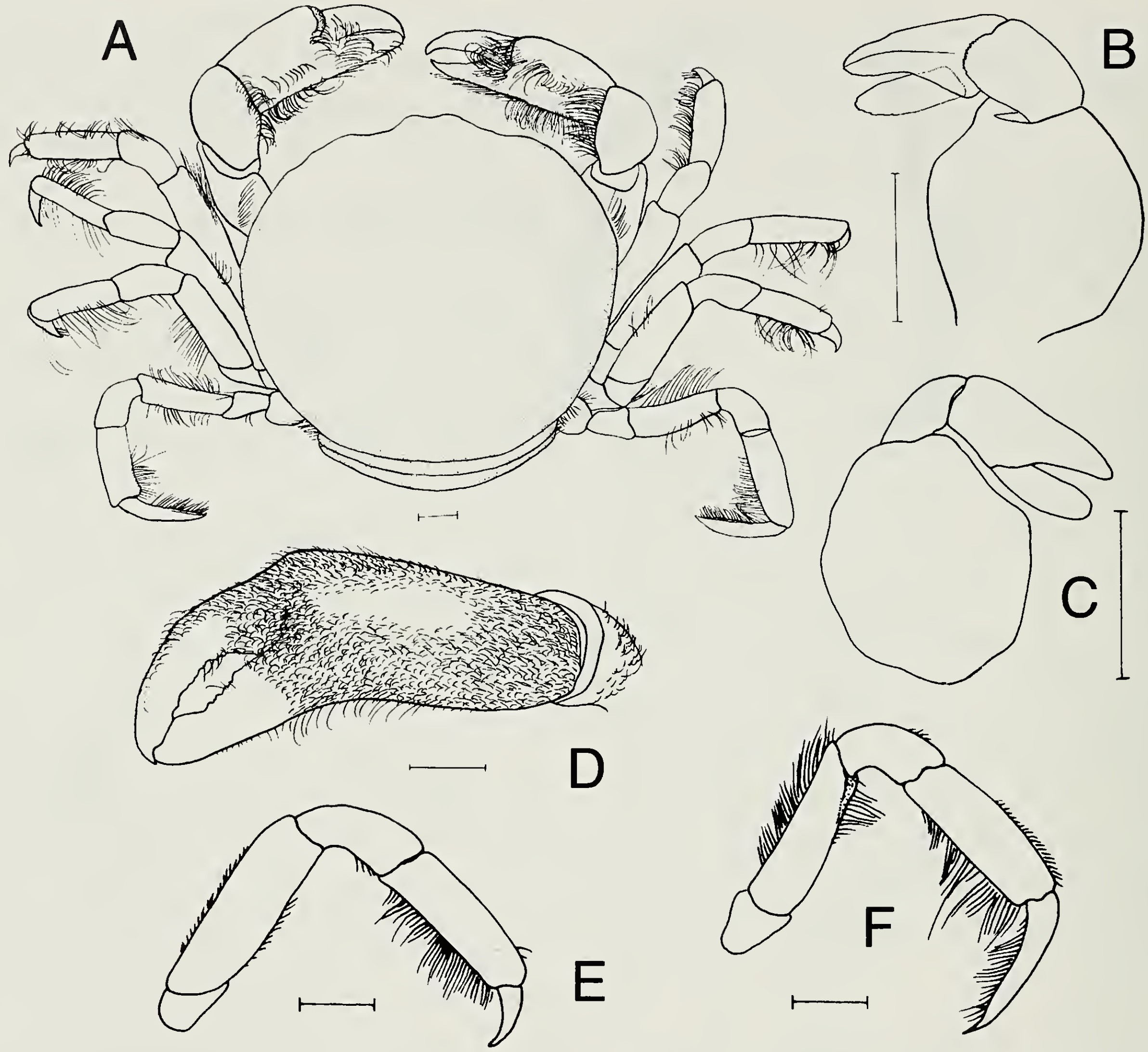

Fig. 5. *Buergeres holothuriae* (Semper, 1880). Lectotype female (10.1 by 9.3 mm) (USNM 032433a). A, overall view of specimen; B, left MXP3 (denuded), outer view; C, left MXP3 (denuded), inner view; C, left chela, outer view; D, WL3 (partially denuded); E, WL4 (partially denuded). Scales = 1.0 mm.

philus (sensu Manning 1993b) although they are clearly not congeneric. We prefer to exclude *P. pilumnoides* from the present discussion until we have an opportunity to examine specimens of the species. Certainly, as things are, *P. pilumnoides* does not fit into any of the Indo-West Pacific pinnotherid genera now recognized.

Alain Manning, 1998, can be distinguished from both *Holotheres* and *Buergeres,* as well as *P. holothuriensis* and *P. pilumnoides,* in the following characters: the spatuliform dactylus of MXP3 is inserted medially rather than proximally on the propodus; the carapace is subcircular, ornamented with few setae dorsally; WL2 and 3 are the longest; the species lives at slope depths of 399–405 and 457–461 m; the male abdomen comprises only six somites, with the second and third fused; and the apex of male first pleopod is complex rather than simple.

Notes on *Pinnaxodes* and *Holothuriophilus*

The following material has been examined for the following notes. *Pinnaxodes chilensis*: 2 females (14.4 by 12.7 mm, 13.4 by 12.4 mm, carapace broken) (ZMUC), parasite, in rectum of echinoid *Loxechinus albus* (Molina), Chile. *Pinnaxodes major*: 1 female (13.1 by 11.1 mm) (ZMUC), inland sea, from bivalve, coll. K. Hatonaka, 7 May

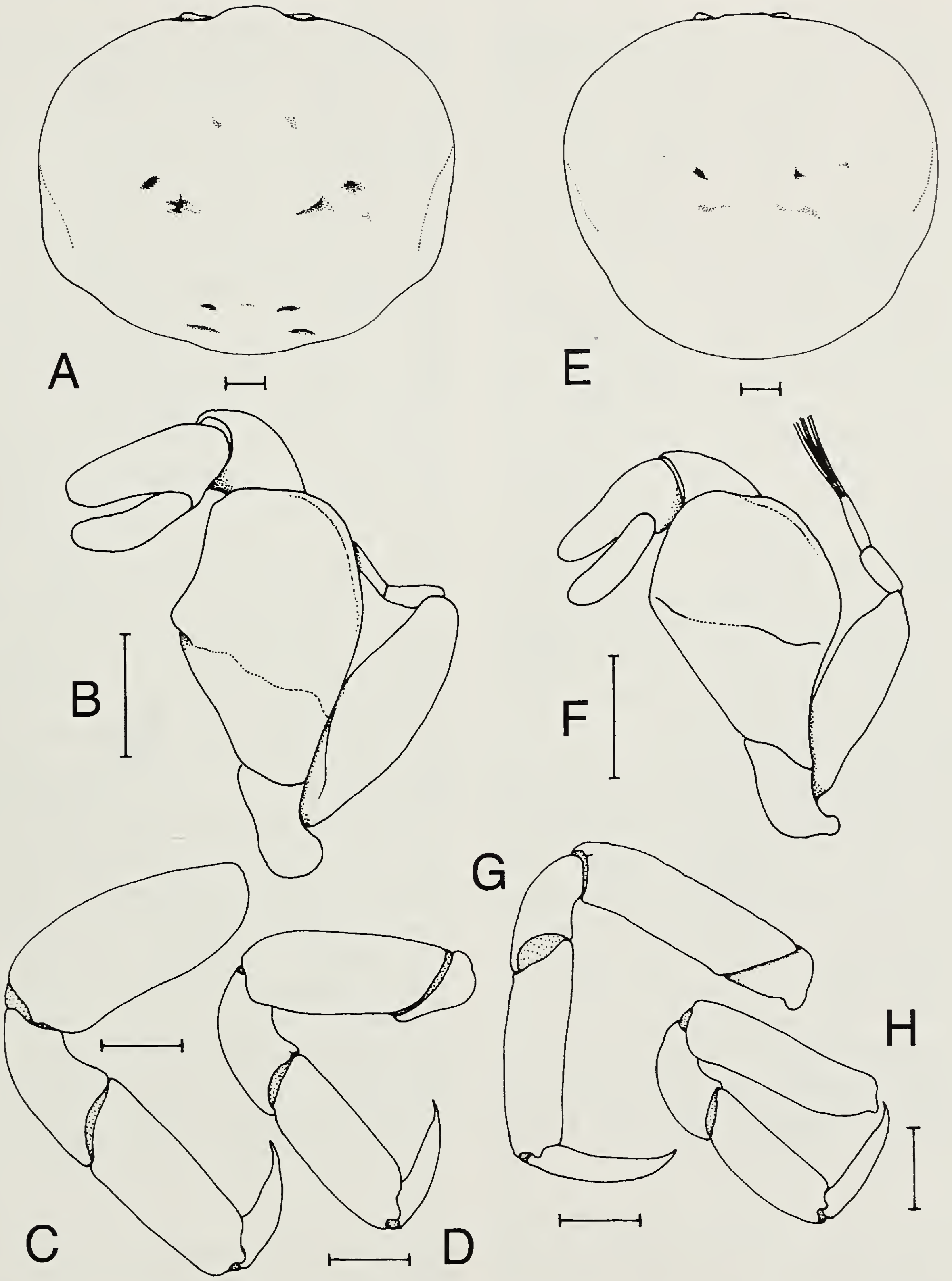

Fig. 6. A–D, *Pinnaxodes major* Ortmann, 1894, female (15.4 by 13.0 mm) (ZRC 1999.39a); E–H, *Pinnaxodes mutuensis* Sakai, 1939, female (14.2 by 12.6 mm) (NSMT). A, E, dorsal views of carapaces; B, F, left MXP3 (outer view); C, G, WL3; D, H, WL4. (All structures denuded.) Scales = 1.0 mm.

1935; 2 females (14.7 by 12.5 mm, 15.4 by 13.0 mm) (ZRC 1999.39), 4 females (NSMT), from *Atrina pectinata,* Hokkaido, Japan, coll. Tsukiji Market, Tokyo, P. K. L. Ng & M. Takeda, 3 February 1999. *Pinnaxodes mutuensis*: 1 female (14.2 by 12.6 mm) (NSMT), from *Mytilus gallprovincialis,* northern Japan, coll. 19 May 1982.

Some comments on the genus *Pinnaxodes* Heller, 1865 (type species *Pinnaxodes* *hirtipes* Heller, 1865, a subjective junior synonym of *Pinnaxodes chilensis* (H. Milne Edwards, 1837)), are necessary as one Indo-West Pacific species, *P. major* Ortmann, 1894, has been reported from a holothurian (Sakai 1939, 1976), although its preferred host seems to be bivalves. Manning (1993b:524, 525) separated *Pinnaxodes* from *Holothuriophilus* on the basis of the carapace shape (greatest width posterior to the midlength, in *Holothuriophilus* it is anterior to the midlength), relatively slender and elongate dactyli of the WL (short and stout in *Holothuriophilus*), and the presence of a suture between the ischium and merus of MXP3 (absent in *Holothuriophilus*). Campos et al. (1998:374) discussed the taxonomy of the American *P. gigas* Green, 1992, and *P. floridensis* Wells & Wells, 1961, including illustrations, and suggested that *Opisthopus* Rathbun, 1893, be regarded as a separate genus (it had been a junior synonym of *Pinnaxodes*).

Takeda & Prince Masahito (2000) discussed the taxonomy of *Pinnaxodes chilensis* (an obligate symbiont of sea urchins), *P. major* and *P. mutuensis* Sakai, 1939 (known only from bivalves), and commented that the latter should be transferred to *Holothuriophilus.* They noted that for *P. mutuensis,* the "fusion of the ischium-merus of the third maxilliped was not mentioned in the original description; it is essentially complete, and a quite imperfect suture may be traceable only on the external surface under special light control." (Takeda & Prince Masahito 2000:110). This, however, is not obvious from their figure (Takeda & Prince Masahito 2000: fig. 2G) that does not show any trace of a suture between the ischium and merus, with only a suture shown between the ischium and basis. We compared specimens of all three species, and the MXP3 of *P. major* (Fig. 6B) is essentially similar to that of *P. mutuensis* (Fig. 6F), with a distinct suture present between the ischium and basis, but the ischium and merus are completely fused, with only the faint trace of a suture demarcating the two segments, most clearly seen under transmitted light. This is the same as in *P. chilensis,* although the suture between the ischium and merus in the present specimen cannot be easily seen (Fig. 7A), being very faint. However, the MXP3 of *P. major* and *P. mutuensis* differ from that of *P. chilensis* in that the latter has the dactylus and propodus proportionately shorter (Fig. 7A, B). Campos et al. (1998) had commented that *P. gigas* and *P. floridensis* have the male telsons "basally expanded", forming a more rounded or pentagonal structure (Campos et al. 1998: fig. 3A, C). This is also the case for *P. major* (see Takeda & Prince Masahito 2000: fig. 4B), but not *P. mutuensis* (see Takeda & Prince Masahito 2000: Fig. 5L). In addition, while *P. gigas, P. floridensis* and *P. major* have their fronts distinctly produced anteriorly (Fig. 6A; Campos et al. 1998: fig. 2A, C; Takeda & Prince Masahito 2000: fig. 4A), the front barely extends beyond the orbits in *P. mutuensis* (Fig. 6E; Takeda & Prince Masahito 2000: Fig. 5A, I, J). These differences suggest that *P. mutuensis* is not a true *Pinnaxodes.* However, to refer *P. mutuensis* to *Holothuriophilus* as suggested by Takeda & Prince Masahito (2000) is also unsatisfactory. Species of *Holothuriophilus* have quadrate carapaces which are clearly wider than long (rather than round) and the WL are proportionally shorter (Fig. 7D–F; Manning 1993b: figs. 2a, 3). It is also pertinent to note that while members of *Holothuriophilus* are symbiotic in holothurians, *P. mutuensis* is only known from bivalves. For the moment, we retain *Pinnotheres mutuensis* in *Pinnaxodes* for lack of a better classification. It may need to be referred to its own genus at a later date.

The MXP3 of *P. chilensis* (Fig. 7A, B) actually closely resembles that of *Holothuriophilus* (see Manning 1993b: fig. 2b, c; present Fig. 7C), and interestingly, both taxa are from the eastern Pacific. With regards to the other supposed differences between *Pinnaxodes* and *Holothuriophilus* mentioned by Manning (1993b), we find

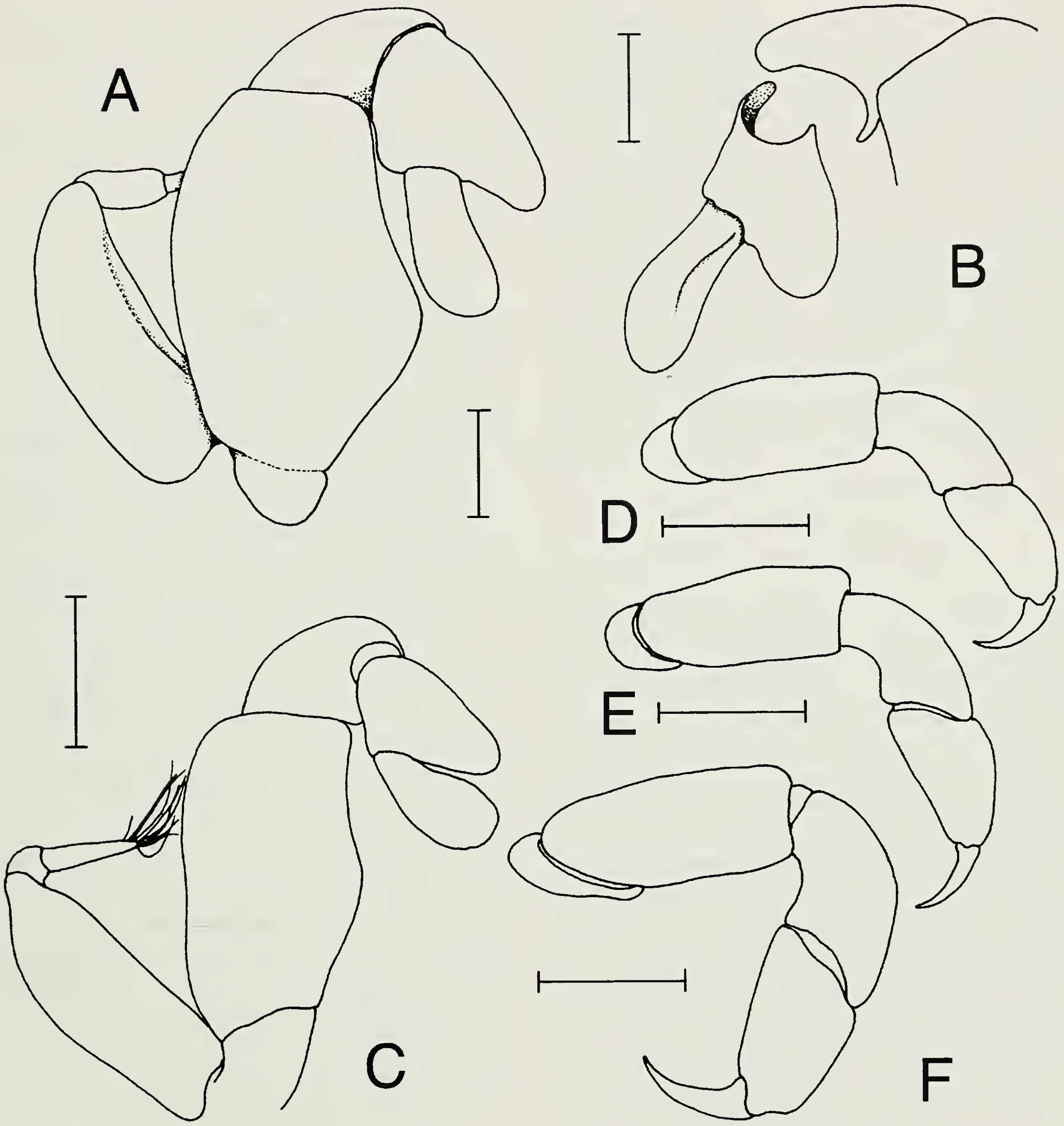

Fig. 7. A, B, *Pinnaxodes chilensis* (H. Milne Edwards, 1837), female (14.4 by 12.7 mm) (ZMUC), A, outer surface of right MXP3, setae removed, suture between ischium and merus very faint, not drawn; B, inner surface of right MXP3, setae removed, propodus and dactylus detached. C–F, *Holothuriophilus trapeziformis* Nauck, 1880, lectotype female (7.7 by 4.8 mm) (SMF); C, right MXP3; D–F, WL2–4 respectively. (All structures denuded.) Scales = 1.0 mm.

the difference in carapace shape not at all obvious, especially between *P. major* and *H. trapeziformis.* The proportions of the dactyli of the WL are also not that distinct, with those of *Holothuriophilus* only slightly shorter than those of the three *Pinnaxodes* species examined here (Fig. 7D–F).

With regard to the specimen of *Holothuriophilus trapeziformis* in the SMF, it carries the old catalogue number "ZMG 67/565a" and was collected from Mazatlán, Sinaloa, in México. Nauck (1880:24, 66) did not state how many specimens he had or even where it was from, commenting only that it was a "Parasit in Holothuria maxima Semper" (Nauck 1880:66). Bürger (1895:380) subsequently listed one female (as *Pinnotheres trapeziformis*) measuring 8.5 by 5.0 mm from Mazatlán, from *Holothuria maxima* Semper. De Man (1887: 722) also measured one specimen from Nauck, noting it was a female 13.8 by 10.5

mm. The size discrepancy between Bürger's and De Man's specimens is difficult to reconcile and suggests that Nauck may have had more than one specimen. As such, we prefer to regard the present SMF specimen as a syntype and we here designate it as the lectotype of *Holothuriophilus trapeziiformis* Nauck, 1880. The present female specimen in the SMF (Fig. 7C–F) measures approximately 7.7 by 4.8 mm, closer to Bürger's data. This specimen is in poor condition, with the carapace removed, very soft and somewhat deformed (making precise measurements difficult).

Acknowledgements

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Literature Cited

Baker, W. H. 1907. Notes on South Australian Decapoda Crustacea. Part V.—Transactions, Proceedings and Report of the Royal Society of South Australia 31:173–191, pls. 23–25.

Bosc, L. A. G. 1802. Histoire naturelle des Crustacés, contenant leur description et leurs moeurs, avec figures dessinées d'apres nature. Deterville, Paris, 1:1–258, pls. 1–8; 2:1–296, pls. 9–18.

Bürger, O. 1895. Ein Beitrag zur kenntniss der Pinnotherinen.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 8:361–390, pls. 9. 10.

Campos, E. 1989. *Tumidotheres,* a new genus for *Pinnotheres margarita* Smith, 1869, and *Pinnotheres maculatus* Say, 1818 (Brachyura: Pinnotheridae).—Journal of Crustacean Biology 9:672–679.

———. 2002. Two new genera of pinnotherid crabs from the tropical eastern Pacific (Decapoda: Brachyura: Pinnotheridae).—Journal of Crustacean Biology 22:328–336.

———, & R. B. Manning. 2000. The identities of *Pinnotheres nudus* Holmes, 1895, and *P. nudus* sensu Weymouth, 1910 (Crustacea: Decapoda: Pinnotheridae).—Proceedings of the Biological Society of Washington 113:799–805.

———, & ———. 2000. Authorship and diagnosis of the genus *Arcotheres* Manning, 1993 (Crustacea: Brachyura: Pinnotheridae).—Raffles Bulletin of Zoology 49:167–170.

———, V. Díaz, & J. A. Gamboa-Contreras. 1998. Notes on distribution and taxonomy of five poorly known species of pinnotherid crabs from the eastern Pacific (Crustacea: Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 111:372–381.

Chopra, B. 1931. Further notes on Crustacea Decapoda in the Indian Museum. II. On some decapod crustacea found in the cloaca of holothurians.—Records of the Indian Museum 33(3):303–324.

Chuang, S. H. 1961. On Malayan Shores. Muwu Shosa, Singapore, 225 pp.

Doflein, F. 1904. Brachyura. Wissenschaften Ergebenisse Deutschen Teifsee 'Valdivia' Expedition 6: i–xiv, 1–314, figs. 1–68, pls. 1–57.

Garth, J. S. 1957. The Crustacea Decapoda of Chile. Reports of the Lund University Chile Expedition 1948–49, 29.—Lunds Universitets Arsskrift, new series (2)53(7):1–130.

Green, T. M. 1992. *Pinnaxodes gigas,* a new species of pinnotherid crab from the Gulf of California (Decapoda: Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 105:775–779.

Hamel, J.-F., P. K. L. Ng, & A. Mercier. 1999. Life cycle of the pea crab *Pinnotheres halingi* sp. nov., an obligate symbiont of the sea cucumber *Holothuria scabra* Jaeger.—Ophelia 50(3):149–175.

Heller, C. 1865. Crustaceen. *In* Reise der österreichischen Fregatte 'Novara' um die Erdre, in den Jahren 1857, 1858, 1859, unter den Befehlen des Commodore B. von Wüllerstorf–Urbair. Zoologische Theil 2(3):1–280, pls. 1–25.

Lanchester, W. F. 1900. On a collection of crustacea made at Singapore and Malacca.—Part I. Crustacea Brachyura.—Proceedings of the Zoological Society of London 1900:719–770, pls. 44–47.

Man, J. G. De. 1887. Uebersicht der Indo-pacifischen Arten der Gattung *Sesarma* Say nebst einer Kritik der von W. Hess und E. Nauck in den Jahren

1865 und 1880 beschriebenen Decapoden.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 2: 639–689, pl. 1.

Manning, R. B. 1993a. West African pinnotherid crabs subfamily Pinnotherinae (Crustacea, Decapoda, Brachyura).—Bulletin du Muséum national d'Histoire naturelle, Paris (4)15A(1–4):125–177.

———. 1993b. Three genera removed from the synonymy of *Pinnotheres* Bosc, 1802 (Brachyura: Pinnotheridae).—Proceedings of the Biological Society of Washington 106:523–531.

———. 1998. A new genus and species of pinnotherid crab (Crustacea, Decapoda, Brachyura) from Indonesia.—Zoosystema, Paris 20(2):357–362.

Milne Edwards, H. 1837. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. Atlas [1834, 1837, 1840]: 1–32, plates 1–14, 14 bis, 15–25, 25 bis, 26–42. Librairie Encyclopédique de Roret, Paris.

Nauck, E. 1880. Das Kaugerust der Brachyuren (mit beschreibung neur gattungen und arten, Z. T. von C. Semper).—Zeitscrift wissenschaften Zoologische Leipzig 34:1–69, pl. 1.

Nobili, G. 1901. Decapodi raccolti dal Dr. Filippo Silvestri nell'America meridonale.—Bolletino dei Museo di Zoologia ed Anatomia comparata della R. Universita di Torino 16(402):1–16.

———. 1905. Décapodes nouveaux des côtes d'Arabie et du Golfe Persique. (Diagnoses préliminaires).—Bulletin du Muséum national d'Histoire naturelle, Paris 11(3):158–164.

———. 1906. Faune carcinologique de la Mer Rouge. Décapodes et stomatopodes.—Annales de Sciences Naturelles Zoologie, Paris (9)4(1–3):1–347, pls. 1–11.

Ortmann, A. 1894. Die Decapoden—Krebse des Strassburger Museums, mit besonderer Berücksichtigung der van Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. VIII. Theil. Abtheilung: Brachyura (Brachyura genuine Boas) III. Unterabtheilung: Cancroidea, 2. section: Cancrinea, 2. Gruppe: Catametopa.—Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere 7:683–772, pl. 23.

Poeppig, E. 1836. Crustacea chilensia nova aut minus nota descripsit.—Archiv für Naturgeschichte 2(1):134–144, pl. 4.

Pregenzer, C. 1988. A redescription of *Pinnotheres holothuriensis* Baker, 1907 and *Pinnotheres subglobosus* Baker, 1907 with a reassignment to the genus *Ostracotheres* (Decapoda, Brachyura).—Crustaceana 55:17–28.

Rathbun, M. J. 1893. Scientific results of explorations by the U.S. Commission Steamer 'Albatross'. XXIV. Description of new genera and species of crabs from the west coast of North America and the Sandwich Islands.—Proceedings of the United States National Museum 16:223–260.

———. 1900. The catametopous or grapsoid crabs of North America.—American Naturalist 34:583–592.

———. 1918. The grapsoid crabs of America.—Bulletin of the United States National Museum 97: 1–461.

Sakai, T. 1939. Studies on the crabs of Japan. IV. Brachygnatha, Brachyrhyncha. Tokyo, pp. 365–741, pls. 42–111.

———. 1976. Crabs of Japan and the adjacent seas. In three volumes; English text, pp. xxix+773pp., Japanese text, pp. 1–461, Plates volume, pp. 1–16, pls. 1–251. Kodansha Ltd., Tokyo.

Schmitt, W. L., J. C. McCain, & E. Davidson. 1973. Decapoda I. Brachyura I. Fam. Pinnotheridae. Crustaceorum Catalogus, Dr. W. Junk, Den Haag 3:1–160.

Semper, K. 1880. Natürlichen existenzbedingungen de Thiere. Erster theil. F. A. Brockhaus, Leipzig. Pp. 98–100.

Takeda, M., & Prince Masahito. 2000. Systematic notes on the pinnotherid crabs of the genus *Pinnaxodes* (Crustacea: Decapoda: Brachyura).—Bulletin of the National Science Museum, Series A (Zoology) 20:99–112.

Tesch, J. J. 1918. Decapoda Brachyura II. Goneplacidae and Pinnotheridae.—Siboga Expeditie Monographite 39c1:149–295, pls. 7–18.

Van den Spiegel, D., & M. Jangoux. 1989. Sur la symbiose entre le Pinnotheride *Pinnotheres villosissimus* (Crustacea, Decapoda) et l'Holothurie *Actinopyga mauritiana* (Echinodermata).—Vie Marine, Marseille 10:205–213.

Wells, H. W., & M. J. Wells. 1961. Observations on *Pinnaxodes floridensis*, a new species of pinnotherid crustacean in holothurians.—Bulletin of Marine Science of the Gulf and Caribbean 11:267–279.

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A new crayfish of the genus *Cambarus* Erichson, 1846 (Decapoda: Cambaridae) from the Cape Fear River basin in the Sandhills of North Carolina

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Abstract.—*Cambarus* (*Puncticambarus*) *hystricosus* is a new species of crayfish that appears to be endemic to certain streams of the Cape Fear River basin that originate in or flow through the xeric Sandhills district of the Atlantic Coastal Plain of North Carolina. It shares a number of unusual characters with *C.* (*P.*) *spicatus* Hobbs of the Broad River basin, and is in many ways similar to an undescribed *Cambarus* of the same subgenus with which it is syntopic. It is readily distinguished from these and other members of the subgenus by a combination of multiple cervical spines, hepatic spines, an obtuse to subacute suborbital angle that is almost always devoid of a tubercle or spine, and the absence of marginal spines or tubercles on the rostrum.

The crayfish whose description follows is another of the undescribed species in the complex previously subsumed under the name *Cambarus* (*Puncticambarus*) *acuminatus* Faxon, 1884 (Cooper 2001). The North Carolina populations of this complex have also been referred to as *Cambarus* (*Puncticambarus*) sp. C (Hobbs and Peters 1977, Cooper and Braswell 1995), since probably none are legitimately referable to *C.* (*P.*) *acuminatus.* This new crayfish is currently known only from certain streams within or near that part of the Cape Fear River basin that lies in the xeric Sandhills district of the Inner Atlantic Coastal Plain. This is a physiographically distinctive region of Eocene sediments (Pinehurst Formation) that sit atop Cretaceous strata (Middendorf Formation) at the eastern margin of the Fall Zone of the Piedmont Plateau, bordered on the east by the Orangeburg Scarp, a marine escarpment that "is generally considered to be an early Pliocene wave-cut feature." (Cabe et al. 1992:177). In contrast to the flatness of the rest of the Coastal Plain, the district is characterized by dissected topography, consisting of broad, discontinuous ridges and adjacent slopes. In North Carolina it is traversed by streams in parts of the Cape Fear, Lumber, and Yadkin-Pee Dee river basins. The distinguishing terrestrial floral community of the Sandhills is the *Pinus palustris*/*Quercus catesbyi*/*Aristida stricta* association. Aquatic animals known to be endemic to the district, in addition to the crayfish described herein, are the fishes *Etheostoma mariae* (Fowler), which appears to occur only in the Lumber basin, and *Semotilus lumbee* Snelson and Suttkus, which occurs in all three river basins. An undescribed salamander of the genus *Eurycea* is also endemic to the Sandhills, where it is known from in and near streams in both the Cape Fear and Lumber river basins.

Since at least one other member of the *C.* (*P.*) species C complex, ostensibly another undescribed species, occupies some of the same streams as the new species, no reliable synonymy can at this time be presented.

Measurements of crayfish structures were made to the nearest 0.1 mm with a Fowler precision dial caliper, following the methods of Hobbs (1981:9–10) unless otherwise noted. Abbreviations used in the text are as follows: j, juvenile; NC, North Carolina State highway; NCSM, North Carolina State Museum of Natural Sciences, Raleigh; PCL, postorbital carapace length; R, river; SR, state secondary (county) road; TCL, total carapace length; US, United States highway; USGS, United States Geological Survey; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UTM, Universal Transverse Mercator coordinates; and WRC, North Carolina Wildlife Resources Commission.

Cambarus (*Puncticambarus*) *hystricosus*, new species

Fig. 1, Table 1

Diagnosis.—Body and eyes pigmented, eye large ($\bar{X}$ adult diam 2.3 mm, n = 21). Rostrum with narrow, moderately elevated margins, slightly or strongly converging to base of acumen, which is not delimited by tubercles or spines; margins not constricted at base of acumen, converging and concave from there to acute or subacute, cephalodorsally directed apical tubercle or spine; acumen comprising 36.3 to 47.3% ($\bar{X}$ = 43.2%, n = 26) of rostrum length, latter constituting 21.8 to 26.9% ($\bar{X}$ = 22.7%, n = 26) of TCL; floor (dorsal surface) of rostrum broadly concave. Areola 3.3 to 4.9 ($\bar{X}$ = 4.0, n = 26) times as long as broad (broader in juveniles), constituting 30.3 to 34.0% ($\bar{X}$ = 32.7%, n = 26) of TCL and 38.8 to 43.3% ($\bar{X}$ = 41.8%, n = 26) of PCL, with 5 or 6 punctations across narrowest part. Thoracic section of carapace dorsally punctate, dorsolaterally granulate, laterally cobbled with tubercles; cephalic section laterally with many tubercles, hepatic region with strong spines or spiniform tubercles. Cervical spines strong, 2–4 each side of carapace, plus one to several tubercles. Postorbital ridge strong, cephalic margin tapered and with strong spine or acute tubercle. Suborbital angle obtuse to subacute, almost always without tubercle or spine; branchiostegal spine strong. Antennal peduncle with 2 strong spines; antennal scale 2.4–2.9 ($\bar{X}$ = 2.6, n = 24) times as long as wide, greatest width at midlength; lateral margin thickened and terminating distally in long spine.

Palm of chela 1.5–1.8 ($\bar{X}$ = 1.7, n = 22) times wider than deep; width of palm 1.2–1.7 ($\bar{X}$ = 1.4, n = 19) times length of mesial margin, latter constituting 29.0–32.2% ($\bar{X}$ = 30.4%, n = 19) of total chela length; mesial margin with subserrate mesial row of 7–9 (usually 8) large, semierect tubercles, subtended dorsally by row of 6–8 (usually 7) tubercles of same size or slightly smaller, and other smaller but produced tubercles immediately dorsal to this row; 1–3 small tubercles ventral to mesial row. Fixed finger of chela costate laterally, with moderately developed dorsal and ventral ridges; opposable surface of finger with row of 6–9 (usually 7 or 8) tubercles, in addition to subconical tubercle ventral to denticles; dactyl length 1.8–2.3 ($\bar{X}$ = 2.0, n = 20) times length of mesial margin of palm, with moderately to poorly developed ridges dorsally and ventrally; mesial surface of dactyl with strong tubercles on proximal half or more; opposable surface with row of 9–12 (usually 10) tubercles. Carpus with strong dorsomesial tubercles, mesial surface with massive subdistal spine, ventral surface usually with 2 strong distal spines; merus with pair of prominent subdistal dorsal spines.

Hook on ischium of third pereiopod of males, that of form I male uniramous, massive, tapered, overreaching basioischial articulation by most of length, opposed by large tubercle on basis; coxa of fourth pereiopod of males with vertically disposed, caudomesial boss.

In situ gonopods (first pleopods) of form

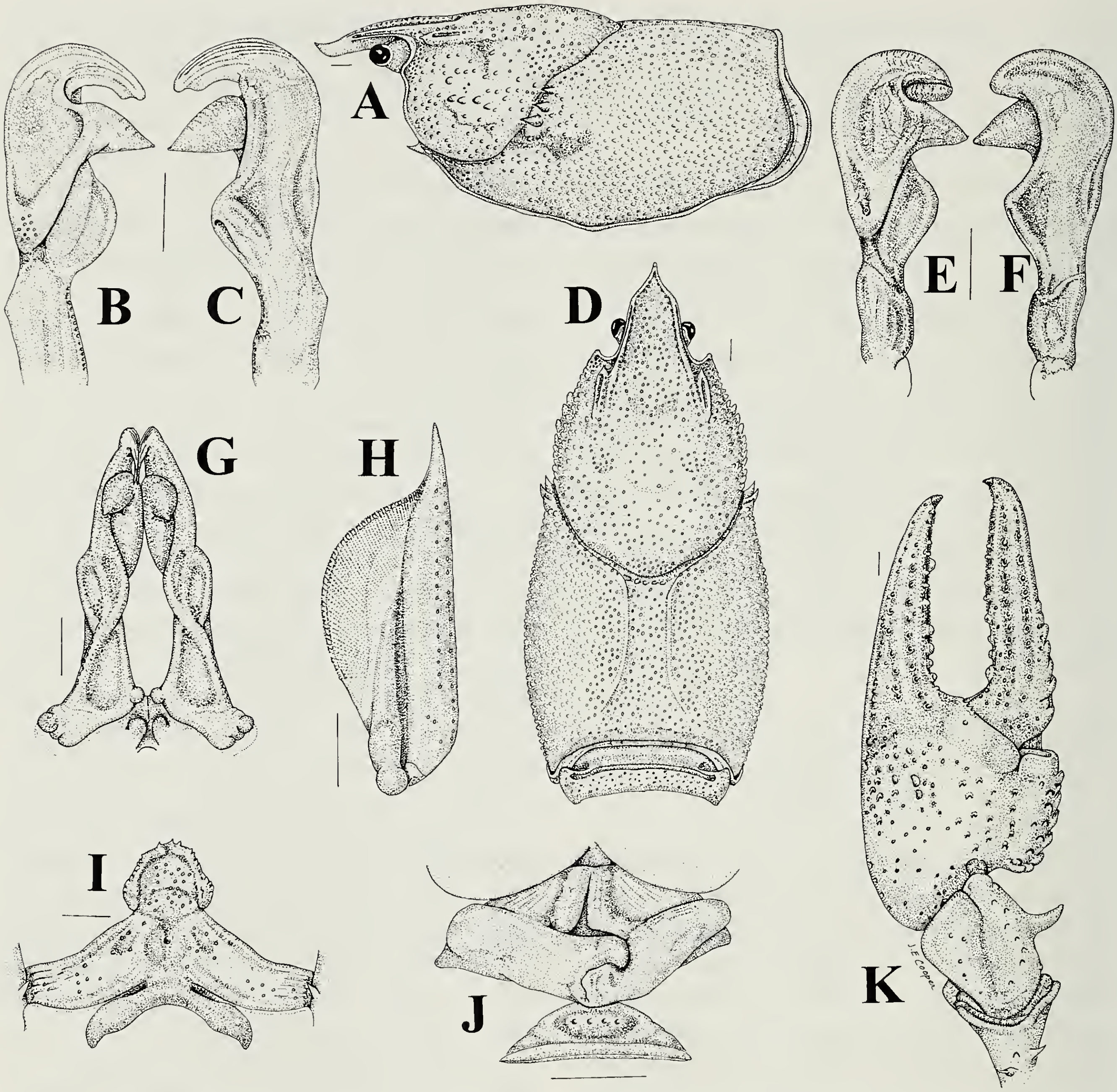

Fig. 1. *Cambarus* (*Puncticambarus*) *hystricosus,* new species. All from holotypic male, form I (NCSM 5115), except E, F, from morphotypic male, form II (NCSM 5120), and J, from allotypic female (NCSM 5004): A, lateral aspect of carapace; B, E, mesial aspect of left gonopod (first pleopod); C, F, lateral aspect of left gonopod; D, dorsal aspect of carapace; G, caudal aspect of in situ gonopods; H, right antennal scale; I, epistome; J, annulus ventralis and postannular sclerite; K, dorsal aspect of distal podomeres of left cheliped. Setae not illustrated. Scale line = 2 mm.

I male (based on holotypic male; Fig. 1G) symmetrical; proximomesial apophyses moderately developed, subglobose, slightly separated; central projection directed caudally; mesial process directed caudally and slightly laterally, with acute tip recurved caudally; in lateral aspect (Fig. 1C), central projection curved over 90° to plane of shaft, untapered, bearing proximally directed subapical notch, tip not extending as far caudally as tip of mesial process; latter inflated, tapered, tip acute; distal margin convex near shaft and inclined caudoproximally, proximal margin inclined slightly caudodistally; in mesial aspect (Fig. 1B), distal portion of gonopod relatively plane, with sparse setae at midlength. Total length of gonopod 22.6% of TCL (28.3% of PCL).

Table 1.—Measurements (mm) of types of *Cambarus* (*Puncticambarus*) *hystricosus*, new species.

	Holotypic male, form I	Allotypic female	Morphotypic male, form II
Carapace			
Total length	46.8	40.7	39.7
Postorbital length	37.4	32.3	31.7
Width	24.7	20.8	20.3
Depth	14.2	13.8	14.0
Length rostrum	10.2	9.1	8.7
Length acumen	3.7	4.1	3.7
Length areola	15.9	13.2	13.1
Width areola	3.7	2.7	3.5
Antennal scale			
Length	8.9	8.6	7.9
Width	3.4	3.1	3.0
Abdomen			
Length	44.6	43.8	41.5
Width	22.0	20.2	18.6
Cheliped			
Length lateral margin chela	42.4*	28.5	31.6
Length mesial margin palm	12.3	8.9	9.5
Width palm	20.5	12.4	14.3
Depth palm	11.5	7.7	8.5
Length dactyl	27.8	17.5	19.1
Gonopod length	10.6	N/A	8.9

* Regenerated.

Annulus ventralis (based on allotypic female; Fig. 1J) about 1.6 times wider than long, subsymmetrical, subrhomboidal in shape; cephalic half depressed, sloping, with narrow median trough not dissecting cephalic margin, trough flanked each side by low ridge; dextral ridge straight, proceeding caudally to meet cephalic margin of caudodextral wall; sinistral ridge less well defined, straight, proceeding caudally to about midlength of annulus before making abrupt turn to join upper arm of reverse C-shaped caudosinistral wall; caudodextral wall fairly thick, straight, slanted about 30–35° from horizontal plane; caudosinistral wall rounded, margin directed about 55° from horizontal; transverse tongue originating from caudodextral wall, proceeding sinistrally, curving slightly before plunging into deep fossa beneath sinistral wall; sinus nearly dissecting caudal margin in midline, caudal wall with weak median labiellum. Mirror image of this configuration present in 29 of 52 females.

Measurements of type specimens provided in Table 1.

Description of holotypic male, form I.—Body and eyes pigmented, eye 2.6 mm diameter. Cephalothorax (Fig. 1A, D) subcylindrical, thoracic section wider than deep. Areola 4.3 times longer than wide, constituting 34.0% of TCL (42.5% of PCL), quite punctate, 6 punctations across narrowest part. Rostrum with narrow margins slightly converging nearly to base of acumen, where not constricted, but more convergent and concave to apical tubercle, which reaching base of distal two-thirds of ultimate podomere of antennular peduncle; acumen comprising 36.3% of rostrum length, latter constituting 21.8% of TCL; floor of rostrum broadly concave, proximal three-fourths of surface punctate; usual row of deep punctations along inner surface of dorsal ridge;

subrostral ridge weak, narrowly visible to base of acumen in dorsal aspect; ventral keel of rostrum devoid of tubercles or spines.

Postorbital ridge strong, straight, laterally grooved, cephalic margin with acute tubercle, caudal terminus somewhat inflated. Suborbital angle rounded, without spine or tubercle; branchiostegal spine strong. Thoracic section of carapace dorsally punctate, dorsolaterally granulate, laterally cobbled with tubercles; row of small tubercles along ventral margin of anterior part of cervical groove; cephalic section of carapace 1.9 times longer than areola, constituting 66.0% of TCL, laterally covered with small to large tubercles, most acute or subacute; gastric region punctate. Cervical spine region on each side of carapace with 2 strong spines, 1 smaller spine dorsal to them, and some tubercles.

Abdomen slightly narrower and shorter than cephalothorax; abdominal pleura truncate ventrally, subangular caudoventrally, slightly rounded caudally; terga very punctate, except articular surfaces glabrous. Proximal podomere of uropod with spine on lateral lobe, larger spine on mesial lobe; mesial ramus of uropod with weak median ridge bearing submarginal caudomedian spine; caudolateral spine of ramus moderate; cephalic section of lateral ramus of uropod with broad, curved median ridge bearing terminal spine at transverse flexure, latter on right with total of 14 fixed spines and 1 long, articulated sublateral spine along caudal margin. Telson with 2 strong spines in each caudolateral corner of cephalic section, mesialmost articulated (tip of fixed spine on left side bifurcate); caudal margin domelike.

Epistome (Fig. 1I) with cephalic lobe basically subcordiform in ventral outline, but cephalic margin slightly curved, not peaked, and lateral margin on each side with weak concavity; most of margin crenulate, with tuberclelike protuberances; lateral corners inflated; floor (ventral surface) of lobe moderately convex, punctate, with setae; central depression of body broad, deep, with cephalomedian fovea; lamellae punctate, lateral corners subtruncate, without tubercles; zygoma moderately arched. Antennal peduncle with strong cephalolateral spine on basis, similar spine on ventral surface of ischium; antennular peduncle with small subdistal median spine on ventral surface of basal podomere. Antennal scale (Fig. 1H) 2.6 times longer than wide, broadest near midlength; lateral margin thickened, straight, terminating in long distal spine, tip of which reaching midlength of ultimate podomere of antennular peduncle; lamella about 1.5 times as wide as thickened lateral margin, with declivous distal margin and broadly curved mesial margin.

Third maxilliped with tip reaching slightly beyond midlength of penultimate podomere of antennal peduncle; exopodite hirsute, tip reaching nearly to midlength of merus of endopodite; distolateral corner of ischium produced as acute tubercle; lateral half of ischium with some punctations, short setae present along inner margin of lateral ridge; mesial half of ischium with eroded bristles, mesial margin on right with 21 denticles, 22 on left. Incisor ridge of right mandible with 6 denticles, 5 on left.

Both chelipeds regenerated (left more nearly normal; deviations noted in following). Left chela (Fig. 1K) 2.1 times longer than wide; palm 1.8 times broader than deep, width 1.7 times length of mesial margin (normal range 1.2–1.7, $\bar{X}$ = 1.4); latter 29.0% of total chela length, 44.2% of dactyl length. Dorsal surface of palm punctate, those punctations on mesial third with small tubercles at proximal bases; longitudinal dorsomesial sulcus shallow, with row of moderate, produced tubercles; distolateral margin of palm costate for about a third of length (continuous onto fixed finger), with moderate impression and aggregation of large punctations with tubercles at proximal bases; lateral eminence of articular ridge with several small distal protuberances; lateral margin of palm rounded, with large, widely spaced punctations. Ventral surface of palm less punctate than dorsal, some punctations on mesial half with minuscule basal tubercles; distolaterally with broad depression (continuous onto fixed finger) and scattered punctations without tubercles; lateral eminence of articular ridge with 1 subdistal tubercle and 1 distal protuberance; 2 tubercles proximal to ridge. Mesial margin of left palm with subserrate mesial row of 8 tubercles, row subtended dorsolaterally by row of 6 tubercles, and others dorsal to this row; 2 tubercles ventral to mesial row.

Fingers gaping most of length, greatest width of gape about equal to width of base of dactyl. Left fixed finger costate laterally; dorsal surface with moderately strong longitudinal median ridge, flanked each side by row of punctations; proximolateral area with moderate impression and large punctations, some with basal tubercles; lateral margin with row of large punctations; ventral surface with weak, rounded longitudinal ridge, flanked each side by row of punctations; opposable margin with usual subconical tubercle (worn) ventral to denticles, located at base of distal fourth of finger, and another smaller ventral tubercle distal to subconical one (abnormal); row of 11 tubercles dorsal to denticles (normal range 6–9, usually 7 or 8), first of these very small, fifth from base largest; denticles eroded, in 2 rows distally. Dorsal surface of dactyl with low ridge, flanked each side by row of punctations; mesial surface with strong tubercles on proximal half, basal tubercles in 2–3 rows, encroaching dorsally; ventral surface with obsolete longitudinal ridge, defined by 2 rows of punctations; opposable surface with 13 tubercles (normal range 9–12, usually 10), first and fourth from base largest; denticles eroded, in 2 rows on distal third of finger.

Left carpus (Fig. 1K) 1.4 times as long as wide, 1.3 times as long as mesial margin of palm; dorsal surface of carpus with shallow, oblique sulcus, lateral to which surface punctate, mesial to which surface with 8 or 9 dorsomesial tubercles; mesial margin with stout, curved distal spine and minuscule proximal tubercle; ventral surface with 2 strong distal spines (tip of distolateral spine broken) and 1 proximomesial tubercle. Left merus 1.7 times longer than deep, dorsal surface with 2 strong, suberect subdistal spines and 1 minuscule tubercle; ventrolateral ridge with 1 small tubercle, 2 stout spines, and moderate distal spine; ventromesial ridge with 4 subacute tubercles, 4 spines, and broken distal spine; ischium with 5 small ventral tubercles.

Gonopods as described in "Diagnosis."

Description of allotypic female.—Except for secondary sexual characters, differing from holotypic male in following respects: Areola 4.9 times wider than long, constituting 32.4% of TCL (40.9% of PCL), with 4 or 5 large punctations across narrowest part. Acumen long, spiniform, comprising 45.1% of rostrum length, tip reaching midlength of ultimate podomere of antennular peduncle; rostrum comprising 22.4% of TCL; subrostral ridge narrowly visible only along proximal half of rostrum. Cephalic margin of postorbital ridge with strong spine. Cephalic section of carapace 2.1 times longer than areola, constituting 67.6% of TCL; hepatic region with spiniform tubercles. Cervical spine region on left side of carapace with 1 long spine, 2 smaller spines dorsal to it, and several tubercles; right side with 2 long and 1 small spine.

Telson with 1 fixed and 1 articulated spine in caudolateral corner of cephalic section on right, 1 fixed and 2 articulated spines on left, all spines strong.

Floor of cephalic lobe of epistome with long setae; lamellae with single caudal tubercle each corner. Antennal scale 2.8 times longer than wide; lamella about 1.2–1.3 times as wide as thickened lateral margin. Third maxilliped with cephalolateral corner of ischium produced as spine.

Both chelipeds appear normal. Right chela 2.3 times longer than wide; palm 1.6 times broader than deep, width 1.4 times length of mesial margin, which is 31.2% of total chela length and 50.9% of dactyl length. Lateral eminence of ventral articular ridge with subacute distal tubercle; single tubercle proximal to ridge. Mesial margin of palm with staggered mesial row of 7 tubercles, row subtended dorsolaterally by staggered row of 8 tubercles (6 on left), and several small tubercles dorsal to this row. Fingers only slightly gaping in proximal half, opposable base of fixed finger with sparse long setae. Opposable surface of right fixed finger with small subconical tubercle ventral to denticles at base of distal fourth of finger, and row of 8 tubercles dorsal to denticles, fourth tubercle from base largest (on left finger, third and fourth from base largest and same size). Mesial surface of right dactyl with strong tubercles on proximal two-thirds of finger; opposable surface with 11 tubercles, basalmost one largest, fourth from base offset ventrally (left dactyl with 12 tubercles).

Dorsal surface of carpus with row of 5 dorsomesial tubercles; mesial surface with long, curved spine at about midlength, no proximal tubercle. Right merus 1.9 times longer than deep; ventrolateral ridge with 3 strong spines; ventromesial ridge with 8 spines or spiniform tubercles (7 on left merus) and strong distal spine.

Annulus as described in "Diagnosis." In addition, first pleopods present, fairly long; postannular sclerite about one-third width of annulus, ridgelike, ventral surface pitted.

Description of morphotypic male, form II.—Differing from holotypic male in following respects: Areola 3.7 times longer than wide, constituting 33.0% of TCL (41.3% of PCL). Acumen comprising 42.5% of rostrum length. Cephalic margin of postorbital ridge with strong spine. Cephalic section of carapace with several strong hepatic spines on each side of body. Cervical spine area with 3 spines and a tubercle.

Cephalic lobe of epistome subcordiform in outline, margins crenulate, with some short setae; floor plane, with setae. Tip of spine of antennal scale reaching distal margin of ultimate podomere of antennular peduncle; lamella about 1.6 times width of thickened lateral margin. Incisor ridge of right mandible with 7 denticles.

Right cheliped replaced by regenerating bud. Left chela 2.2 times longer than wide; palm 1.7 times broader than deep, width 1.5 times length of mesial margin; latter 30.1% of total chela length, 49.7% of dactyl length. Lateral eminence of ventral articular ridge with 2 distal tubercles; 2 tubercles proximal to ridge. Mesial margin of palm with subserrate mesial row of 7 tubercles, row subtended dorsolaterally by staggered row of 7 tubercles, and others dorsal to this row; 2 produced tubercles ventral to mesial row. Fingers gaping in proximal three-fourths of length, greatest width of gape about four-fifths width of base of dactyl. Dorsal surface of fixed finger with strong median ridge, flanked mesially by punctate groove; opposable margin with strong subconical tubercle ventral to denticles, and row of 8 tubercles dorsal to denticles, fourth tubercle from base largest. Opposable surface of dactyl with 12 tubercles, basalmost largest. Mesial surface of carpus with long, curved subdistal spine and small proximal tubercle; ventral surface with 2 strong distal spines and large proximomesial tubercle. Merus 1.8 times longer than deep; ventrolateral ridge with 3 strong spines and moderate distal spine; ventromesial ridge with 4 small tubercles and 6 spines.

Hook on ischium of third pereiopod small, tuberclelike, not overreaching basioischial articulation, not opposed by tubercle on basis. Gonopod (Fig. 1E, F) length 22.4% of TCL (28.1% of PCL). In situ gonopods with small, separated proximomesial apophyses; central projection directed caudally; mesial process inflated, directed caudolaterally and inclined slightly proximally; in lateral aspect, central projection curved 90° to plane of shaft, broad, tapered; mesial process tapered, tip slightly extruded.

Color notes.—Ground color of carapace and abdomen (except tailfan) gray-green to olive. Thoracic section of carapace with large, pale greenish blotches, one such blotch in median third of carapace at caudal end of areola; laterally darker, with small, light blotches and white granules; cervical spines ivory or roseate. Cephalic section of carapace nearly uniform olivaceous dorsally, darker laterally, with large tan or whitish blotch along cephalolateral margin between suborbital area and white branchiostegal spine; hepatic spines and tubercles on lateral surface white. Postorbital ridge pale grayish-green, cephalic spine tan to yellowish. Antennal scale bluish, but mesial margin of thickened lateral portion tan; antennal and antennular flagellae variable in color, with dark brown, reddish tan, or tan articles, and brown or pale green interstices.

Dorsal surfaces of palm and fingers of cheliped blue-green; lateral margin of entire propodus creamy orange, or yellowish with blue-gray areas; ventral surfaces of palm and fingers pale grayish-green or blue-green, but mesial third of palm and most of dactyl usually darker; tips of fingers orange or tannish-orange, color not subtended by black band; tubercles on mesial margin of palm and dactyl pale green, tubercles on opposable surfaces of both fingers ivory, pale green, or blue-gray. Dorsal and mesial surfaces of carpus gray-green, dorsal tubercles same color but paler; proximal and distal margins of carpus with narrow russet band. Dorsal surface of merus gray-green on distal half, fading to white on proximal half, distal membrane blue, spines ivory; ventral merus nearly white, spines white with amber tips; proximal two-thirds of mesial surface ivory, darker on distal third; lateral surface white. Dorsal surfaces of second through fifth pereiopods pale greenish-blue or blue, articulations brownish; fingers of chelae of second and third pereiopods blue with amber tips.

Abdominal terga grayish-green, caudal margin of each with transverse black or iodine band, which broader on cephalicmost tergite; latter also with pale (usually yellowish) blotch at each lateral terminus; pleura generally darker green with bluish overtones, each with large, diagonal yellowish or tannish blotch near ventral border and dark oblique dorsolateral mark. Telson and uropods aquamarine dorsally and ventrally, dorsal surface of telson with tan overtones; both rami of uropods with narrow transverse subcaudal band of orange-tan, subtended caudally by narrow blue band; transverse flexure of lateral ramus of uropod also with narrow orange-tan band.

Ventrally, all cephalic structures of body blue-green or bluish, except zygoma white, and mandible and parts of third maxilliped lighter in color, sometimes pale yellowish; other ventral surfaces of body white or translucent blue, ventral abdomen usually with blue markings.

Juveniles with same general pattern, but paler. Ventral margins of carapace often distinctly blue; dorsal abdomen pale greenish, terga with very prominent dark banding.

Type locality.—North Carolina, Hoke County, Puppy Creek at SR 1409, ca. 2.4 air km E of Wayside (Nicholson Creek 7.5′ USGS quadrangle, UTM Zone 17, coordinates 670662E/3876690N).

Disposition of types.—The holotypic male, form I, allotypic female, and morphotypic male, form II, are in the NCSM crustacean collection (catalogue numbers 5115, 5004, and 5120, respectively), as are paratopotypes consisting of 3j ♂, 3 j♀ (5055); 2 ♀ (5060); 1 ♀ (5117); 1 ♂ II (5119); 4 j♂, 2 j♀ (5118); 1 ♀ (5254); 1 j♂ (5288); 5 j♂, 3 j♀ (6206); and paratypes consisting of 1 ♂ II, 1 ♀ (2524); 1 ♂ II, 2 j♂, 2 ♀, 2 j♀ (6371); 9 j♂, 1 ♀, 8 j♀ (5057). Paratypes consisting of 1 ♂ II, 4 j♂, 4 ♀, 5 j♀ have been deposited at USNM (1004633).

Range and specimens examined.—North Carolina endemic; currently known from twelve creeks in the Rockfish Creek and Little River subdrainages, and one creek that forms an independent subdrainage, of the Cape Fear River basin in and near the Sandhills district of the Atlantic Coastal Plain. More than 250 voucher specimens have been collected from the following localities (collectors names given in first usage, initials thereafter): *Cumberland Co.*—(1) upper trib Bones Crk at SR 1400; 1 ♂ II, 1 ♀ (2524), 30 Jan 1989, coll. T. MacPherson, D. R. Lenat (DRL); (2) Little Rockfish Crk at SR 1102 (Gillis Hill Rd); 2 j♂, 1 j♀ (WRC 000830.1jaj), 30 Aug 2000, coll. B. T. Watson (BTW), A. H. Fullerton (AHF), J. A. Johnson (JAJ); (3) Little Rockfish Crk at Cameron Rd; 1 j♀ (WRC 001031.4jaj), 31 Oct 2000, coll. BTW, AHF; (4) Rockfish Crk at boundary Fort Bragg Military Reservation (35.08.04N/79.21.06W); 1 ♂ II (2716), date unknown, coll. P. W. Havens (PWH); (5) Stewarts Crk at SR 1102 (Gillis Hill Rd); 1 intersex adult (6395), 30 Aug 2000, coll. BTW, AHF, JAJ; (6) Grays Crk at SR 2234 (Blossom Rd), ca. 3.7 air km W of Lena; 1 ♂ I, 2 ♂ II, 6 j♂, 3 ♀, 2 j♀ (23584), 31 Oct 2000, coll. AHF, BTW. *Hoke Co.*—(7) Horse Crk, Fort Bragg Military Reservation (35.11.30N/77.12.00W); 1 ♂ II (2712), date unknown, coll. PWH; (8) Rockfish Crk at US 401 Bypass, 2.7 km NE of Raeford; 1 ♂ II, 2 j♂, 2 ♀, 2 j♀ (6371), 26 Oct 2000, coll. W. C. Starnes, M. Raley, G. Hogue, L. Fullbright; (9) Rockfish Crk, 3.2 km N of Raeford; 1 ♂ I (5255), 9 Jul 1962, coll. D. Louder; (10) Rockfish Crk at firebreak 32 off Moore County road, Fort Bragg Military Reservation, 13.0 air km NW of Raeford; 2 j♂, 1 j♀ (23873), 20 Aug 2002, coll. C. Bryan (CB), A. Young (AY); (11) Puppy Crk at SR 1406, ca. 4.8 air km W of center town Rockfish; 1 j♂ (5006), 3 Feb 1999, coll. D. G. Cooper (DGC), D. A. Jackan (DAJ); 9j ♂, 1 ♀, 8 j♀ (5057), 1 j♂ (5061), 21 Mar 1999, coll. DGC, DAJ; 2 ♂ II, 3 ♀ (4993), 1 ♂ II (5120), 21 May 1998, coll. M. Hale, DRL, N. Medlin, B. Tracy (BT); (12) Puppy Crk at SR 1409 (type locality), ca. 2.4 air km E of Wayside; 2 ♀ (5060), 1 ♀ (5254), 3 j♂, 3 j♀ (5055), 26 Mar 1999, coll. DGC, DAJ; 1 ♀ (5117), 1 ♂ II (5119), 4 j♂, 2 j♀ (5118), 1 ♂ I (5115), 3 Jun 1999, coll. DGC; 1 j♂ (5288), 4 Nov 1999, coll. DGC; 5 j♂, 3 j♀ (6206), 9 Sep 2000, coll. DGC, S. Yirka; 1 ♀ (5004), 3 Feb 1999, coll. DGC, DAJ; (13) Rockfish Crk at firebreaks 3–5, Fort Bragg Military Reservation, ca. 8 air km NNW of Raeford; 1 ♂ II, 4 j♂, 4 ♀, 5 j♀ (USNM 1004633), 5 Nov 2001, coll. CB, B. Ball (BB); 1 ♂ II, 5 j♂, 11 j♀ (7990), 6 Nov 2001, coll. CB, BB; 2 j♂, 6 j♀ (23582), 7–8 Nov 2001, coll. CB, BB; (14) Little R, ca. 11.2 air km SE of Vass; 2 ♀ (7985), 25 Oct 2001, coll. CB, AY; (15) Rockfish Crk at Sandy Grove Church Rd, ca. 8 air km NNW of Raeford; 1 j♂ (23583), 5 Nov 2001, coll. CB, BB; 4 j♂, 2 ♀, 11 j♀ (23791), 9 Aug 2002, coll. CB, AY; (16) Piney Bottom Crk at Southern Pines Rd, ca. 15.5 air km NNW of Raeford; 1 ♂ II, 1 j♂ (23781), 24 Sep 2002, coll. CB, AY; (17) Gum Branch at Chicken Rd, ca. 12.4 km NNW of Raeford; 1 ♀ (23777), 24 Sep 2002; 1 j♂ (23776), 6 Sep 2002, coll. CB, AY; (18) Juniper Crk at Chicken Rd, 12.3 air km NNW of Raeford; 1 ♀ (23868), 7 Oct 2002, coll. CB, AY; (19) Juniper Crk at firebreak 13, Fort Bragg Military Reservation, 10.6 air km NNW of Raeford; 1 ♀ (23864), 1 Nov 2002; 1 ♂ II, 2 j♂, 3 j♀ (23829), coll. CB, AY; (20) Juniper Crk at firebreak 29, Fort Bragg Military Reservation, 7.7 air km NNW of Raeford; 3 ♂ II, 9 j♂, 5 ♀, 14 j♀ (23867), 1 Oct 2002; 2 ♂ I, 1 ♂ II, 1 j♂, 14 j♀ (23827), 1 Nov 2002, coll. CB, AY; (21) Juniper Crk at Plank Rd, 8.8 air km NNW of Raeford; 1 ♂ II, 5 j♂, 1 ♀, 4 j♀ (23865), 23 Sep 2002; 1 ♂ II (23866), 1 Nov 2002, coll. CB, AY; (22) Nicholson Crk at firebreak 15, Fort Bragg Military Reservation, 10.4 air km N of Raeford; 1 ♂ II, 2 j♂, 1 ♀, 6 j♀ (23869), 20 Oct 2002; 2 ♂ II, 2 j♂ (23870), 1 Nov 2002, coll. CB, AY; (23) Nicholson Crk at firebreak 29, Fort Bragg Military Reservation, 6.9 air km N of Raeford; 4 ♂ II, 6 j♂, 2 ♀, 3 j♀ (23871), 19 Oct 2002, coll. CB, AY; (24) James Crk at boundary road, Fort Bragg Military Reservation, 6.4 air km SSW of Vass; 1 j♂ (23872), 2 Nov 2002, coll. CB, AY. *Moore Co.*—(25) Nicks Crk at NC 22, ca. 3.7 air km W of Whispering Pines; 1 ♂ II, 2 ♀, 1 j♀ (3308), 31 May 1996, coll. DRL, BT.

Variations.—In addition to those addressed elsewhere in this paper, intraspecific variations include the following. The degree of convergence of the margins of the rostrum, from its base to the base of the acumen, varies from subparallel to strongly convergent, and in some individuals the rostrum is nearly caret-shaped. Although the floor of the rostrum is usually moderately concave, in some specimens it approaches being plane. The suborbital angle is obtuse (very seldom subacute or obsolete) and only rarely bears a tubercle or small spine. Six specimens show disparities in this character from one side of the carapace to the other, displaying varying combinations of obtuse or subacute angles with or without tubercles. The hepatic ornaments vary from strong spines to subacute tubercles, and are weak, if present, in the sample from Grays Creek, a small, independent subdrainage of the Cape Fear River at what appears to be the southernmost periphery of the range of specimens assignable to *C.* (*P.*) *hystricosus*.

In about half the specimens examined the distal margin of the lamella of the antennal scale is subtransverse for about half its width before curving proximomesially, while in the others this margin is gently or moderately declivous from the base of the spine to the widest part of the scale at about midlength. In nearly all specimens the shape of the cephalic lobe of the epistome is subcordiform or subtriangular, but in a few it approaches subpentagonal or semicircular. The margins of the lobe are almost always strikingly crenulate, bearing from several to many subacute protuberances, but in a few specimens the margins are only moderately uneven. The carpus usually has from three to eight moderate or strong dorsomesial tubercles, but in some specimens these tubercles are weak, and they are fewest and weakest in the sample from Grays Creek. The mesial surface of the carpus normally lacks a proximal tubercle, but this is present in a number of specimens, and others have two or three very small tubercles at this site. The usual ventral armature of the carpus consists of two strong distal spines, but in four specimens the distomedian spine is weak or obsolete, and in three others it is reduced to a rounded tubercle, with or without an acute nipple. The dorsal surface of the merus almost always bears two strong subdistal spines, and occasionally these may be accompanied by from one to several small tubercles. Two specimens have three strong subdistal spines on the dorsal merus. The ventrolateral ridge of the merus usually bears two or three spines, plus a strong or moderate distal spine. In some specimens there may be an additional tubercle or two on this ridge, and in several individuals the distal spine is small. The ventromesial ridge of the merus may have from six to nine ornaments, a combination of acute tubercles and moderate spines, along with a strong distal spine.

The largest tubercle on the opposable surface of the dactyl is usually the first from the base, but often is the second and occasionally the fourth; the fourth tubercle is always displaced toward the ventral surface, and not infrequently lies distinctly ventral to the denticles. The largest tubercle on the opposable surface of the fixed finger (not counting the usual subconical tubercle that lies ventral to the denticles) is generally the fourth from the base, occasionally the third or fifth.

Nearly all specimens have two spines in each cephalolateral corner of the telson, but eight have three in one corner and two in the other, six have three spines in each corner, and three have two in one corner and one in the other.

Anomalies.—In a subadult female from Puppy Creek, the distance between the base of the acumen and its apex is greater on the right side than on the left, and the base of the acumen on the right side is delimited by a strong, laterally directed spine. A juvenile male from Rockfish Creek has a deformed, probably regenerated, rostrum with a long, cephalolaterally directed spine projecting from the left side near the base. These are the only individuals in which a "marginal spine" has been observed. A juvenile female (9.4 mm TCL) from Rockfish Creek has a small fixed spine projecting from the base of the lateral side of the regular fixed spine on the right side of the telson.

A female from Rockfish Creek lacks oviduct apertures. An adult animal (TCL 43.7 mm) from Stewarts Creek is gynandromorphic. It has a normal annulus ventralis, female first and second pleopods, and postannular sclerite, but lacks oviduct apertures in the coxae of the third pereiopods. It has male sperm duct openings in the coxae of the fifth pereiopods.

Size.—The largest specimen is a female measuring 52.6 mm TCL (43.0 mm PCL). The largest form I male measures 46.8 mm TCL (37.4 mm PCL); the only other form I males have TCLs of 30.8, 35.0, and 38.0 mm (25.4, 27.7, and 30.2 mm PCL, respectively). The largest form II male measures 39.7 mm TCL (31.7 mm PCL).

Life history and ecological notes.—Form I males were found in early June and July, and in October and November. No ovigerous females or those with attached young have yet been seen.

On 21 May 1998, Puppy Creek was a "clear blackwater stream with a white sand bottom" (B. Tracy, pers. comm.). Specific conductance on that date was 18 μmhos/cm, pH 4.9, water temperature 22°C, and dissolved oxygen content 6.9 ppm. In February and March 1999, the creek at the type locality was about 3 m wide, with fairly shallow water and a few deeper sections. The bottom was sandy, with some sticks and detritus, several large submerged logs, and dense growths of long, slender submerged vegetation in which the crayfish were found. At some points the banks were undercut and covered with overhanging roots, but passing a dipnet through these produced no crayfish. In June of the same year, water levels had dropped significantly, the vegetation was not completely submerged, and the few crayfish collected were found only among sticks and detritus in areas with the greatest current.

Other members of the aquatic community at the type locality included the fishes *Ameiurus* sp., *Aphredoderus sayanus* (Gilliams), *Enneacanthus chaetodon* (Baird), *Etheostoma olmstedi* Storer, *E. serrifer* (Hubbs and Cannon), *Lepomis gulosus* (Cuvier), *Notropis cummingsae* Myer, and *Noturus insignis* (Richardson); the neotenic salamander *Necturus punctatus* (Gibbes); and the watersnake *Nerodia taxispilota* (Holbrook).

Crayfish associates.—The only other crayfishes yet found at sites occupied by *C.* (*P.*) *hystricosus* are an undescribed member of the subgenus, and *Procambarus* (*Ortmannicus*) *acutus* (Girard, 1852). *Cambarus* (*Depressicambarus*) *latimanus* (LeConte, 1856) occurs in some other streams of the area, but has not yet been found in those occupied by *C.* (*P.*) *hystricosus.*

Affinities.—On the basis of its extensive spinal armature, which we consider a plesiomorphic character state (and see Hobbs 1962:276, 1969:116–118), *C.* (*P.*) *hystricosus* appears to have strong affinities with *Cambarus* (*Puncticambarus*) *spicatus* Hobbs, 1956. Both species characteristically have hepatic spines, or strong spiniform or very acute tubercles, a rare feature in epigean *Cambarus*; strong cervical spines that are multiple in *C.* (*P.*) *hystricosus* and sometimes so in *C.* (*P.*) *spicatus*; long branchiostegal spines; and strong, multiple spines on the antennal peduncle, ventral carpus, and dorsal and ventral merus. Major differences between the two species are the presence of marginal spines or strong tubercles on the rostrum of *C.* (*P.*) *spicatus,* which are never normally present in *C.* (*P.*) *hystricosus*; a spine or tubercle on the suborbital angle of *C.* (*P.*) *spicatus,* which is rarely seen in *C.* (*P.*) *hystricosus*; the structure of the central projection of the form I male gonopod, which in *C.* (*P.*) *spicatus* is scarcely curved beyond 90° to the shaft and has a very weak subapical notch; and the more symmetrical annulus of that species.

The other member of the subgenus that occurs in some streams with *C.* (*P.*) *hystri-*

cosus lacks hepatic spines and multiple cervical spines, although it may display acute or subacute cervical tubercles along with a single strong spine. The suborbital angle in this species is almost always acute or subacute and bears a tubercle or spine. Only two of forty-five specimens examined had an obtuse suborbital angle, and in only one of them did the angle lack a tubercle. The postorbital ridge of adults seldom bears more than a small cephalic tubercle, although some smaller specimens have a cephalic spine. This species also has a shorter acumen and a broader areola than *C.* (*P.*) *hystricosus,* and the base of its acumen is more angular.

Remarks.—Both *C.* (*P.*) *hystricosus* and *C.* (*P.*) *spicatus* occupy limited, circumscribed ranges, the former in streams of the Cape Fear River basin in the Sandhills of North Carolina, the latter in streams of the Broad River basin in the Piedmont Plateau of North and South Carolina. The ranges of both are surrounded by the ranges of other, presumably more derived, members of *Puncticambarus.* In the Sandhills, this is comparable to the distributions of two other endemic animals. Populations of *Semotilus lumbee* there are surrounded by its more broadly distributed relative, *Semotilus atromaculatus* Mitchill, and populations of the undescribed *Eurycea* are surrounded by its close relative, *Eurycea cirrigera* (Green).

It seems reasonable that the forerunner of *C.* (*P.*) *spicatus* and *C.* (*P.*) *hystricosus* was one of the few members of the genus *Cambarus* to expand its range eastward from the Blue Ridge escarpment—which then lay farther east than it does today—or from farther west. Colonization of the Piedmont Plateau and the eastern extremity of the Inner Coastal Plain would have met with little opposition, but continued eastward expansion would have brought this putative progenitor into conflict with procambaroid stocks. The latter crayfishes were adapted to the warm, lentic or low-gradient habitats of the broad, base-leveled Coastal Plain, habitats that likely would have been inimical to exploitation by more cold- and lotic-adapted cambaroid stocks. The later radiation into the Piedmont of more highly competitive and closely related forms could have fragmented the ranges of the earlier inhabitants into a number of allopatric populations that evolved into distinctive relicts. Other such populations may await discovery.

The "residual" genetic influences of a once widespread, presumably plesiomorphic *Puncticambarus* could help explain the occasional appearance of hepatic spines, marginal spines, and even instances of multiple cervical spines, observed in some individuals from a number of populations of more derived forms in the subgenus (JEC, pers. obs.).

Etymology.—Species *hystricosus,* meaning prickly, from the Latin *hystrix,* porcupine, in reference to its extremely spinose body parts.

Suggested vernacular name: Sandhills spiny crayfish.

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Literature Cited

Cabe, S., J. G. Nickerson, C. W. Hoffman, & K. M. Farrell. 1992. Cretaceous and Tertiary stratigraphy of the northern Sandhills area, North Carolina. Pp. 177–188 *in* J. M. Dennison and K. G. Stewart, eds., Geologic field guides to North Carolina and vicinity. Geologic Guidebook No. 1, University of North Carolina at Chapel Hill.

Cooper, J. E. 2001. *Cambarus* (*Puncticambarus*) *hobbsorum,* a new crayfish (Decapoda: Cambaridae) from North Carolina.—Proceedings of the Biological Society of Washington 114(1):152–161.

———, & A. L. Braswell. 1995. Observations on North Carolina crayfishes (Decapoda: Cambaridae).—Brimleyana 22:87–132.

Erichson, W. F. 1846. Uebersicht der Arten der Gattung *Astacus.*—Archiv für Naturgeschichte 12(1): 86–103.

Faxon, W. 1884. Descriptions of new species of *Cambarus,* to which is added a synonymical list of the known species of *Cambarus* and *Astacus.*—Proceedings of the American Academy of Arts and Sciences 20:107–158.

Girard, C. 1852. A revision of the North American Astaci, with observations on their habits and geographical distribution.—Proceedings of the Academy of Natural Sciences of Philadelphia 6: 87–91.

Hobbs, H. H., Jr. 1956. A new crayfish of the Extraneus Section of the genus *Cambarus* with a key to the species of the Section (Decapoda, Astacidae).—Proceedings of the Biological Society of Washington 69:115–122.

———. 1962. Notes on the affinities of the members of the Blandingii Section of the crayfish genus *Procambarus* (Decapoda, Astacidae).—Tulane Studies in Zoology 9(5):273–293.

———. 1969. On the distribution and phylogeny of the crayfish genus *Cambarus.* Pp. 93–178 *in* P. C. Holt, R. L. Hoffman, and C. W. Hart, Jr., eds., The distributional history of the biota of the southern Appalachians, Part I: invertebrates. Research Division Monograph 1, Virginia Polytechnic Institute, Blacksburg, 295 pp.

———. 1981. The crayfishes of Georgia.—Smithsonian Contributions to Zoology 480:1–236.

———, & D. J. Peters. 1977. The entocytherid ostracods of North Carolina.—Smithsonian Contributions to Zoology 247:1–73.

LeConte, J. 1856. Descriptions of new species of *Astacus* from Georgia.—Proceedings of the Academy of Natural Sciences of Philadelphia 7:400–402.

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116(4):933–942. 2003.

A new species of freshwater anomuran crab of the genus *Aegla* Leach, 1821 (Crustacea: Decapoda: Aeglidae) from the Nahuelbuta Coastal Range, Chile

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Abstract.—Aegla occidentalis, a new species of the family Aeglidae, is described from the Tucapel River basin, on the western slope of the Nahuelbuta Coastal Range, in Chile. Morphologically, the new species closely resembles *A. laevis* (Latreille) from Central Chile but differs in having the apex of the carpal lobe of the chelipeds topped by two to four blunt scales mixed with a group of short, stout setae, the dorsum of the palmar crest slightly, if at all, concave, and the distal half of the subligulate rostrum not distorted. The morphological similarity between *A. occidentalis* and *A. laevis* contrasts with the high degree of genetic divergence between these two taxa, based on mtDNA sequence analysis. Our molecular results show *A. occidentalis* and *Aegla bahamondei* Jara to be sister species, with a 1.4%–1.6% average pairwise sequence divergence, compared with 5.9%–7.4% between *A. occidentalis* and *A. laevis.*

The anomuran freshwater crabs of the genus *Aegla* Leach, 1821 are found in rivers and lakes of southern South America (Schmitt 1942), displaying a vast array of minute morphological differences in the shape and ornamentation of carapace and appendages (Bond-Buckup & Buckup 1994). However, the group is constrained to a rather conservative general morphotype that renders the discrimination of most species difficult (Schmitt 1942). By necessity, all known species of *Aegla* have until now been discriminated and diagnosed on the basis of discrete combinations of morphological characters, and therefore the existence of cryptic or sibling species (sensu Mayr & Ashlock 1991) cannot be ruled out. Molecular techniques can potentially reveal levels of genetic differentiation among populations of *Aegla* hidden within morphologically similar populations (Hillis 1987). Such was the case when ~2.6 kb from the mitochondrial genes 12S, 16S, COI and COII were sequenced for most of the *Aegla* species occurring in the continental territory of Chile to reconstruct their phylogenetic relationships (Pérez-Losada et al. 2002).

Some of the specimens collected in the River Tucapel, Province of Arauco, on the western slope of Nahuelbuta Coastal Range, and provisionally assigned by Jara (1996) to *Aegla araucaniensis* Jara, 1980, were subsequently linked to *A. bahamondei* Jara, 1982 by molecular analysis (Pérez-Losada et al. 2002). In this study, the specimens of River Tucapel are described as a new species. The type material and other reference specimens were deposited in the Crustacean Collection of the Instituto de Zoología of the Universidad Austral de Chile (IZUA-C), Valdivia, Chile. The size of specimens was recorded as carapace length (CL), measured between the tip of rostrum and posterior margin of the carapace.

Aegla occidentalis, new species

Figs. 1, 2

Aegla "not yet identified".—Jara, 1982: 235 (see Remarks).

Aegla araucaniensis.—Jara, 1996:63, 194, 195, figs. 42, 43 (in part, see Remarks).

Aegla sp.—Pérez-Losada et al., 2002:305.

Material examined.—Holotype: ♂, CL 28.3 mm, River Tucapel, at Quelen Quelen, 100 m eastward from bridge at national roadway P-60-R, 7 km N of Cañete, 37°44′09″S, 73°22′49″W, 40 m above sea level, Arauco, VIII Región, Chile, 7 Dec 1974, colls. C. G. Jara, C. A. Moreno, and J. N. Arenas, IZUA C-66A. Allotype: ♀, CL 19.0, same data as holotype, IZUA C-66A. Paratypes: 2 ♂♂, CL 17.5, 21.7; ♀, CL 14.3, same data as holotype, IZUA C-66A.

Non-paratype material: 6 ♀♀, CL 16.2, 17.6, 18.2, 18.5, 18.6, 19.5; ♂, CL 15.5, same data as holotype, 19 Nov 1975, coll. C.G.Jara, IZUA C-156. ♀, CL 16.1; 5 ♂♂, CL 17.0, 17.9,18.5, 18.6, 25.5, same data as holotype, 18 Sep 1981, coll. C. G. Jara, IZUA C-429. 2 ♀♀, CL 18.0, 18.9; 4 ♂♂, CL 16.5, 17.4, 18.3, 19.8, same data as holotype but 100 m westward from bridge, 22 Feb 2000, colls. C. G. Jara, M. Pérez-Losada, and A. Riedemann, IZUA C-592. 3 ♀♀, CL 7.9, 19.8, 22.5; 2 ♂♂ CL 17.9, 22.8, River Caramávida, 37°41′16″S, 73°21′27″W, 05 Nov 1981, coll. C. G. Jara, IZUA C-242. 2 ♀♀, CL16.2, 16.9; 4 ♂♂ CL 18.9, 19.8, 21.0, 24.8, River Pocuno, 2 km north from Colonia Antiquina, under bridge of national roadway S-70, 38°02′07″S, 73°23′37″W, 11 Dec 1981, coll. C. G. Jara, IZUA C-428. 2 ♀♀, CL 18.1, 18.7; 4 ♂♂, CL 16.7, 18.8, 19.4, 20.2, Lake Lanalhue, 37°55′37″S, 73°15′18″W, 7 Nov 1974, colls. C. G. Jara, C. A. Moreno, and J. N. Arenas, IZUA C-65. 2 ♀♀, CL 13.6, 13.8; 4 ♂♂, CL 15.8, 15.8, 16.0, 20.8, Lake Lleu Lleu, at Puerto Choque, 38°11′43″S, 73°21′21″W, 8 Dec 1981, coll. R. Arriagada, IZUA C-260.

Diagnosis.—Body contour almond shaped; carapace surface grossly punctated; rostrum triangular to subligulate, short and low profiled, apex with scale surrounded by rosette of short stiff setae and minute acicular scales; orbital spine absent; branchial margins of carapace not expanded, smooth; anterolateral angle of second abdominal epimeron blunt, frequently with small scale hidden among short setae; carpal lobe subpyramidal tipped with row of 1–4 scales in a row mingled with short stiff setae; lobe on proximodorsal end of dactylus of chelae low and blunt; palmar crest subrectangular, slightly expanded and faintly concave, its margin subdenticulate; fourth thoracic sternum flat, unornamented, at most with semicircular swelling ending abruptly at frontal end.

Description of holotype.—Body (Fig. 1a) almond-shaped in contour; precervical portion clearly distinct from postcervical; carapace most protuberant and convex on gastric area. Carapace surface with coarsely, shallow punctae, with pappose setae. Rostrum subligulate, straight, at same level of front; margins, from orbital sinus to tip, with row of tiny scales; rostral carina extended from point equidistant to protogastric eminences to distal third of rostrum, and merging beyond that point into rostrum body (Fig. 1g). Space between carina and margins not noticeably troughed; carina summit with 2 irregular rows of tiny acute scales. Rostrum tip with small, acute, conical scale flanked by flat scales at base; scales interspersed with minute, stiff, pappose setae. Ventral surface of rostrum protruding as blunt keel, reaching deepest point between and behind ocular peduncles. Orbits broad, deeply U-shaped, without orbital spine or extraorbital sinus (Fig. 1a). In place of extraorbital sinus 2 minute scales protruding from slanted margin merging with anterolateral lobe of carapace; lobe tipped with a cuspidate scale, and posterior

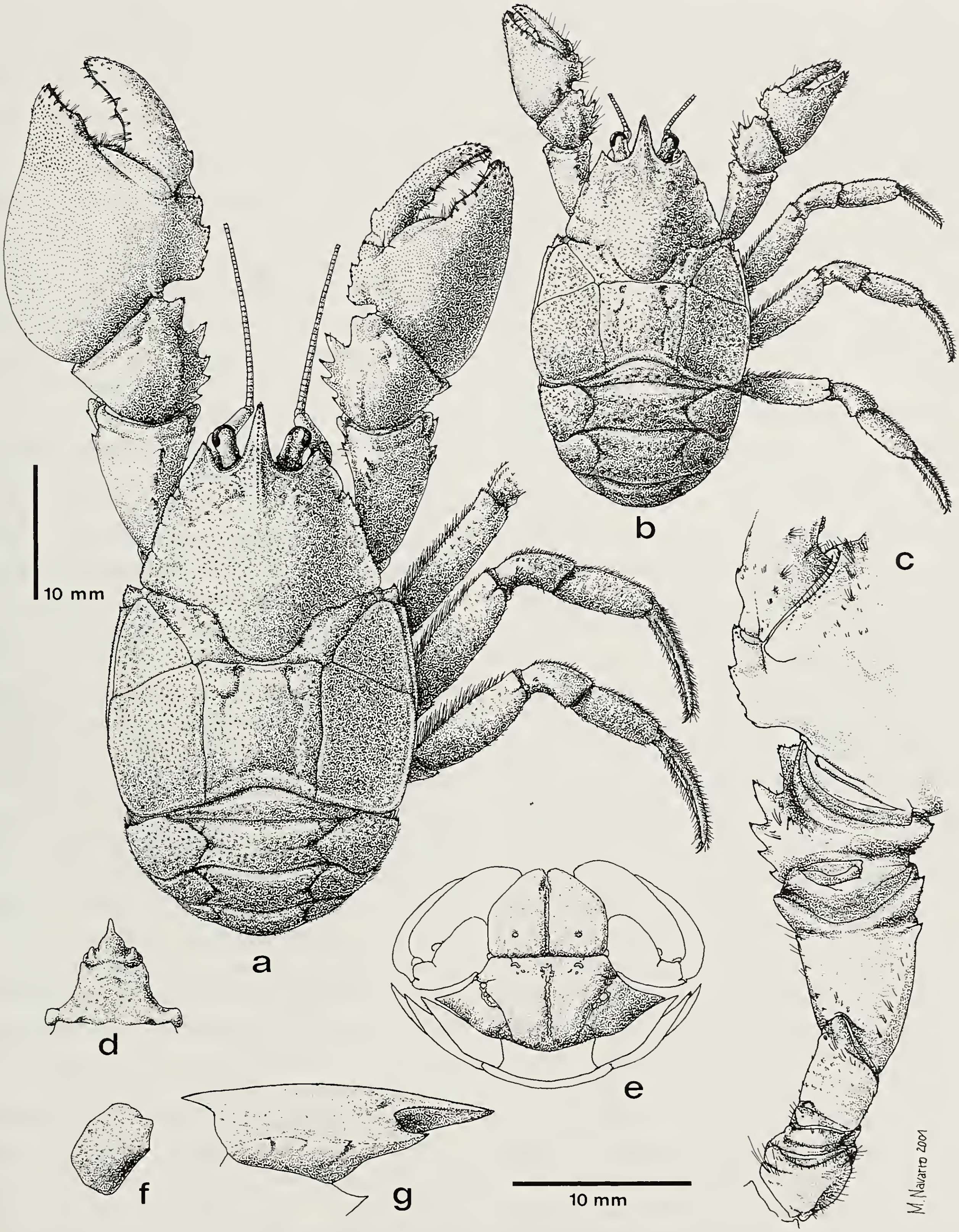

Fig. 1. *Aegla occidentalis,* new species. a, male holotype (IZUA C-66A), dorsal view; b, female allotype, dorsal view; c–g, male holotype; setae mostly omitted: c, left cheliped, ventral view; d, third and fourth sterna, ventral view; e, telson plate and sixth abdominal somite, dorsal view; f, second abdominal epimeron; g, precervical portion of carapace, side view.

to it with row of 12 (left) or 14 (right) minute, size-decreasing scales extending on lateroexternal margin. Protogastric eminences nodular, bearing 6 (left) or 8 (right) irregularly placed minute blunt scales. Epigastric eminences low, rounded, not well defined, bearing patch of minute scales, some arranged in semicircular row on frontal edge with remaining scales spreading backwards over somewhat triangular area. Hepatic area wide, margin slightly upturned and bearing row of minute scales; anterolateral angle of first right hepatic lobe tipped with acuminate scale larger than that on left side. Second and third lobes distinct, blunt. Epibranchial tooth pyramidal, well defined but not particularly elongated, tipped with small acuminate scale followed by row of 5 (right) or 7 (left) tiny scales on lateroexternal margin. Margin of anterior branchial areas thin, almost smooth, slightly expanded, bearing homogeneous band of tiny scales mingled with short stiff pappose setae. Posterior branchial margin non-recurved, somewhat thickened, with band of scales and setae extending to posterior carapace rim. Cardiac area subrectangular, slightly longer than wide. Areola rectangular (length/width ratio = 1.5), not noticeably protuberant. Sternal surface of carapace not ornamented. Central portion of fourth thoracic sternum slightly protuberant (Fig. 1d), bearing patch of long stiff simple setae on frontal edge. Dorsum of abdominal somites covered by short stiff pappose setae especially dense on epimera. Anterolateral angle of second abdominal epimeron as short acuminate tubercle ending in scale concealed by short stiff pappose setae (Fig. 1f). Lateroventral angle of third and fourth epimera also tipped with acute scale. Telson subpentagonal, slightly wider than long, clearly divided by mesial joint (Fig. 1e).

Chelae massive, unequal in size, left larger. Basis-ischium ventromesial edge smooth, slightly nodulated, bearing tiny conical scale on subdistal knob. Merus dorsal edge blunt, bearing row of tubercular denticles tipped with acuminate scale; distodorsal margin smooth, bearing scattered minute scales and short stiff pappose setae more numerous and closely packed on middorsal low profiled tubercle; ventrolateral inner margin slightly sinuous, bearing row of 3 minute scales, and pronounced acuminate conical tubercle distally; ventrolateral outer margin smooth, with 1 (left) or 2 (right) spiniform tubercles distally; with another small acuminate tubercle distally and close to article margin. Carpus markedly convex, globose, almost smooth, bearing scattered minute scales irregularly distributed, larger and more prominent on distal margin; carpal ridge slightly protuberant, and nodulated, bearing few minute scales; tubercles (1 left, 2 right), each with 3 scales in oblique row on apex; dorsomesial margin of carpus with 4 large proximally size-decreasing conical tubercles in a row; tubercles thick, tipped with moderately acute scales; frontmost tubercle on left carpus with accessory scale some distance behind apical one, and separated from low-profiled carpal lobe by wide sinus (Fig. 1c). Carpal lobe broad-based, subtriangular in outline, flattened, tipped with row of 3 or 4 short coalescent scales interspersed with short stiff pappose setae. Ventral face of carpus (Fig. 1c) clean, smooth, bearing 1 short stout acuminate tubercle on central area surrounded by few long stiff simple setae; right carpus with second acuminate tubercle close to base of third tubercle of dorsomesial carpal margin; corresponding site on left carpus with slightly protuberant swelling. Ventral margin of carpus with minute scale on carpus-propodus articular knob. Propodus inflated, markedly convex (particularly left); dorsal surface covered by minute lens-like scales variously arranged, and becoming more dense and protruding on fixed finger. Palmar crest as moderately expanded laminar ridge, with margin irregularly serrated; palmar crest neatly separated from distalmost pyramidal palmar lobe by shallow groove; distal margin of palmar lobe blunt, scaly. Left chela cutting edge of molar process with double row of imbricate short transversal corneous scales. Dactylus with slender molar process; dorsal margin with low broad-based corneous tipped tubercle close to articular furrow.

Dactylus of second, third, and fourth pereiopods long, slender, with elongate, markedly recurved corneous tip, especially at fourth; ventral margin of dactylus with 2–4 needle-like corneous spines in longitudinal row behind tip; distodorsal angle of carpus and merus with 1 or 2 tiny, acute scales concealed by dense band of short stiff pappose setae; frontodorsal margin of carpus and propodus with dense band of short stiff pappose setae; same margin of merus with dense row of long soft plumose setae.

Description of allotype.—Differs from holotype in having rostral carina flanked by troughs on middle third of rostrum. Carapace (Fig. 1b) worn out, blackened by deposition of organic matter. Chelae less massive, unequal in size, left larger. Dorsomesial margin of carpus of chelipeds with only 3 conical tubercles. Ventral face of carpus of right cheliped with 2 coalescent blunt tubercles, 1 on left cheliped. Lobe on proximodorsal end of dactylus of chelae slightly prominent. Ventral margin of dactylus of left second pereiopod with row of 5 slender acuminate scales behind tip, and row of 3 scales in the remaining dactyli.

Morphometrics.—Descriptive morphometrics of the type series specimens (see Bond-Buckup & Buckup 1994) are recorded in Table 1.

Variations.—Typically lacking extraorbital sinus, but in two of the smallest paratypes both orbits have thickened margin bearing one small tubercle delimiting a very narrow extraorbital sinus.

Apex of carpal lobe of chelipeds typically with row of two to four scales mixed with short stiff pappose setae. In the smallest paratype, both carpal lobes are monocuspidate.

Anterolateral angle of second abdominal epimeron; it typically protrudes as small tubercle tipped with acuminate scale surrounded by short stiff pappose setae. However, the largest male paratype has blunt angles bearing an almost imperceptible scale hidden by setae.

Table 1.—Morphometric ratios of the type series specimens of *Aegla occidentalis*, new species. CL, carapace length, between tip of rostrum and median point on rear margin of carapace; RL, rostral length, between tip of rostrum and median point between proximal end of orbits; AL, areola length, between frontal and caudal midpoints; AW, areola width, between midpoint of lateral grooves of areola; PCL, precervical length, between tip of rostrum and midpoint of cervical groove; FW, frontal width, between tips of anterolateral angles of carapace.

Ratios	N	Range	Mean	Mean confidence limits ($P \leq 0.05$)
CL/RL	5	5.5–5.6	5.5	5.2–5.8
AL/AW	5	1.3–1.5	1.4	1.2–1.6
PCL/FW	5	2.1–2.2	2.1	1.9–2.4

Ventromesial margin of merus of chelipeds with ornamentation varying from completely lacking, as in the smallest female paratypes, to a row of small tubercles, some of which are tipped with a small scale, as in the smallest male paratype.

Ornamentation of fourth thoracic sternum, in both male paratypes, with frontal margin sharp, and convex, forming a rim that is not apparent in the remaining type specimens.

The morphological variation among non-paratype specimens of *A. occidentalis* is summarized in Table 2. In addition, among the specimens from Lake Lanalhue and Lake Lleu Lleu, the rostral carina varies from a sharp elevated ridge, stretched along the whole rostrum, to a ridge restricted to the proximal third or half of the rostrum; beyond that it appears flat and apically recurved. The same specimens have a faintly marked ridge, with variable intensity, along the midline of the gastric area behind the protogastric eminences. This ridge is also present in the specimens of River Caramávida and River Pocuno but only sporadically among the specimens of River Tucapel.

Distribution.—Known from the River Paicaví drainage system, which includes the

Table 2.—Variation of morphotypic characters in *A. occidentalis,* new species. Relative frequencies (%) refer to the number of specimens from each locality examined as non-paratype material, irrespective of sex. River Tucapel (n = 19), River Caramávida (n = 5), Lake Lanalhue (n = 6), River Pocuno (n = 6), and Lake LleuLleu (n = 6).

	Localities				
	Tucapel	Caramávida	Lanalhue	Pocuno	LleuLleu
Shape of rostrum:					
Triangular	36.8	80.0	33.3	33.3	33.3
Subligulate	63.2	20.0	66.7	66.7	66.7
Troughs both sides of rostrum:					
Well marked	52.6	60.0	50.0	50.0	50.0
Faintly marked	47.4	40.0	50.0	50.0	50.0
Orbits:					
Without spine/tubercle	47.4	60.0	16.7	83.3	50.0
With spine/tubercle	52.6	40.0	83.3	16.7	50.0
Apex of carpal lobe of chelipeds:					
With two or more scales	73.7	60.0	83.3	83.3	66.7
With one scale	26.3	40.0	16.7	16.7	33.3
Frontalmost tubercle of dorso-medial margin of carpus of chelipeds:					
Monocuspid	94.7	80.0	83.3	100.0	100.0
Bicuspid	5.3	20.0	16.7	0.0	0.0
Anterolateral angle second abdominal epimeron:					
Armed with scale	63.2	60.0	33.3	50.0	83.3
Unarmed	36.8	40.0	66.7	50.0	16.7
Angle of third abdominal epimeron:					
With acuminate scale	15.8	0.0	50.0	0.0	0.0
Blunt	84.2	100.0	50.0	100.0	100.0
Angle of fourth abdominal epimeron:					
With acuminate scale	89.5	100.0	83.3	66.7	66.7
Blunt	10.5	0.0	16.7	33.3	33.3

River Tucapel, the River Caramávida and Lake Lanalhue, and from the River Lleu Lleu drainage system, which includes the River Pocuno and Lake Lleu Lleu (Fig. 2). Both systems drain contiguous sections of the western slope of the Nahuelbuta Costal Cordillera, between 37°40′S and 38°15′S.

Notes on natural history.—The general description of the biotope where *A. occidentalis,* new species, lives was published by Jara (1982) with the description of *A. bahamondei,* a species with which the former coexists.

The females of *A. occidentalis* collected in the River Caramávida (IZUA C-242) were ovigerous. Their eggs contained embryos in advanced state of development, probably close to hatching. Also, five of the six females from River Tucapel (IZUA C-156) had fresh, empty egg-shells, indicating that the juveniles hatched only a few days before collection. Therefore, it is likely that recruitment in populations of *A. occidentalis* occurs in springtime (September to November), as in other species of *Aegla* (see Bahamonde & López 1961, López 1965, Rodrigues & Hebling 1978).

Etymology.—The specific name is from the Latin *occidentalis*, western, in allusion to the geographic distribution of the new species, which is apparently restricted to a section of the drainage system of the western slope of the Nahuelbuta Coastal Cordillera.

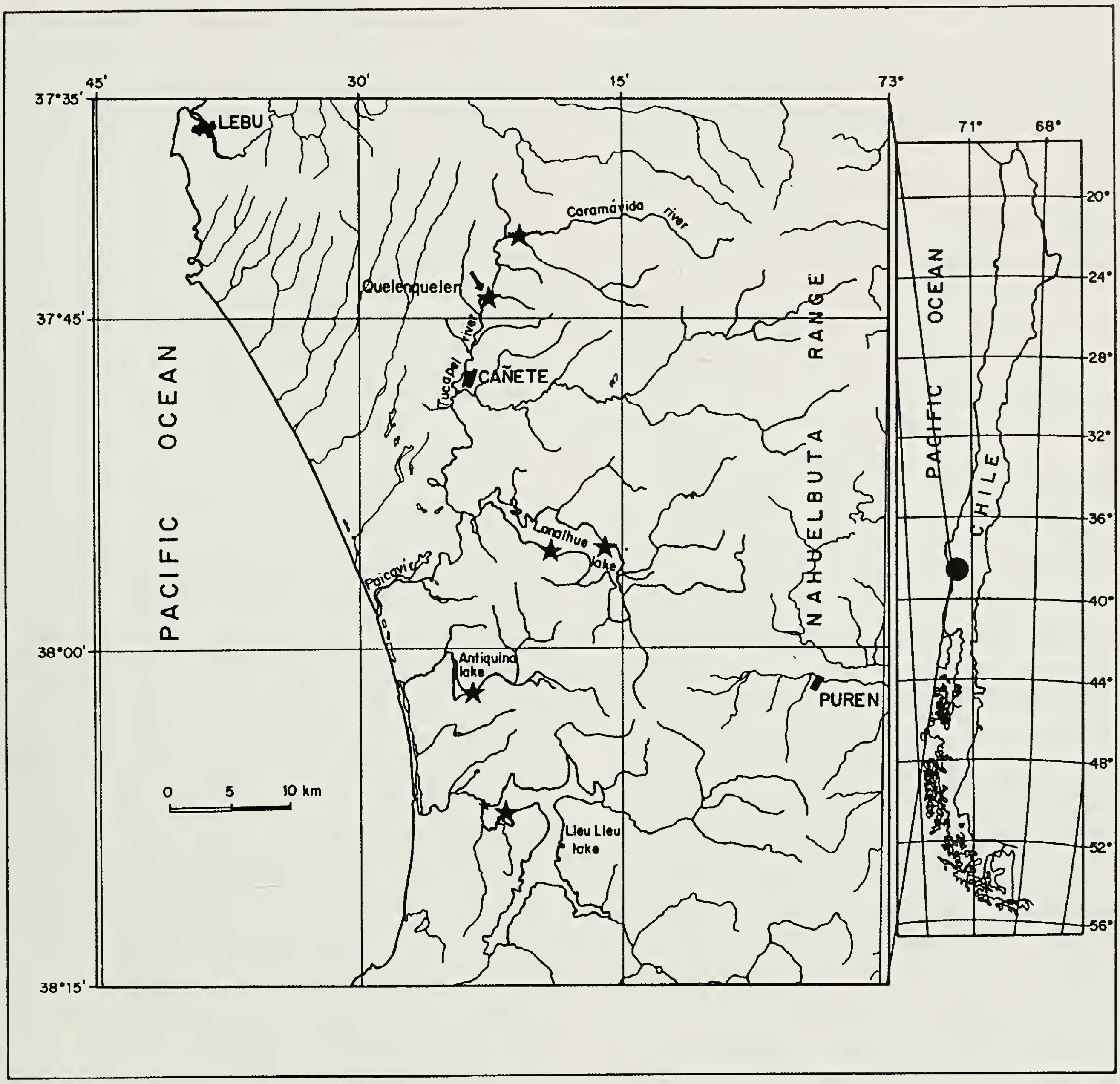

Fig. 2. Collection localities (stars) of *Aegla occidentalis,* new species, in the Tucapel and Pocuno river systems. Arrow indicates type locality.

Comparisons.—*Aegla occidentalis,* new species, closely resembles *A. laevis* (Latreille, 1818), and *A. araucaniensis.* The new species shares with those two species the almond-shaped body contour, the relatively short precervical section and narrow front, the absence of orbital spine, the elevated gastric area, the broad areola, the unornamented branchial margins, the scale ending rostral apex surrounded by rosette of short stiff pappose setae and minute acicular scales, the subligulate rostrum, the subrectangular denticulate palmar crest, and the tubercular lobe on the dorsum of the dactylus of the chelae. Furthermore, with *A. laevis* it shares the blunt slightly protruding epigastric eminences, the non-recurved posterior branchial margin, and the low profiled carpal lobe.

Aegla occidentalis differs from the other almond-shaped species by having the dorsal surface of the carapace grossly punctated, a feature most evident in specimens with old, darkened carapaces, and by having the anterolateral angle of the second abdominal epimeron rounded and frequently without an apical scale (see Table 2). The palmar crest in *A. occidentalis,* although subrectangular, is slightly to moderately expanded, with the margin weakly serrate, and faintly concave on the dorsum. In that respect it differs from *A. araucaniensis,* in which the palmar crest is clearly expanded, markedly indented, and dorsally concave especially at its posterior end; and from *A. laevis,* which has a less expanded but similarly concave posterior ending palmar crest. The morphological differences between *A. occidentalis* and the above mentioned species are subtle, and subject to considerable variation but still enough to distinguish the species. From *A. bahamondei* it differs in lacking acute, apically elongate, conical rostrum; denticulate branchial margin; protuberant protogastric eminences; anterolateral angle of second abdominal epimeron spiniform; fourth thoracic sternum with median acute, conical, tubercle; and spine-like dactylar lobe of chelae (Jara 1982).

Genetically, *A. occidentalis* shows clear differences from all other Chilean species analyzed by Pérez-Losada et al. (2002). According to those authors, the interspecific degree of average pairwise genetic divergence estimated from the corrected genetic distances ranges from 1.3%–9.9%. The pair *A. occidentalis–A. bahamondei* has the lowest divergence, 1.4% to 1.6%, a value similar to that observed for other pairs (e.g., *A. cholchol* Jara & Palacios, 1999–*A. rostrata* Jara, 1977 = 1.3% to 1.5%), and higher than that observed in pairs of subspecies (e.g., *A. denticulata lacustris* Jara, 1989–*A. denticulata denticulata* Nicolet, 1849 = 0.3% to 0.4%), or in populations of a single species (e.g., *A. affinis* Schmitt, 1942 = 0.2%). Thus, these data suggest that the genetic differences observed between *A. occidentalis* and *A. bahamondei* are indicative of species distinctness within the Aeglidae.

Remarks.—The discovery of the new species *A. occidentalis* was facilitated by the application of molecular techniques in the study of phylogenetic relationships among the Chilean species of *Aegla* (Pérez-Losada et al. 2002), which provided a high-resolution approach to assess taxonomic limits. The existence of similar morphologies in two or more species may be due to close phylogenetic relationship (descendents from a common recent ancestor), or to morphological convergence. Convergence may result from the independent evolution of the same specialized (adaptive) features in response to similar selective pressures, or to retention of a generalized ancestral morphotype (Moore & Willmer 1997). In the present case, the comparison of *A. occidentalis* with other species of *Aegla* indicates that the morphotype of the new species is markedly similar to that of *A. laevis* and *A. araucaniensis.* The genetic divergence and phylogenetic analysis (Pérez-Losada et al. 2002) of four mitochondrial genes from 16 Chilean aeglids suggest that the species most closely related to *A. occidentalis* is *A. bahamondei,* a species from which the former clearly differs in morphology (Jara 1982), and the two occupy the same biotope. The high degree of genetic divergence between *A. occidentalis* and *A. araucaniensis* (3.5%–3.7%) and between *A. occidentalis* and *A. laevis* (5.9%–7.4%), and their clearly separated phylogenetic positions in the maximum likelihood and maximum parsimony trees (see Pérez-Losada et al. 2002), suggest the possibility of morphological convergence rather than the sharing of a generalized ancestral morphotype. In contrast, the inferred close relationship between *A. occidentalis* and *A. bahamondei,* and the fact that they share the same biotope with no appreciable differences in density (C. G. Jara, pers. obs.), suggest an evolutionary and geographic scenario that allowed for the allopatric speciation of both taxa, and for their subsequent concurrence in the same river basin.

The specimens of *Aegla* "not yet identified" mentioned by Jara (1982) have proven to represent the new species *A. occidentalis.* As previously mentioned, part of the material of *A. araucaniensis* reported by

Jara (1996), contains specimens of *A. occidentalis*.

Conservation.—From a conservation perspective, *A. occidentalis* qualifies as "Vulnerable" (VU) according to the criteria included in the IUCN (2001) Red List Categories, because, with only five recognized localities, its populations are likely fragmented and restricted in distribution due to severe perturbations in the river basins of the western slope of the Coastal Cordillera by intense logging activities (criterion D2).

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Literature Cited

Bahamonde, N., & M. T. López. 1961. Estudios biológicos en la población de *Aegla laevis laevis* (Latreille) de El Monte (Crustacea, Decapoda, Anomura).—Investigaciones Zoológicas Chilenas 7:19–58.

Bond-Buckup, G., & L. Buckup. 1994. A família Aeglidae (Crustacea, Decapoda, Anomura).—Arquivos de Zoologia, Museu de Zoologia da Universidade de Sao Paulo, 32(14):159–346.

Hillis, D. M. 1987. Molecular versus morphological approaches to systematics.—Annual Review of Ecology and Systematics 18:23–42.

IUCN. 2001. IUCN Red List Categories (2001): version 3.1. Prepared by the IUCN Species Survival Commission. IUCN, Gland, Switzerland and Cambridge, UK.

Jara, C. G. 1977. *Aegla rostrata* n.sp., (Decapoda, Aeglidae), nuevo crustáceo dulceacuícola del Sur de Chile.—Studies on Neotropical Fauna and Environment 12:165–176.

———. 1980. Dos nuevas especies de *Aegla* Leach (Crustacea, Decapoda, Anomura) del sistema hidrográfico del Río Valdivia.—Anales del Museo de Historia Natural de Valparaíso (Chile) 13:255–266.

———. 1982. *Aegla bahamondei,* new species (Crustacea: Decapoda: Anomura) from the Coastal Mountain Range of Nahuelbuta, Chile.—Journal of Crustacean Biology 2: 232–238.

———. 1989. *Aegla denticulata lacustris,* new subspecies, from Lake Rupanco, Chile (Crustacea: Decapoda: Anomura: Aeglidae).—Proceedings of the Biological Society of Washington 102:385–393.

———. 1996. Taxonomía, sistemática y zoogeografía de las especies chilenas del género *Aegla* Leach (Crustacea: Decapoda: Anomura: Aeglidae). Ph.D. thesis, Escuela de Graduados, Universidad de Concepción, Concepción, Chile, 223 pp.

———, & V. L. Palacios. 1999. Two new species of *Aegla* Leach (Crustacea: Decapoda: Anomura: Aeglidae) from southern Chile.—Proceedings of the Biological Society of Washington 112:106–119.

Latreille, P. A. 1818. Crustacés, Arachnides et Insectes. Pp. 24, pl. 308 *in* Tableau Encyclopédique et Méthodique de Trois Règnes de la Nature, 24, Paris.

Leach, W. E. 1821. Galatéadées. Pp. 49–56 *in* F. G. Levrault, ed., Dictionnaire des Sciences Naturelles, 18(1820), Strasbourg.

López, M. T. 1965. Estudios biológicos en *Aegla odebrechtii paulensis,* Schmitt.—Boletim da Facultade de Filosofia, Ciências e Letras da Universidade de São Paulo, Zoologia 25:301–314.

Mayr, E., & P. D. Ashlock. 1991. Principles of systematic zoology, 2nd edition. McGraw-Hill, Inc., New York, 475 pp.

Moore, J., & P. Willmer. 1997. Convergent evolution in invertebrates.—Biological Review 72:1–60.

Nicolet, H. 1849. Crustáceos. Pp. 200–201 *in* C. Gay, ed., Historia física y política de Chile, Zoología 3; Atlas Zoológico (1854), Crustáceos, pl. 2, figs. 1a, b.

Pérez-Losada, M., C. G. Jara, G. Bond-Buckup, & K. A. Crandall. 2002. Phylogenetic relationships among the species of *Aegla* (Anomura: Aeglidae) freshwater crabs from Chile.—Journal of Crustacean Biology 22:304–313.

Rodrigues, W., & N. Hebling. 1978. Estudos biológicos em *Aegla perobae* Hebling & Rodrigues, 1977 (Decapoda, Anomura).—Revista Brasileira de Biologia 38:383–390.

Schmitt, W. L. 1942. The species of *Aegla,* endemic South American freshwater crustaceans.—Proceedings of the United States National Museum 91:431–520, pl. 25–28.

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116(4):943–955. 2003.

A new genus and new species of the family Paguridae (Crustacea: Decapoda: Anomura), from Hachijo-jima Island, Japan, with a list of hermit crab species found in the same collection sites

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Abstract.—A new genus and new species of pagurid hermit crab, *Hachijopagurus rubrimaculatus,* is described and illustrated on the basis of three specimens from Hachijo-jima Island in the Izu Islands, Japan. The new genus *Hachijopagurus* appears close to *Pygmaeopagurus* McLaughlin, 1986, but differs from the latter in having the eighth thoracic sternite with a pair of ventrally flattened lobes in male and female, and a rod-like sexual tube on the coxa of the right fifth pereopod in male. The distinct concavity at the dorsomesial distal angle of the palm of the right cheliped can be regarded as unique for *H. rubrimaculatus* since such the structure has not been described for any known pagurid species. A list of the hermit crab species found in the collection sites of the present new species is provided.

Kato & Okuno (2001) introduced the richness of the shallow-water decapod crustacean fauna around Hachijo-jima Island of the Izu Islands, Japan, in their local guidebook "Shrimps and crabs of Hachijo Island", with many underwater photographs. Their book contains a photograph of an unusual hermit crab, "Paguridae sp.", taken at the depth of 40 m. The photographed specimen could be collected, and was found to have a characteristic right cheliped with a distinct concavity at the dorsomesial distal angle of the palm. In addition to this specimen, two hermit crabs proved to be conspecific with Kato & Okuno's (2001) "Paguridae sp." from Hachijo-jima Island were made available for close taxonomic study. The examination of the three specimens revealed that they represent an undescribed species that can not be assigned to any known pagurid genera. Thus, we herein describe and illustrate these specimens as a new genus and new species.

General terminology used in the description follows that of McLaughlin (1974:9), with the exception of the posterior carapace (see Lemaitre 1995:2), fourth pereopod (see McLaughlin 1997:435), and gill structure (see McLaughlin & de Saint Laurent 1998: 161). The submedian grooves on the shield are termed "paragastric grooves" (see Komai & Osawa 2001:1291). Forest et al. (2000:24) is followed in the interpretation of the ocular peduncle, which is provided basally with a small calcified plate referred to as the "ocular acicle". The sternites of the third maxillipeds and third and fifth pereopods are each shown as "third", "sixth", and "eight" thoracic sternites. Shield length (sl), as measured from the tip of the rostrum to the midpoint of the posterior margin of the shield, indicates specimen size. The lengths of the segments of the chelipeds were measured along the dorsomesial margin except for the chelae, which were measured along each the dorsal midline from the proximal margin of the palm to the level of the distal tip of the fixed finger. The widths of the chelae were measured at the dorsoproximal points of the fingers. The lengths of the segments of the ambulatory legs were measured along the dorsal margins, but for the propodus, excluding the proximal oblique margin and distal projection. The heights of the propodi and meri of the ambulatory legs were measured along the lateral transverse midline. The drawings were made with the aid of a drawing tube mounted on a Leica MZ8 stereomicroscope. The type material of the new species is deposited in the Coastal Branch of Natural History Museum and Institute, Chiba (CMNH, with code of ZC), and National Science Museum, Tokyo (NSMT, with code of Cr).

A list of hermit crabs found in the collection sites of the present new species is given in "Appendix", with the specimen and collection data. The specimens are deposited in CMNH.

Hachijopagurus, new genus

Diagnosis.—Eleven pairs of biserial, phyllobranchiate gills. Shield with moderately well developed, broadly triangular rostrum. Ocular acicles subtriangular, not elongate. Antennal peduncles with supernumerary segmentation. Maxillule with endopod bearing subtriangular external lobe. Third maxilliped with ischium bearing developed crista dentata and accessory tooth. Chelipeds markedly unequal, right much stronger. Fourth pereopod semichelate, propodal rasp composed of single row of corneous scales, dactyl lacking preungual process. Sixth thoracic sternite with semicircular anterior lobe. Eighth thoracic sternite with pair of ventrally flattened lobes. Male with coxae of fifth pereopods slightly asymmetrical, right larger; each with sexual tube rod-like, distally curved, longer than coxal length measured on ventral surface; 3 unpaired, unequally biramous left pleopods on third to fifth abdominal somites. Female with unpaired left gonopore; no paired pleopods; 4 unpaired, unequally biramous left pleopods on second to fifth abdominal somites. Abdomen well developed, dextrally coiled. Uropods markedly asymmetrical. Telson with midlateral transverse identations on lateral margins; posterior lobes with terminal margins separated by shallow median cleft.

Type species.—*Hachijopagurus rubrimaculatus,* new species, by present designation.

Etymology.—The genus name is a combination of "*Hachijo*", meaning the locality where the type species was collected, and "*pagouros,*" meaning crab in Greek. Gender is masculine.

Remarks.—*Hachijopagurus* shares with certain species belonging to the genera *Alainopagurus* Lemaitre & McLaughlin, 1995, *Decaphyllus* de Saint Laurent, 1968, *Iridopagurus* de Saint Laurent-Dechancé, 1966, *Nematopaguroides* Forest & de Saint Laurent, 1968, *Nematopagurus* A. Milne-Edwards & Bouvier, 1892, and *Solitariopagurus* Türkay, 1986, a pair of sexual tubes being longer than the coxa of the fifth pereopod in male measured on the ventral surface. Among these genera, *Hachijopagurus* resembles *Nematopaguroides* or *Nematopagurus* in that the right sexual tube is slender and distally filamentous, but differs from the latter two genera in having markedly unequal chelipeds in both male and female, and unpaired left gonopore in female. Species of *Nematopaguroides* and *Nematopagurus* have subequal or somewhat unequal chelipeds, and paired gonopores in female (see McLaughlin 1997, 2003; Wang & McLaughlin 2000).

Hachijopagurus rather appears close to *Pygmaeopagurus* McLaughlin, 1986 currently recognized as monotypic (type species: *P. hadrochirus* McLaughlin, 1986 from Hawaii), in sharing a set of characters as follows: eleven pairs of biserial gills; shield with a moderately well developed, broadly triangular rostrum; crista dentata of the third maxilliped with an accessory tooth; semichelate fourth pereopods with a single row of corneous scales in the propodal rasp; male with a rod-like sexual tube on the coxa of the left fifth pereopod and three unpaired left biramous pleopods; and female with unpaired left gonopore, no pair of pleopods modified as goponods on the first abdominal somite, and four unpaired left biramous pleopods. However, the shape of the eighth thoracic sternite in both male and female and the coxa of the right fifth pereopod in male immediately distinguish the two genera. The eighth thoracic sternite consists of a pair of ventrally flattened lobes in *Hachijopagurus,* whereas it is produced as two closely-set lobes in *Pygmaeopagurus.* The coxa of the right fifth pereopod has a rod-like sexual tube in *Hachijopagurus,* but lacks a sexual tube and gonopore in *Pygmaeopagurus.*

Hachijopagurus is also allied to *Anapagurides* de Saint Laurent-Dechancé, 1966, but the structure of sexual tubes in male is different in the two genera. *Hachijopagurus* has a rod-like sexual tube on each the right and left coxae of the fifth pereopods, but *Anapagurides* possesses a pair of short or very short sexual tubes or only a right tube (see Komai 1999:25). On the coxa of the left fifth pereopod, *Anapagurides facetus* (Melin, 1939) from the Ogasawara Islands of Japan has a slightly protruded vas deferens (see McLaughlin & Sandberg 1995: 583); while *A. reesei* (McLaughlin, 1986) from Hawaii possesses frequently a vestige of sexual tube (see McLaughlin 1986:801, as *Nanopagurus* McLaughlin, 1986), and *A. aequalis* Komai, 1999 from off Torishima Island of Japan has a very short sexual tube (see Komai, 1999:24).

The monotypic *Trichopagurus* de Saint Laurent, 1968 (type species: *Catapaguroides? trichophthalmus* Forest, 1954 from Tahiti) is somewhat similar to *Hachijopagurus,* but has quadriserial gills with lamellae weakly divided distally, and a rudimentary left sexual tube in male (see de Saint Laurent 1970:210, figs. 11, 16). *Hachijopagurus* has biserial gills, and a rod-like left sexual tube.

Hachijopagurus rubrimaculatus
new species
Figs. 1–3

Paguridae sp.: Kato & Okuno 2001:83, unnumbered fig.

Type material.—Holotype: male (sl 1.6 mm), Nazumado, Hachijo-jima Island, Izu Islands, 45 m, 25 Nov 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 470. Paratypes: 1 female (sl 1.4 mm), Nazumado, Hachijo-jima Island, Izu Islands, 40 m, 17 Dec 2000, SCUBA dive, coll. S. Kato, NSMT-Cr 14556 [specimen of "Paguridae sp." photographed by Kato & Okuno (2001)]. 1 female (sl 1.3 mm), Kyokucho-hama, Hachijo-jima Island, Izu Islands, 40 m, 9 Jul 2002, SCUBA dive, coll. J. Okuno & K. Tanaka, CMNH-ZC 930.

Description.—Eleven pairs of biserial phyllobranchiate gills; 2 moderately well to well developed arthrobranchs on each third maxilliped to fourth pereopod; single moderately well developed pleurobranch on seventh thoracic somite.

Shield (Fig. 1A) slightly longer than broad or slightly broader than long, not strongly calcified; anterior margin between rostrum and lateral projections concave; anterolateral margins sloping; posterior margin roundly truncate; dorsal surface weakly convex in general but concave laterally along conspicuous paragastric grooves, with short setae behind rostrum and lateral projections. Rostrum moderately well developed, broadly triangular, terminating in small spine directed ventrally at slight angle, overreaching lateral projections, dorsal surface with weak, short median ridge. Lateral projections broadly subtriangular, each with small submarginal spine. Accessory portions along cervical groove (not illustrated) narrow, generally membranous but slightly calcified along cervical groove. Posterior carapace membranous, with few tufts of short setae; posteromedian plate very weakly calcified, with pair of tufts of short setae in posterior half; cardiac sulci weakly marked, subparallel in anterior half

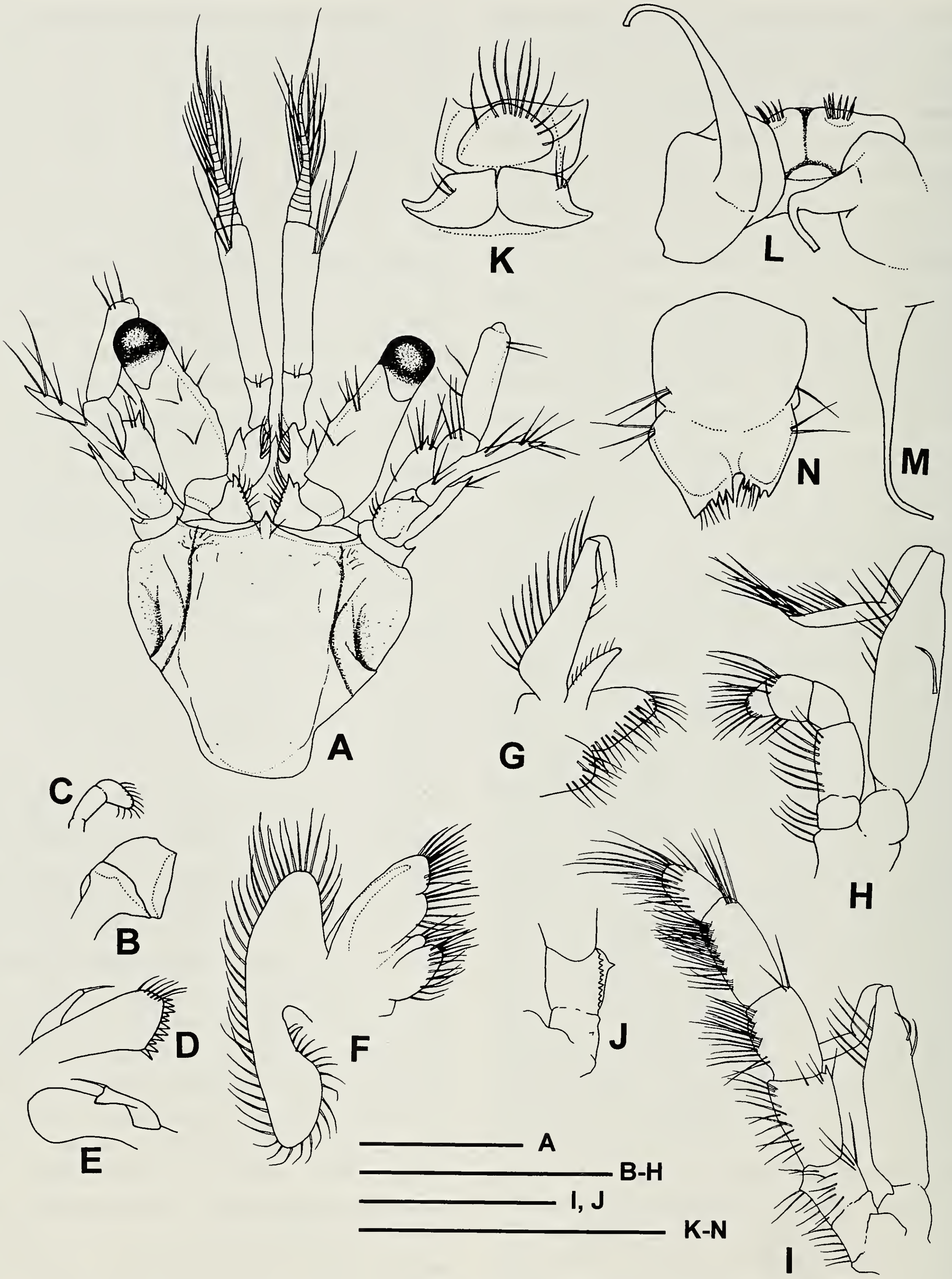

Fig. 1. *Hachijopagurus rubrimaculatus,* new genus and new species. Holotype male (sl 1.6 mm) from Hachijo-jima Island, Izu Islands, Japan, CMNH-ZC 470. A, shield and cephalic appendages, dorsal; B, left mandible, internal; C, same, palp, internal; D, right maxillule (coxal endite missing), external; E, same, lateral; F, right maxilla, external; G, right first maxilliped (flagellum of exopod missing), external; H, left second maxilliped, external; I, left third maxilliped, lateral; J, same, ischium and basis, dorsal (internal); K, sixth thoracic sternite, ventral; L, eighth thoracic sternite, ventral; M, left sexual tube, lateral; N, telson, dorsal. Scales equal 1.0 mm.

but divergent in posterior half, extending to posterior margin; sulci cardiobranchialis extending posteriorly along posterior margin of branchiostegite. Branchiostegites membranous; anterior margins broadly rounded, unarmed, fringed with short setae.

Ocular peduncles (Fig. 1A) stout, subcylindrical, 0.7 times as long as shield; dorsal surface with 2 rows of sparse tufts of short setae mesially; basal portion inflated; median portion concave laterally but slightly convex mesially; corneas occupying 0.3 length of peduncle, not dilated, semispheric, pigmented. Ocular acicles well developed, subtriangular, each with distinct marginal spine terminally, separated basally by half basal width of 1 acicle; dorsal surface convex; mesial margin with short and moderately long setae.

Antennular peduncles (Fig. 1A), when fully extended, exceeding ocular peduncles by 0.9 length of ultimate segment. Ultimate segment elongate, 1.8 times longer than penultimate segment, somewhat deeper distally, with 3 long setae near dorsodistal margin. Penultimate segment with few short setae on dorsodistal margin. Basal segment elongate; statocyst lobe produced laterally, with spine on lateral margin; ventrodistal margin with minute spine and short setae. Upper flagellum elongate, slightly longer than ultimate peduncular segment; lower flagellum reaching midlength of upper flagellum.

Antennal peduncles (Fig. 1A), when fully extended, exceeding distal margins of corneas by approximately half length of fifth segments. Fifth and fourth segments with few scattered, moderately long setae. Third segment with few moderately long setae and small spine at ventromesial distal angle. Second segment with dorsolateral distal angle strongly produced, reaching midlength of fourth segment, terminating in small spine; dorsomesial distal angle with small spine; mesial margin with few short setae. First segment with small spine on ventrolateral margin distally; ventrodistal margin unarmed. Antennal acicles slender, arcuate, reaching midlength of fifth peduncular segment and overreaching bases of corneas, each terminating in small spine; mesial margin with tufts of moderately long setae. Antennal flagella (missing in holotype) approximately 3.0 times longer than shield, with 4 short setae distally on every article.

Mandible (Fig. 1B, C) with incisor process without distinct teeth on mesial margin. Maxillule (Fig. 1D, E) with external lobe of endopod subtriangular, not recurved; internal lobe with apical bristle. Maxilla (Fig. 1F) with endopod overreaching anterior margin of scaphognathite. First maxilliped (Fig. 1G) with endopod less than half length of exopod, exopod inflated proximally. Second maxilliped (Fig. 1H) with basis-ischium fusion incomplete. Third maxilliped (Fig. 1I, J) with carpus unarmed on dorsodistal margin; merus bearing small distolateral spine; ischium with crista dentata composed of row of small corneous teeth, accessory tooth small but distinct; basis-ischium fusion incomplete; basis with few small denticles on mesial margin.

Chelipeds (Figs. 2A–F, 3A–D) considerably unequal, right much stronger than left. Right cheliped of male holotype (Fig. 2A–D) massive, dactyl articulating obliquely with palm, propodal-carpal articulation not twisted. Chela with general outline subovate in dorsal view, 1.6 times longer than wide; dactyl and fixed finger weakly curved ventrally, each terminating in small corneous claw. Dactyl slightly longer than fixed finger, 0.9 length of palm; cutting edge with rounded calcareous teeth on proximal 0.8 and small corneous teeth on distal 0.2; dorsal surface convex, with closely-set, small rounded tubercles and several short setae; dorsomesial margin delimited by subacute ridge of rounded tubercles; mesial surface with irregular rows of small rounded tubercles along dorsal and ventral margins; ventromesial margin delimited by subacute ridge of rounded tubercles, with several short setae; ventral surface with small rounded tubercles and double row of tufts

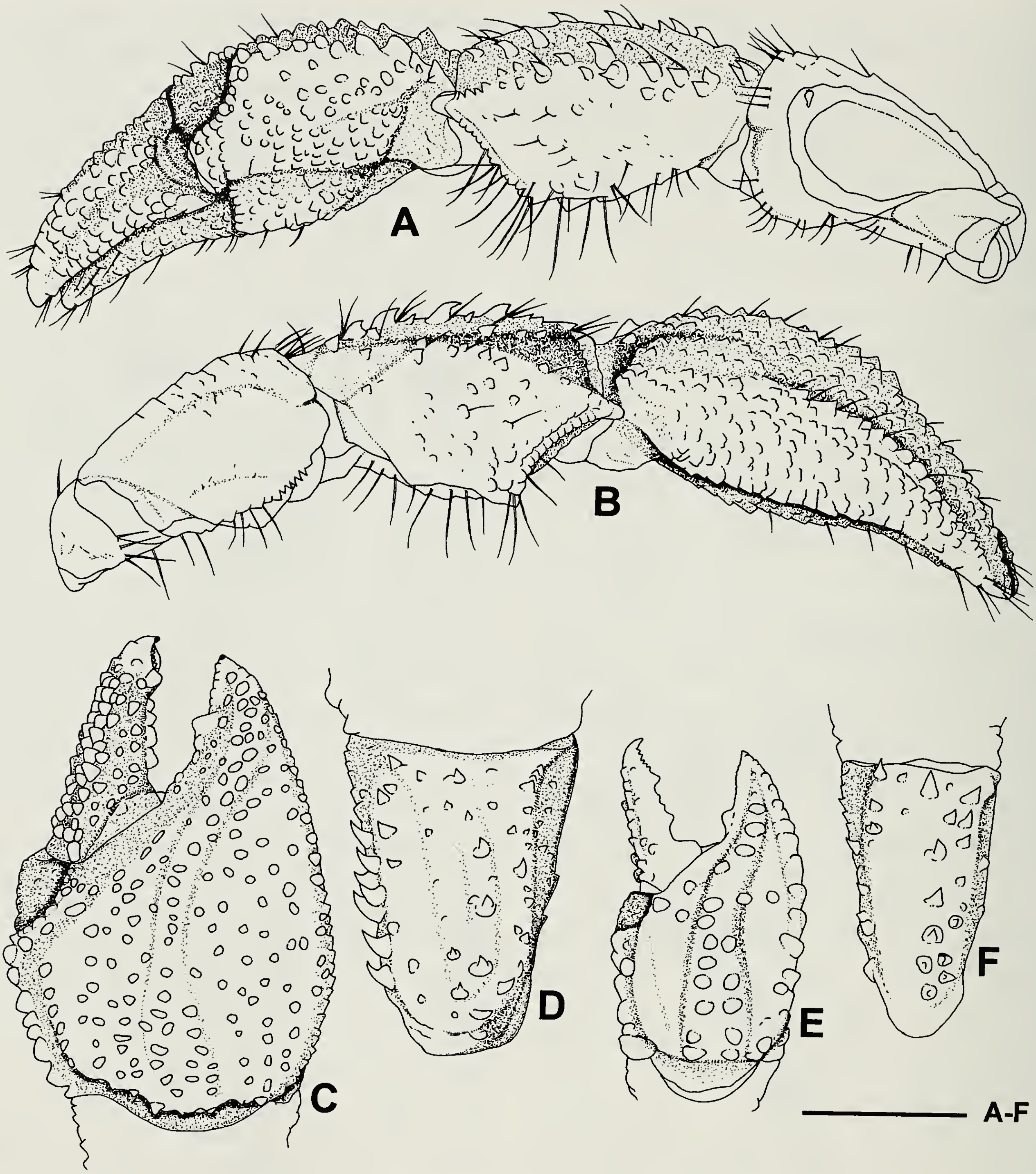

Fig. 2. *Hachijopagurus rubrimaculatus,* new genus and new species. A–D, holotype male (sl 1.6 mm) from Hachijo-jima Island, Izu Islands, Japan, CMNH-ZC 470; E, F, paratype female (sl 1.4 mm), same locality as holotype, NSMT-Cr 14556. Right cheliped. A, entire cheliped, mesial; B, same, lateral; C, E, chela, dorsal, setae omitted; D, F, carpus, dorsal, setae omitted. Scale equals 1.0 mm.

of short setae along cutting region. Palm slightly shorter than carpus; dorsomesial margin subacute, distinctly delimited by row of moderately large tubercles, bearing few short setae, dorsomesial distal angle with prominent concavity; dorsal surface of palm and fixed finger convex, with numerous small rounded tubercles each occasionally accompanied by tuft of few short setae, palm with weakly elevated longitudinal row of tubercles on midline and extending onto fixed finger along cutting edge; dorsolateral margin convex, delimited by subacute ridge of rounded tubercles and low protuberances, with several short setae; mesial surface with numerous, small tubercles; lateral surface with numerous, small low protuberances; ventromesial and ventrolateral margins each delimited by subacute ridge of low protuberances; ventral surface with numerous, small low protuberances and tubercles, and several short setae, larger protuberances present on longitudinal midline of palm, several tufts of setae present along cutting region; cutting edge of fixed finger with low, rounded calcareous teeth on proximal 0.6 (distalmost tooth well developed) and small rounded calcareous teeth each with minute corneous tip on distal 0.4. Carpus broad, becoming broader distally in dorsal view, 1.2 times longer than merus; dorsomesial margin depressed, with irregular row of curved spines accompanied by few short setae, distal part with small tubercles, distal angle produced bluntly; dorsodistal margin unarmed; dorsal surface with short row of curved spines distally on mesial half, row of curved spines adjacent to dorsolateral margin, and scattered smaller spines and tubercles, each spine occasionally accompanied by few short setae; dorsolateral margin weakly delimited, with irregularly arranged small spines and tubercles, distal angle produced bluntly; mesial face with few scattered short setae, distal margin with tuberculate ridge; ventromesial margin protuberant, with tufts of moderately long setae; lateral face with small low protuberances, distal margin with tuberculate ridge; ventrolateral margin smooth, distal part produced, subtriangular ventrally, bearing moderately long setae; ventral surface slightly concave, with scattered, moderately log setae, distal margin without spines or tubercles. Merus subtriangular in dorsal view; dorsal surface roundly ridged along midline, with row of short transverse ridge; dorsodistal margin unarmed but with row of short setae; mesial face with few short setae; lateral face with few small flattened tubercles; ventromesial margin unarmed but with short setae; ventrolateral margin with row of small spines on subdistal part and short setae; ventral surface with few very short setae. Ischium unarmed on dorsal surface; surfaces with scattered short setae. Coxa unarmed but with long setae on ventromesial margin. On carpus and merus, setae on ventromesial and ventrolateral margins and ventral face plumose; setae on other faces and on chela and coxa apparently simple.

Right cheliped of each female paratype (Fig. 2E, F) smaller than that of male holotype; chela narrower and less tuberculate on dorsal surface than that of male holotype, 1.7–1.8 times longer than wide; dactyl 0.9–1.0 length of palm; palm 0.7 length of carpus, with more strongly elevated, longitudinal median row of larger tubercles irregularly arranged in single or double, and more strongly elevated dorsomesial and dorsolateral margins than those of male holotype.

Left cheliped (Fig. 3A–D) moderately slender, reaching (female paratypes) or not reaching (male holotype) to proximal margin of dactyl of right cheliped; dactyl articulating obliquely with palm; propodal-carpal articulation not twisted. Chela elongate, 3.2–3.4 times longer than wide; dactyl and fixed finger slightly curved ventrally, each terminating in small corneous claw. Dactyl slightly longer than fixed finger, 1.2 length of palm; cutting edge with row of sharply pointed, small corneous teeth on distal 0.7; dorsal surface weakly convex, with few very short ridges each bearing short setae along cutting region; dorsomesial margin delimited by small low protuberances and short transverse ridges each bearing tuft of few short and moderately long setae, proximal part subacute; mesial surface with few very short ridges bearing short and moderately long setae; ventromesial margin rounded; ventral surface with row of tufts of few short and moderately long setae along cutting region. Palm 0.5–0.6 times as long as carpus; dorsomesial margin delimited, with row of irregularly arranged small tubercles and several moderately long setae, proximal tubercles spinulose; dorsal surface convex, with elevated row of spines and spinulose tubercles on midline of palm and

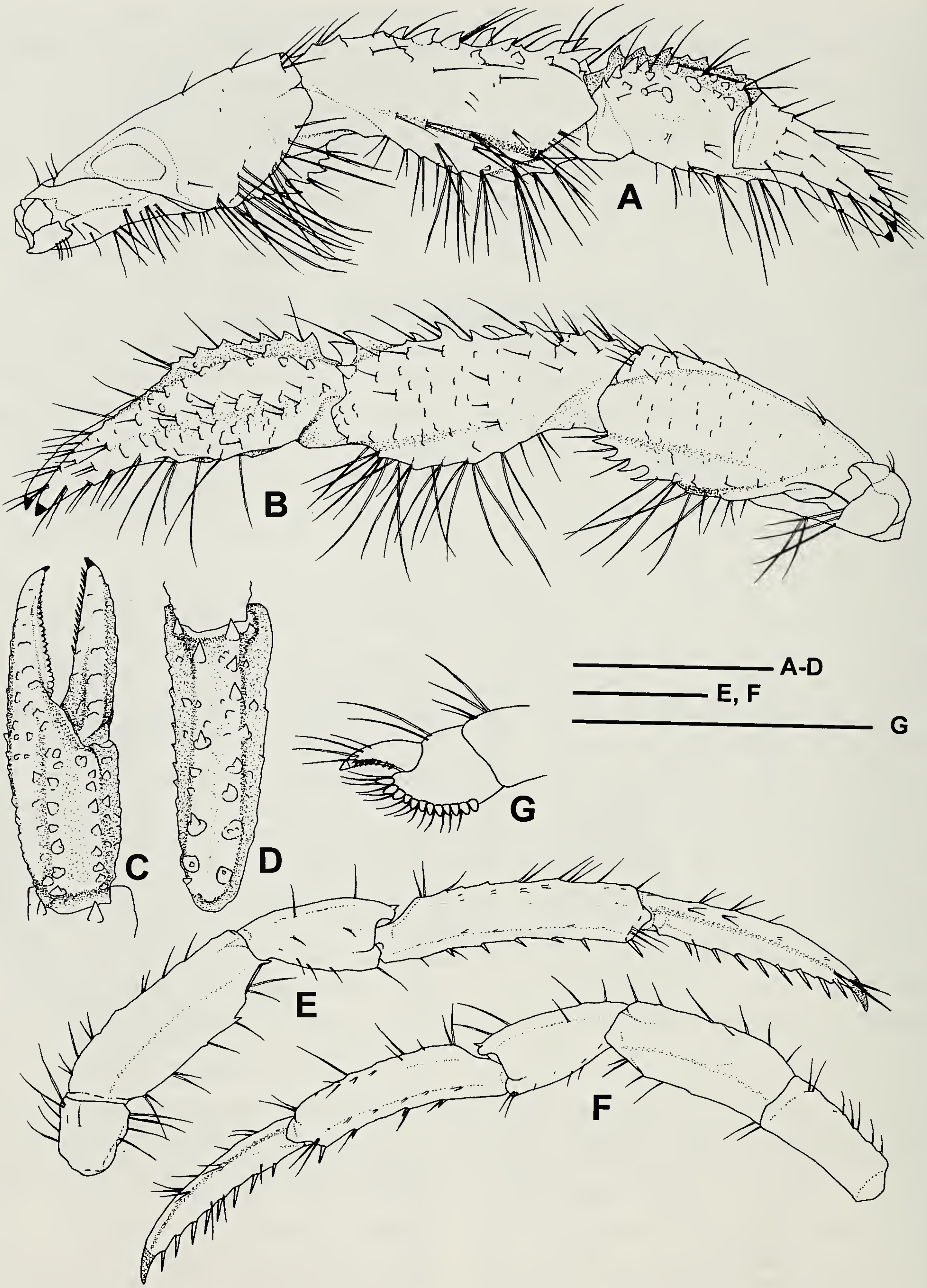

Fig. 3. *Hachijopagurus rubrimaculatus,* new genus and new species. Holotype male (sl 1.6 mm) from Hachijo-jima Island, Izu Islands, Japan, CMNH-ZC 470. A, left cheliped, mesial; B, same, lateral; C, same, chela, dorsal, setae omitted; D, carpus of same, dorsal, setae omitted; E, right second pereopod, lateral; F, left third pereopod, lateral; G, left fourth pereopod, dactyl and propodus, lateral. Scales equal 1.0 mm.

extending onto fixed finger along cutting region, tubercles on fixed finger reduced, lateral part of fixed finger with irregularly arranged small protuberances and tubercles, spines and tubercles accompanied by few short or moderately long setae; dorsolateral margin not delimited; mesial face with small flattened tubercles and short oblique ridges dorsally; lateral face with small low protuberances, short oblique ridges, and several short and moderately long setae; ventral surface roundly crested on longitudinal midline, with several short transverse ridges bearing long and short setae on palm and longitudinal double row of irregularly arranged tufts of short and moderately long setae on fixed finger; cutting edge of fixed finger with row of small calcareous teeth interspersed with very short corneous teeth. Carpus 1.1–1.2 times longer than merus; dorsomesial and dorsolateral margins each with row of strong spines and several moderately long setae, spine at each distal angle largest; dorsodistal margin unarmed; dorsal surface with few small tubercles; mesial face with row of small spinulose protuberances and moderately long setae adjacent to dorsomesial margin; lateral face with short or very short transverse ridges sometimes bearing short setae; ventromesial margin with few tufts of long setae; ventrolateral margin with small tubercles, protuberances, and tufts of long setae; ventral surface slightly concave, with tufts of long and moderately long setae. Merus subtriangular in dorsal view; dorsal surface roundly ridged along midline, with few short transverse ridges bearing short setae; dorsodistal margin unarmed but with row of moderately long setae; mesial face nearly naked; ventromesial margin unarmed but with transverse tufts of long setae; lateral surface with short and very short transverse ridges; ventrolateral margin with strong spines distally, and long and short setae; ventral surface with several long setae. Ischium unarmed on dorsal surface; ventral surface with moderately long setae. Coxa unarmed but with long setae on ventromesial margin. On carpus and merus, setae on ventromesial and ventrolateral margins and ventral face plumose; setae on other faces and on chela and coxa apparently simple.

Second and third pereopods (Fig. 3E, F) generally similar from left to right but different in length, right subequal to or slightly longer than left; right second pereopod slightly overreaching tip of right cheliped. Dactyls 1.2 times as long as propodi in second, 1.2 times as long in third, moderately slender, weakly curved ventrally in lateral view, straight in dorsal view, each terminating in corneous claw; lateral and mesial surfaces unarmed but each with shallow sulcus along midline and tufts of sparse short setae along dorsal margin; ventral margins each with 6–8 (second) or 6–9 (third) slender corneous spines and few short setae. Propodi 1.3 times longer than carpi and 3.8 times longer than high in second, 1.2–1.4 times longer than carpi and 3.5 times longer than high in third; lateral and mesial surfaces with few tufts of very short setae along each dorsal and ventral margin; dorsal faces weakly protuberant on right but apparently smooth on left, each with row of sparse, moderately long setae; ventral faces each with row of 4–6 small corneous spines and few short setae, spine at distal angle largest. Carpi 0.7 length of meri in second, 0.8–0.9 length in third, each with spinule near dorsodistal angle; lateral and mesial surfaces with few short setae; dorsal and ventral faces with sparse setae, setae on dorsal face longer. Meri 2.9 times longer than high in second, 2.4–2.7 times longer in third; lateral surfaces apparently naked; ventral margins each with few small protuberances, and small spine at each distal angle and distal third on second, but unarmed on third; dorsal and ventral surfaces each with row of sparse short and moderately long setae; mesial faces naked. Ischia with short and moderately long setae on dorsal and ventral surfaces. Coxae unarmed, with few tufts of short and moderately long setae; female with gonopore only on left side.

Fourth pereopods (Fig. 3G) subequal in size, semichelate, with scattered tufts of moderately long, simple and plumose setae marginally. Dactyl moderately curved, with row of tiny corneous teeth on lateral face ventrally, no preungual process at base of terminal claw. Propodus with strongly convex ventral margin; propodal rasp composed of single row of small ovate and lanceolate, corneous scales on distal 0.8 of ventral margin. Carpus unarmed on dorsal surface.

Fifth pereopods chelate; size of coxae (Fig. 1L) slightly asymmetrical with right larger in male, but equal in female. Male with right coxa with membranous, rod-like sexual tube approximately 2.2 coxal length measured on ventral surface, directed anteriorly; distal part recurved posteriorly, naked; left coxa (Fig. 1M) with membranous, rod-like sexual tube directed ventromesially, slightly shorter and slenderer than right; distal part recurved posteriorly, naked.

Third thoracic sternite unarmed on anterior margin. Sixth thoracic sternite (Fig. 1K) with semicircular anterior lobe slightly skewed to left and bearing moderately long setae on anterior margin. Eighth thoracic sternite (Fig. 1L) with pair of ventrally flattened lobes separated by shallow median depression, each with tuft of short bristles (male holotype) or moderately long setae (female paratypes) anteriorly.

Male with 3 left pleopods subequal in size; each endopod 0.3 length of exopod. Female (posterior half of abdomen missing in paratype, CMNH-ZC 930) with 4 left pleopods; pleopods on second to fourth somites well developed, pleopods on fourth somite slightly smaller than precedences; pleopod on fifth somite much smaller; anterior 2 pleopods each with endopod half length of exopod, posterior 2 pleopods each with endopod 0.3 length of exopod.

Telson (Fig. 1N) with distinct, midlateral transverse identations on lateral margins indicating division of anterior and posterior lobes; posterior lobes slightly asymmetrical, separated by shallow median cleft; terminal margins oblique, each with 3 small spines and short setae (male holotype) or apparently lacking spines but bearing short stiff setae (female paratypes), lateral angles acute; lateral margins convex, each with weakly delimited ridge.

Color in flesh specimens.—Shield pale pink or reddish. Ocular peduncles and acicles, antennular and antennal peduncles, third maxillipeds, left cheliped, and second to fourth pereopods greenish or pale yellow with scattered small red speckles. Antennal flagella semitransparent with interspaced few red articles. Right cheliped pale pink or reddish with yellow and orange tints.

Habitat.—Small gastropod shells, *Gyrineum pusillum* (Broderip) or *Gyrineum* species, family Ranellidae.

Distribution.—So far known only from Hachijo-jima Island in the Izu Islands, Japan; 40–45 m.

Etymology.—The specific name is a combination of the Latin, "*ruber*", meaning red, and "*maculatus*", meaning spotted, in reference to the scattered red speckles on most parts of the body.

Remarks.—The specimen of "Paguridae sp." depicted in a color photograph by Kato & Okuno (2001:83) is a female paratype of this new species (NSMT-Cr 14556).

Hachijopagurus rubrimaculatus shows intraspecific variations in the structure of the right cheliped. The chela and carpus of the male holotype are broader than those of two smaller female paratypes. The palm of the male is much more tuberculate, has a less elevated longitudinal row of smaller tubercles on the dorsal surface, and less elevated dorsomesial and dorsolateral margins than those of the females.

As noted in the remarks for the genus, *Hachijopagurus* resembles *Pygmaeopagurus*. Both *H. rubrimaculatus* and *P. hadrochirus* have relatively large right chelipeds, but the size is different in comparison to the total body mass. The cheliped is mentioned to be at least twice the mass in *P. hadrochirus* (see McLaughlin 1986:790), whereas it is approximately as same as or less than the mass in *H. rubrimaculatus. Hachijopagurus rubrimaculatus* also seems to differ from *P. hadrochirus* in having a prominent concavity at the dorsomesial distal angle of the palm of the right cheliped. *Pygmaeopagurus hadrochirus* may have a similar structure in the mentioned part from dorsal view (see McLaughlin, 1986:792, fig. 2b). However, the dorsomesial margin of the right palm is described as having two or three broad, thin, plate-like projections, and the mesial surface apparently has a sulcus along the dorsomesial margin, judging from McLaughlin (1986:792, fig. 2c). The distinct concavity at the dorsomesial distal angle of the palm of the right cheliped can be regarded as unique for *H. rubrimaculatus* since such the structure has not been described for any known pagurid species. The shape of the corneas of the ocular peduncles is also different between *H. rubrimaculatus* and *P. hadrochirus*. It is semispheric in *H. rubrimaculatus,* but cone-like and bluntly pointed in *P. hadrochirus.*

Available field observations with SCUBA equipment in Hachijo-jima Island revealed that *Hachijopagurus rubrimaculatus* occurred among or under stones on shelly sand bottom at depths of around 40 m. In the collection sites of this species, the following hermit crab species were also found: *Calcinus anani* Poupin & McLaughlin, 1998; *Dardanus lagopodes* (Forskål, 1775); *Pagurus lophochela* Komai, 1999; *Pylopaguropsis furusei* Asakura, 2000; *Pylopaguropsis speciosa* McLaughlin & Haig, 1989; and *Pylopaguropsis zebra* (Henderson, 1893) (see Appendix). Individuals of *Hachijopagurus rubrimaculatus* are much smaller in size than those of other species found except for *Pagurus lophochela.* The small size of the specimens of this new species makes it rather difficult to find them in the field.

Acknowledgments

We thank Mr. Shoichi Kato of the "Regulus Diving", a well-known service shop for local SCUBA divers in Hachijo-jima Island, for first finding this unusual hermit crab in the field, and kindly providing us with the specimens for study. Mr. Kotaro Tanaka of the "Diving Club Con:color" in Hachijo-jima Island also assisted the second author in collecting additional material. Mr. Masahiro Aizawa of the Coastal Branch of Natural History Museum and Institute, Chiba, kindly identified the gastropod shells carried by the hermit crabs for us. We are grateful to Dr. Patsy A. McLaughlin of the Shannon Point Marine Center, Western Washington University, Dr. Rafael Lemaitre of the National Museum of Natural History, Smithsonian Institution, and Dr. Akira Asakura of the Natural History Museum and Institute, Chiba, for their valuable comments and suggestions to improve the manuscript. This study was supported in part by a research fellowship for young scientists from the Japan Society for the Promotion of Science, to the first author.

Literature Cited

Asakura, A. 2000. A review of Japanese species of *Pylopaguropsis* Alcock, 1905 (Decapoda: Anomura: Paguridae).—Crustacean Research 29: 70–108.

Forest, J. 1954. Crustacés Décapodes Marcheurs des Iles de Tachiti et des Tuamotu. I. Paguridea (suite).—Bulletin du Muséum national d'Histoire naturelle, Paris, 2ᵉ série, 26:71–79.

———, & M. Saint Laurent. de. 1968. Résultats scientifiques des campagnes de la "Calypso". Part VIII. Campagne de la Calypso au large des côtes Atlantiques de l'Amérique du Sud (1961–1962). 6. Crustacés Décapodes: Pagurides.—Annales de l'Institut océanographique de Monaco, n. s. 45:47–172.

———, ———, P. A. McLaughlin, & R. Lemaitre. 2000. The marine fauna of New Zealand: Paguridea (Decapoda: Anomura) exclusive of the Lithodidae.—National Institute of Water and Atmospheric Research Biodiversity Memoir 114:1–250.

Forskål, P. 1775. Descriptiones animalium avium, piscium, amphibiorum, insectorum, vermium; quae in itinere orientali observavit: 1–19, i–xxxii, 1–164.

Henderson, J. R. 1893. A contribution to Indian carcinology.—Transactions of the Linnean Society of London, Zoology (2)5:325–458.

Kato, S., & J. Okuno. 2001. Shrimps and crabs of Hachijo Island. TBS-BRITANNICA Co., Ltd., Tokyo, 160 pp. (in Japanese).

Komai, T. 1999. Hermit crabs of the families Diogenidae and Paguridae (Crustacea: Decapoda: Anomura) collected during Shin'yo-maru cruise to the Ogasawara Islands and Torishima Island, oceanic Islands in Japan.—Natural History Research, Chiba, Special Issue 6:1–66.

———, & M. Osawa. 2001. A new distinctive species of pagurid hermit crab (Crustacea: Decapoda: Anomura) from Japan.—Zoological Science 18: 1291–1301.

Lemaitre, R. 1995. A review of the hermit crabs of the genus *Xylopagurus* A. Milne Edwards, 1880 (Crustacea: Decapoda: Paguridae), including descriptions of two new species.—Smithsonian Contributions to Zoology 570:i–iii, 1–27.

———, & P. A. McLaughlin. 1995. *Alainopagurus crosnieri* n. gen., n. sp. (Decapoda: Anomura: Paguridae) from the western Pacific.—Bulletin Muséum national d'Histoire naturelle, Paris 4^{e} sèrie, section A, 17:273–282.

McLaughlin, P. A. 1974. The hermit crabs (Crustacea, Decapoda, Paguridea) of northwestern North America.—Zoologische Verhandelingen 130:1–396.

———. 1986. Three new genera and species of hermit crabs (Crustacea, Anomura, Paguridae) from Hawaii.—Journal of Crustacean Biology 6: 789–803.

———. 1997. Crustacea Decapoda: Hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia *in* A. Crosnier, and P. Bouchet, eds., Résultats des Campagnes MUSORSTOM, 16.—Mémoires du Muséum national d'Histoire naturelle, Paris 172:433–572.

———. 2003. Illustrated keys to families and genera of the superfamily Paguroidea (Crustacea: Decapoda: Anomura), with diagnoses of genera of Paguridae.—Memoirs of Museum Victoria 60: 111–144.

———, & J. Haig. 1989. On the status of *Pylopaguropsis zebra* (Henderson), *P. magnimanus* (Henderson), and *Galapagurus teevanus* Boone, with descriptions of seven new species of *Pylopaguropsis* (Crustacea: Anomura: Paguridae).—Micronesica 22:123–171.

———, & M. Saint Laurent. de. 1998. A new genus for four species of hermit crabs formerly assigned to the genus *Pagurus* Fabricius (Decapoda: Anomura: Paguridae).—Proceedings of the Biological Society of Washington 111:158–187.

———, & L. Sandberg. 1995. Redescriptions of Gustaf Melin's "*Eupagurus* (*Pagurillus*)" *exiguus*, "*Eupagurus* (*Catapagurus*)" *vallatus*, and "*Eupagurus* (*Spiropagurus*)" *facetus* (Decapoda: Anomura: Paguridae) based on the type material.—Journal of Crustacean Biology 15:569–587.

Melin, G. 1939. Paguriden und Galatheiden von Prof. Dr. Sixten Bocks Expedition nach den Bonin-Inseln 1914.—Kungliga Svenska Vetenskapsakademiens Handlingar, series 3 18:1–119.

Milne-Edwards, A., & E.-L. Bouvier. 1892. Observations préliminaries sur les paguriens recueillis par les expéditions du *Travailleur* et du *Talisman*.—Annales des Sciences Naturelles, Zoologie et Paléontologie, série 7, 13:185–226.

Poupin, J., & P. A. McLaughlin. 1998. Additional records of *Calcinus* species (Decapoda: Anomura: Diogenidae) from French Polynesia with description of three new species and a key to Indo-west Pacific species of the genus.—Crustacean Research 27:9–27.

Saint Laurent, M. de. 1968. Révision des genres *Catapaguroides* et *Cestopagurus* et description de quatre genres nouveaux. I. *Catapaguroides* A. Milne Edwards et Bouvier et *Decaphyllus* nov. gen. (Crustacés Décapodes Paguridae).—Bulletin du Muséum national d'Histoire naturelle, Paris, 2^{e} série, 39 ['1967']:923–954.

———. 1970. Révision des genres *Catapaguroides* et *Cestopagurus* et description de quatre genres nouveaux. V. *Trichopagurus* de Saint Laurent (Crustacés Décapodes Paguridae). VI. Conclusion.—Bulletin du Muséum national d'Histoire naturelle, Paris, 2^{e} série, 42:210–222.

Saint Laurent-Dechancé, M. de. 1966. Remarques sur la classification de la famille des Paguridae et sur la position systématique d'*Iridopagurus* de Saint Laurent. Diagnose d'*Anapagurides* gen. nov.—Bulletin du Muséum national d'Histoire naturelle, Paris, 2^{e} série, 38:257–265.

Türkay, M. 1986. Crustacea Decapoda Reptantia der Tiefsee des Roten Meeres.—Senckenbergiana Maritima 18:123–185.

Wang, Y.-L., & P. A. McLaughlin. 2000. First report of *Nematopaguroides* (Crustacea: Decapoda: Paguridae) in the Indo-Pacific, and the description of a new species.—Proceedings of the Biological Society of Washington 113:956–963.

Appendix

List of hermit crab species found in the collection sites of *Hachijopagurus rubrimaculatus*, new species, at Hachijo-jima Island, Izu Islands, Japan

Family Diogenidae

Calcinus anani Poupin & McLaughlin, 1998. 1 male (sl 3.8 mm), Nazumado, 40 m, 30 Nov 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 516. 1 female (sl 4.2 mm), Nazumado, 45 m, 4 Dec 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 517.

Dardanus lagopodes (Forskål, 1775). 1 male (sl 9.6

mm), Nazumado, 40 m, 1 Dec 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 933. 1 male (sl 10.0 mm), Kyokucho-hama, 40 m, 9 Jul 2002, SCUBA dive, coll. J. Okuno & K. Tanaka, CMNH-ZC 936. 1 juvenile (sl 1.8 mm), same data as CMNH-ZC 936, CMNH-ZC 937.

Family Paguridae

Pagurus lophochela Komai, 1999. 1 male (sl 2.2 mm), Nazumado, 45 m, 4 Dec 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 595. 1 male (sl 1.6 mm), same data as CMNH-ZC 595, CMNH-ZC 596. 1 ovigerous female (sl 1.5 mm), Kyokucho-hama, 40 m, 9 Jul 2002, SCUBA dive, coll. J. Okuno & K. Tanaka, CMHN-ZC 934. 1 male (sl 1.2 mm), sama data as CMHN-ZC 934, CMNH-ZC 935. 1 female (sl 1.6 mm), same data as CMHN-ZC 934, CMNH-ZC 938.

Pylopaguropsis furusei Asakura, 2000. 1 female (sl 3.4 mm), Nazumado, 40 m, 24 Nov 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 874. 1 female (sl 2.5 mm), same data as CMNH-ZC 874, CMNH-ZC 875. 1 female (sl 2.2 mm), Nazumado, 45 m, 4 Dec 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 876. 1 male (sl 2.7 mm), same data as CMNH-ZC 876, CMNH-ZC 877.

Pylopaguropsis speciosa McLaughlin & Haig, 1989. 1 male (sl 3.7 mm), Nazumado, 40 m, 30 Nov 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 522. 1 male (sl 1.9 mm), same data as CMNH-ZC 522, CMNH-ZC 873.

Pylopaguropsis zebra (Henderson, 1893). 1 male (sl 2.4 mm), Nazumado, 40 m, 30 Nov 2000, SCUBA dive, coll. S. Kato, CMNH-ZC 523. 1 male (sl 2.5 mm), same data as CMNH-ZC 523, CMNH-ZC 525.

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A new species of the hermit crab genus *Diogenes* (Decapoda: Anomura: Paguroidea: Diogenidae) from Pakistan, with a comparative diagnosis of *D. guttatus* Henderson, 1888

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Abstract.—Comparison of the holotype of *Diogenes guttatus* Henderson with the Pakistani specimens attributed to that taxon has shown that they are not conspecific. The Pakistani specimens are described herein as *Diogenes tirmiziae,* sp. nov. A diagnosis of *D. guttatus,* based on the holotype, is presented for comparative purposes.

In earlier studies of the hermit crab fauna of Pakistan, Tirmizi & Siddiqui (1981, 1982) identified specimens as *Diogenes guttatus* Henderson, 1888. McLaughlin (2002b) compared Tirmizi & Siddiqui's (1981, 1982) specimens with Henderson's (1888) holotype from H.M.S. *Challenger* station 187 in the Torres Strait, off northern Australia, and with two incomplete specimens collected in the Andaman Sea, west of Phuket, Thailand. McLaughlin (2002b) concluded that while the Andaman Sea specimens were most probably conspecific with Henderson's (1888) species, the Pakistani specimens definitely were not. We have now reexamined Tirmizi & Siddiqui's (1981, 1982) material, together with specimens collected more recently, and find that they cannot be assigned to any known taxon. They are described herein as *Diogenes tirmiziae,* sp. nov. As the left chelipeds were missing from both of the Thai specimens McLaughlin (2002b) illustrated only the shield, cephalic appendages and telson. We include an illustrated diagnosis of *D. guttatus* based on the holotype, including the chela and carpus of the left cheliped.

All of the specimens of *D. tirmiziae,* sp. nov. were collected from shallow depths along the Karachi coastal region. With the exception of two specimens that have been donated to the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA (USNM), all specimens are deposited in the Marine Reference Collection and Resource Centre, University of Karachi (MRCRC) under the catalog prefix ANOM. The holotype of *D. guttatus* was borrowed from The Natural History Museum, London, United Kingdom (NHM).

The seeming inconsistencies between the present species description of *D. tirmiziae,* sp. nov., and the diagnosis presented by Tirmizi & Siddiqui (1982, as *D. guttatus*) are principally a matter of semantics. Inclusion of the family Diogenidae within the superfamily Paguroidea is based on the classification of Martin & Davis (2001). Terminology for the present description and diagnosis follows that of McLaughlin & Clark (1997), except for McLaughlin's (1997) definition of fourth pereopod structure. One measurement, shield length (sl), as measured from the midpoint of the rostral lobe (exclusive of the intercalary rostral process) to the midpoint of the posterior margin of the shield, provides an indication of animal size.

Diogenes tirmiziae, sp. nov.
Figs. 1–3

Diogenes guttatus—Tirmizi & Siddiqui 1981: fig. 17; 1982:57, figs. 30, 31 (not *Diogenes guttatus* Henderson, 1888).
Diogenes sp.—Siddiqui & Kazmi 2003:88.

Material examined.—Holotype, Pache, 22 Apr 2000, ♀ (sl = 2.0 mm), MRCRC ANOM 276.

Paratypes.—Pache: 24 Jul 1997, 1 ♀ (sl = 2.0 mm), MRCRC ANOM 274; 22 Apr 2000, 8 ♂ (sl = 1.0–3.0 mm), MRCRC ANOM 277.

Buleji: 20 Jan 1969, 1 ♂ (sl = 2.0 mm), MRCRC ANOM 125; 12 Dec 1977, 1 ♀ (sl = 2.0 mm), MRCRC AMON 225; 03 Oct 1990, 4 ♂ (sl = 1.8–2.3 mm), MRCRC ANOM 273, 2 ♂ (sl = 2.2, 2.5 mm) USNM 1009965.

Katti Bunder: 28 Jan 1975, 12 ♂ (sl = 1.0–2.5 mm), 2 ♀ (sl = 1.0, 2.0 mm) MRCRC ANOM 186.

Sandpit: 29 Oct 1999, 1 ♂ (sl = 3.5 mm) MRCRC ANOM 275; 24 Apr 2002, 10 ♂ (1.0–2.4 mm), 10 ♀ (sl = 1.0–2.0 mm), MRCRC ANOM 278.

Description.—Shield (Fig. 1A–D) slightly broader than long to slightly longer than broad; anterior margin between very broadly rounded rostral lobe and lateral projections somewhat concave and often with few minute or tiny tubercles; anterolateral angles usually spinulose, lateral margins each usually cut by several transverse, spinulose or tuberculate ridges, each extending onto lateral surfaces of shield; posterior margin truncate; dorsal surface with additional few scattered spinules and tufts of sparse setae. Lateral projections triangular, often with tiny to small marginal or submarginal spine or spinule. Dorsal margins of branchiostegites each with 5–8 moderately small spines, partially obscured by fine setae.

Ocular peduncles 0.6–0.8 length of shield, moderately stout, each with rows of tufts of very sparse setae dorsomesially and mesially; corneal diameter 0.2–0.3 of peduncular length. Ocular acicles subtriangular, anterior margin with 2–4 prominent spines and usually 3 or 4 additional spinules, innermost spine often distinctly thicker and sometimes with curved tip; acicles basally separated by approximately 0.2 or less width of one acicle. Intercalary rostral process stout proximally, frequently drawn out into long slender terminal spine, but not overreaching apices of innermost acicular spines; no ventral spine.

Antennular peduncles moderately slender, when fully extended overreaching corneas by 0.2–0.5 length of ultimate segments. Ultimate and penultimate segments unarmed, but with few tufts of moderately long setae. Basal segment with few shorter setae.

Antennal peduncles (Fig. 1E–H) not quite reaching or slightly overreaching distal corneal margins; with supernumerary segmentation. Fifth segment with scattered setae dorsally and 2 rows of long setae ventrally. Fourth segment unarmed, but with tuft of moderately long setae dorsally. Third segment with tuft of long setae on ventrodistal margin. Second segment with dorsolateral distal angle usually produced into prominent spine, 3–5 additional spines on laterodistal margin ventrally (not visible in dorsal view), dorsomesial distal angle with or without acute spine, mesial margin with tufts of setae. First segment usually with 1 or 2 small spines at dorsolateral distal angle, lateral margin with few tiny spinules ventrally. Antennal acicle short, broad, with distally oblique margin armed with 3–5 very prominent spines and few setae. Antennal flagellum short, often not reaching to proximal margin of palm of left cheliped; each article with pair of long, pinnate setae.

Maxillule with endopod lacking external lobe. Third maxilliped with inner margin of coxal plate denticulate; 1–3 small spines on basis; ischium with crista dentata composed of 6–9 small corneous teeth.

Left cheliped (Fig. 2A–D′) with dactyl slightly shorter to approximately as long as upper margin of palm, prominently arched; cutting edge with row of small calcareous

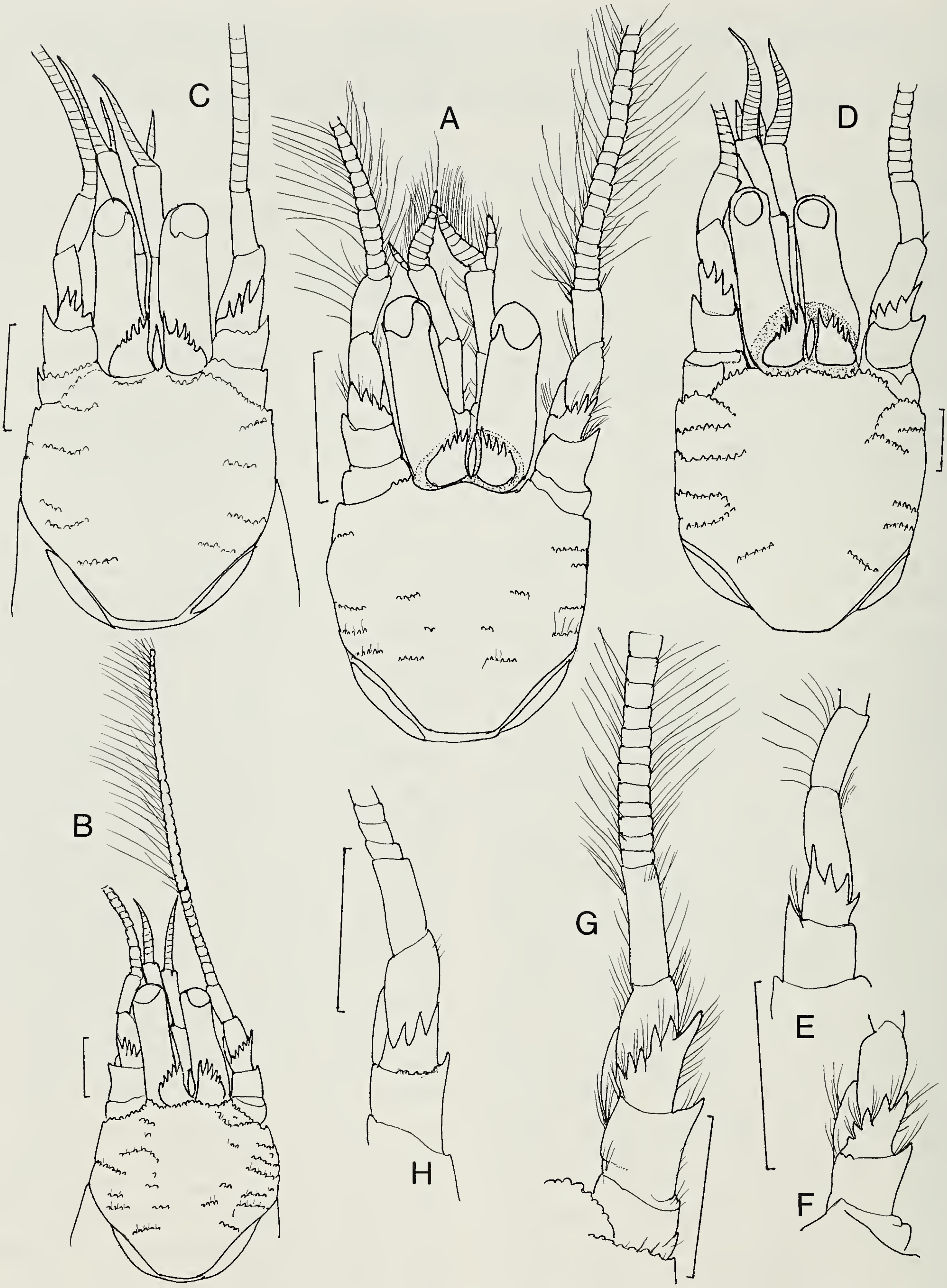

Fig. 1. *Diogenes tirmiziae* sp. nov.. A, E, F, holotype female, sl = 2 mm, MRCRC ANOM Cat. No. 276; B–D, G, H, paratypic males, sl = 2.5–3 mm, MRCRC ANOM Cat No. 277. A–D, shield and cephalic appendages (setae and aesthetascs generally omitted); E–H, antennal peduncle and acicle (setae often omitted). E, H, left; F, G, right. Scales equal 1 mm.

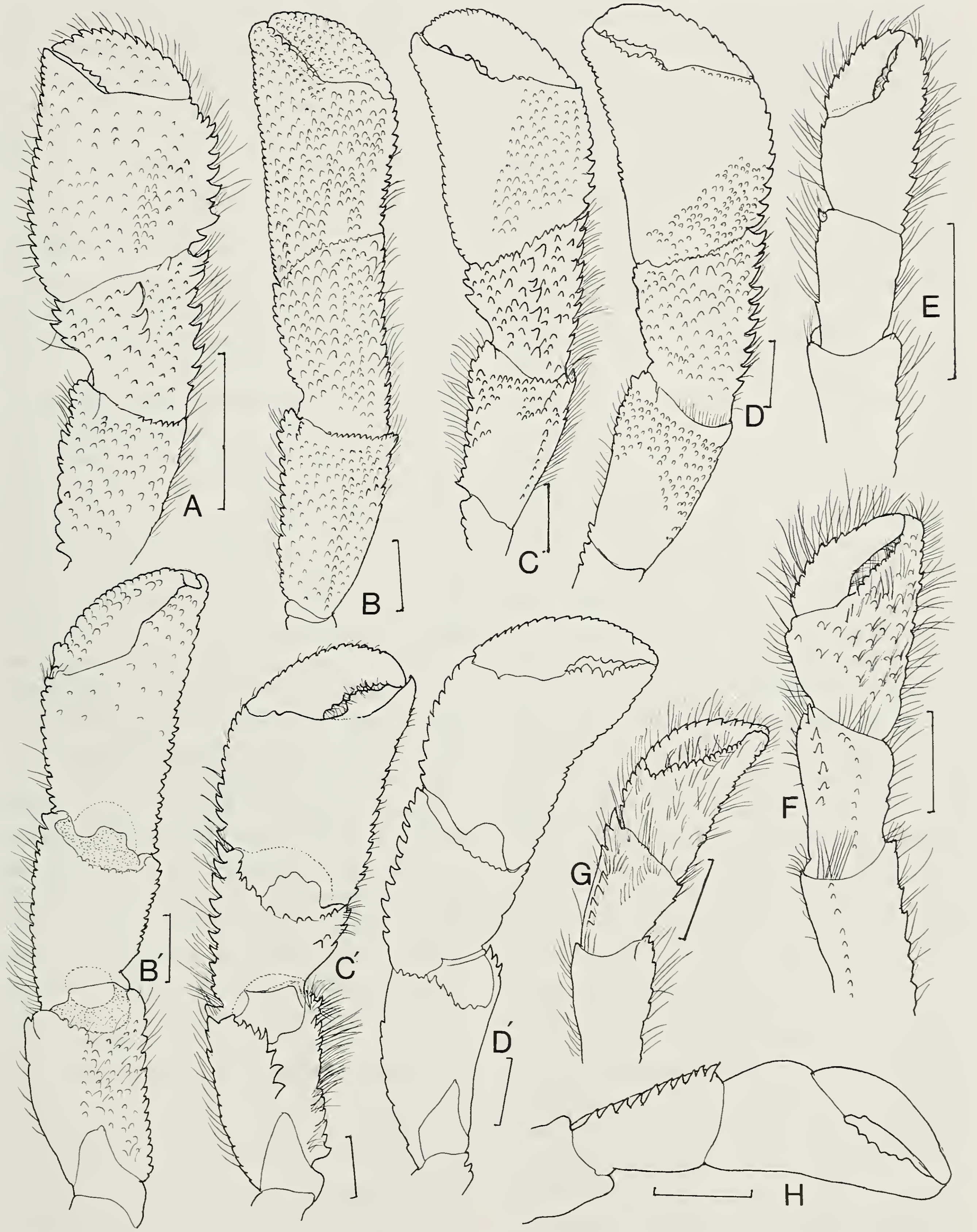

Fig. 2. *Diogenes tirmiziae* sp. nov. A, E, holotype female, sl = 2 mm, MRCRC ANOM Cat. No. 276; B–D, F–H, paratypic males, sl = 2.5–3 mm, MRCRC ANOM Cat No. 277. A–D, left cheliped (dorsolateral view) (setae and full armature sometimes omitted); B′–D′ left cheliped (ventrolateral view) (setae and armature sometimes omitted); E–H, right cheliped (dorsolateral view) (setae and armature sometimes omitted). Scales equal 1 mm.

teeth and frequently 1 larger tooth proximally; terminating in large calcareous claw, sometimes overlapping fixed finger; outer surface generally flattened, armature varying from longitudinal row of moderately small, subacute to blunt, tuberculate spines and short row of small spinules adjacent to cutting edge in distal 0.25 to complete covering of closely-spaced, small, conical tubercles; upper margin with 2 rows, sometimes coalesced, of subacute or blunt spines forming transverse, low ridges over full length of margin; inner surface varying from smooth and glabrous, or with row of shallow pits and sparse very short setae extending nearly to tip and flanked proximally by few very small tubercles, to overall weakly tuberculate. Fixed finger with lower margin often not distinctly delimited, but with almost double row of small rounded tubercles and forming straight line with similarly armed lower margin of palm; outer surface somewhat convex, with covering of small drop-like, spinulose tubercles, sometimes simply ovate tubercles; inner surface often with 2 rows of very shallow pits and sparse tufts of very short setae, rows divergent proximally, but converging toward tip, sometimes with scattered tubercles; cutting edge with row of small calcareous teeth and 1 larger tooth proximally; terminating in large calcareous claw. Palm with outer surface angularly convex and with covering of small, drop-like, frequently spinulose tubercles, often larger near upper margin, short longitudinal row of 4 small, tuberculate spines proximally in upper 0.2 sometimes evident; upper margin with irregular single to double row of small to moderately-sized, subacute, tuberculate spines, ventral margin not delimited and no prominent spines or tubercles at or near ventroproximal angle; inner surface usually tuberculate. Carpus equal to or slightly longer than palm and approximately equal to length of merus; armature of upper margin varying from irregular double row of small, tuberculate spines to similarly double row of prominent acute or subacute spines, outer face angularly convex, upper 0.3 relatively flat and with scattered very small tubercles to well developed spines, angular 0.3 with more numerous and slightly more prominent, larger tubercles or spines, lower 0.4 with covering of much smaller tubercles, lower margin not delimited, but with somewhat larger tubercles or tuberculate spines; inner surface with scattered small tubercles and sparse, moderately long setae. Merus subtriangular; distal margin occasionally with row of prominent spines extending laterally and mesially; dorsal surface tuberculate or with short, transverse, spinulose or spinose ridges and with tufts of moderately long setae; lateral face tuberculate, tubercles often larger near ventral margin, ventromesial margin tuberculate or with row of small spines; mesial face weakly tuberculate, distal margin with several spines or at least with 2 small spines ventrally, ventromesial margin with tubercles and few small tuberculate spines or row of small to prominent spines; ventral surface weakly tuberculate. Ischium with tuberculate ventral surface, ventromesial margin tuberculate or with row of small spines.

Right cheliped (Fig. 2E–H) appreciably shorter than left, usually not reaching proximal margin of palm of left; dactyl and fixed finger with prominent hiatus. Dactyl slightly longer than palm, arched; upper margin with 2 rows of low, spinulose tubercles or small spines, accompanied by numerous long, fine, simple setae and separated by moderately broad, shallow sulcus; outer surface often with 2 rows of low, spinulose tubercles or small spines, also accompanied by long setae; cutting edge with row of small calcareous teeth, at least proximally, terminating in moderately large calcareous claw and slightly overlapped by fixed finger. Palm with irregular rows of spinulose tubercles or small spines on upper surface; outer surface with small, spinulose tubercles or small spines, often forming irregular rows and partially obscured by long setae; outer face of fixed finger similarly armed; lower margin with row of subacute spines and long setae; cutting edge with row of small calcareous teeth, terminating in moderately large calcareous claw. Carpus with row of small to moderately large spines on upper margin and adjacent row of slightly smaller spines on outer face, both partially obscured by numerous long setae, remainder of outer face granular, minutely tuberculate, or spinulose, lower margin not delimited; inner and lower surfaces with scattered long setae. Merus usually with numerous long setae arising from low protuberances or tubercles on dorsal margin; lateral face weakly tuberculate or granular, ventrolateral margin unarmed, with 2 or 3 very small spines distally, or with row of small spines; ventromesial margin with row of small spines or spinulose tubercles and long setae. Ischium with ventromesial margin unarmed or with row of very small spines or tubercles, and with few long setae.

Second and third pereopods (Fig. 3A–H) with dactyls approximately equal to or 0.1–0.2 longer than propodi, somewhat curved, but not twisted; terminating in moderately small corneous claws; dorsal surfaces with numerous long, simple setae, ventral surfaces with each row of tufts of sparse, short setae; mesial and lateral faces each with shallow longitudinal sulcus and scattered, moderately long setae. Propodi each with dorsal row of small spines not obscured by tufts of sparse, long setae, spines smallest on third pereopods or occasionally distinguishable only distally, lateral and mesial faces each with 1 or 2 rows of tufts of sparse setae, surfaces sometimes with tiny tubercles or protuberances. Carpi each with row of small to moderately large spines and long, simple setae on dorsal margin, spines of third pereopods usually appreciably smaller, occasionally only low protuberances; mesial, lateral and ventral surfaces with rows of moderately long setae, lateral faces sometimes also tuberculate. Meri with tufts of moderately long setae on dorsal surfaces, ventral surfaces of second pereopods each with irregular row of small spines or tubercles and tufts of setae, ventral surfaces of third pereopods often with low protuberances and tufts of setae. Ischia with long setae dorsally and ventrally. Fourth pereopods semichelate. Anterior lobe of sternite of third pereopods divided by shallow, longitudinal median groove, each half with 1 small tuberculate spine accompanied by tuft of setae.

Male unpaired left pleopods uniramous, marginally very setose. Female with paired gonopores; unpaired left pleopods 2–4 well developed, biramous; pleopod 5 as in male. Telson (Fig. 3I–K) with median cleft; left terminal margin with row of relatively uniform, small spines, 1–3 much larger spines at or near outer angle and several smaller spines continued down lateral margin; right terminal margin with row of relatively uniform small spines, usually not continued down lateral margin.

Color (in life).—Carapace light orange with pale green and brownish spots. Shield with transverse bands of brown. Intercalary rostral process and ocular acicles green; ocular peduncles brown proximally, bright orange distally with median dark brown bands. Antennular and antennal peduncles and flagella with alternating bands of brown and cream. Left chela dark brown, remaining segments banded green and brown (after Tirmizi & Siddiqui 1982).

Habitat.—Rocky shores (Siddiqui & Kazmi 2003).

Distribution.—Known only from the Karachi coast of Pakistan.

Etymology.—This species is named in honor of Dr. N. M. Tirmizi, former director of the Marine Reference Collection and Resource Centre, and noted Pakistani carcinologist.

Diogenes guttatus Henderson, 1888
Fig. 4

Diogenes guttatus Henderson, 1888:54, pl. 6, fig. 4, 4a.—Alcock 1905:166.—Gordan 1956:317.—Morgan & Forest 1991: 664.—McLaughlin 2002b:411, fig. 1A, B.
Not *Diogenes guttatus*—Tirmizi & Siddiqui

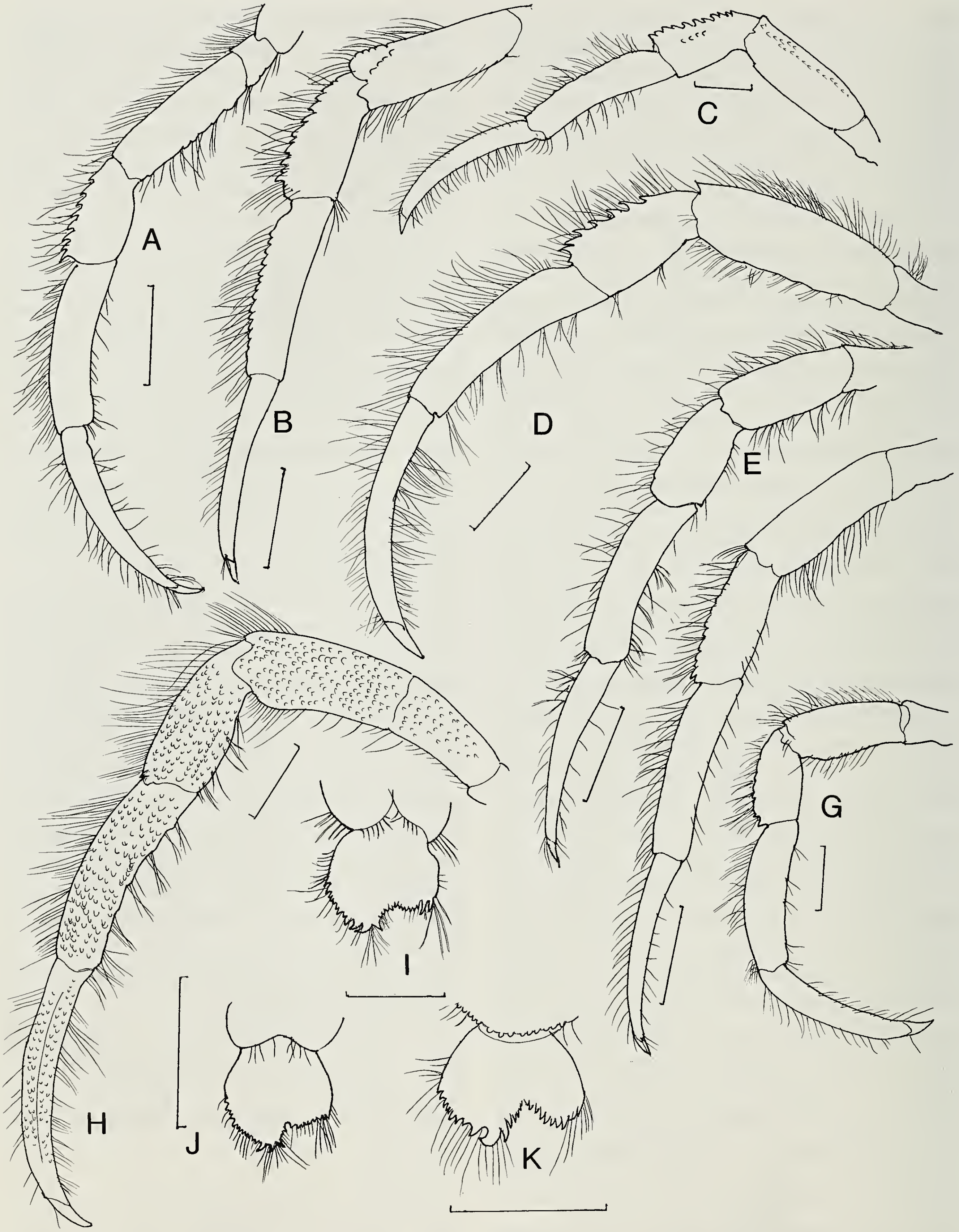

Fig. 3. *Diogenes tirmiziae* sp. nov. A, E, I, holotype female, sl = 2 mm, MRCRC ANOM Cat. No. 276; B–D, F–H, J, K paratypic males, sl = 2.5–3 mm, MRCRC ANOM Cat No. 277. A–D, left second pereopod (lateral view); E–H, left third pereopod (lateral view); I–K, telson (dorsal view). Scales equal 1 mm.

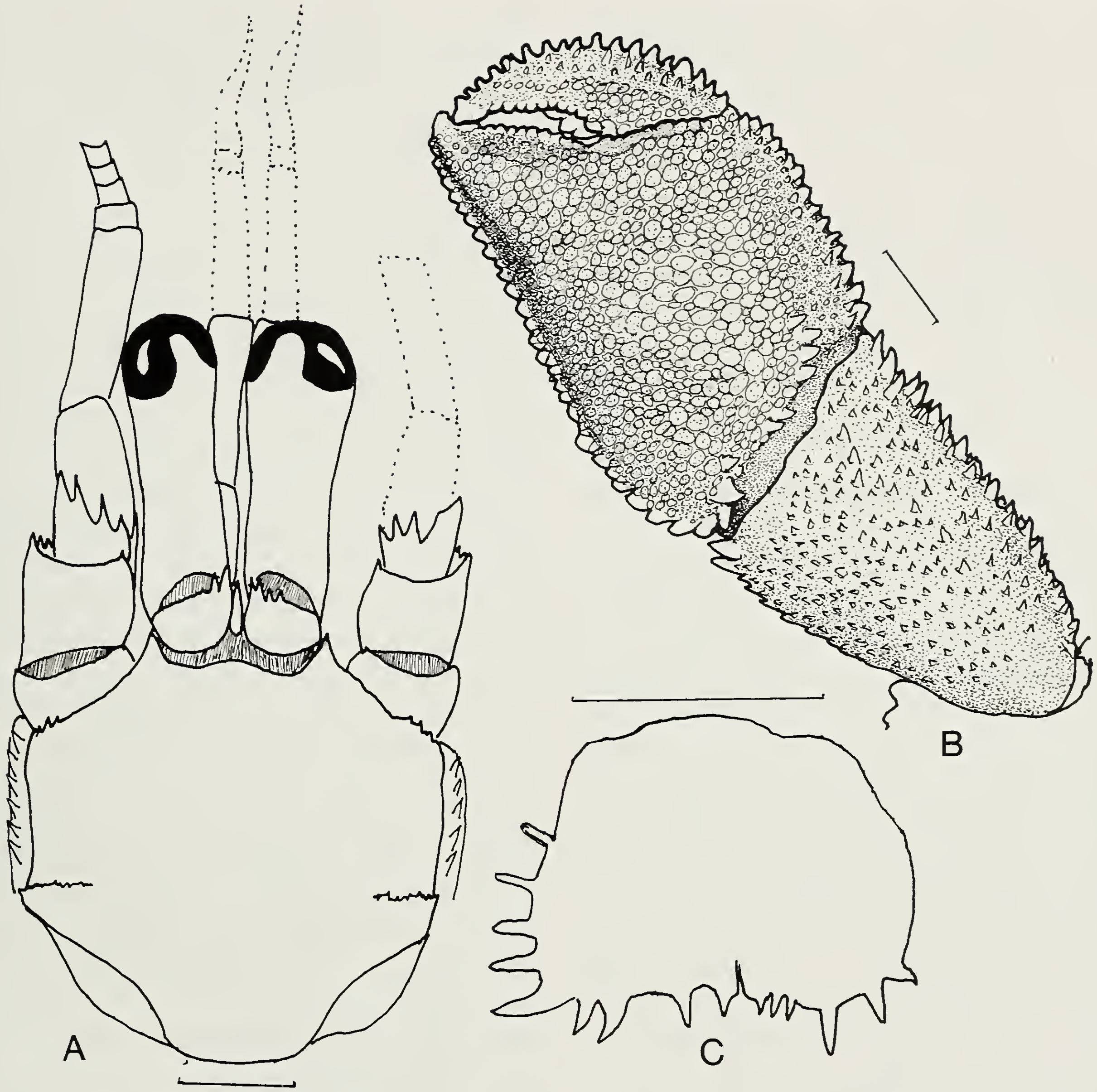

Fig. 4. *Diogenes guttatus* Henderson, 1888. holotype male sl = 3.1 mm, NHM 1888.3.1. A, shield and cephalic appendages (setae and aesthetascs omitted); B, chela and carpus of left cheliped (dorsolateral view); C, telson (dorsal view). Scales equal 1 mm.

1981: fig. 17; 1982:57, figs. 30, 31 (= *Diogenes tirmiziae,* sp. nov.).

Material examined.—Holotype ♂ (sl = 3.2 mm), *Challenger* station 187, 10°36′S, 141°55′E, 11 m, 9 Sep 1874, NHM 1888.33.1.

Diagnosis.—Shield (Fig. 4A) slightly convex, centrally smooth; lateral margins each with protuberant spinulose ridge in proximal half. Rostrum obsolete; lateral projections produced. Margins of branchiostegites with 5 (right) or 6 (left) acute spines. Intercalary rostriform process simple, tapering to acute tip, not reaching to apices of acicular spines. Ocular peduncles (including corneas) reaching approximately to midpoint of ultimate segments of antennal peduncles and proximal margins of ultimate antennular peduncular segments; ocular acicles with 2 or 4 spinules on distal margin, innermost largest. Second segment of antennal peduncle with row of small spines on lateral margin ventrally, 1 small spine at dorsolateral distal angle and smaller spine at dorsomesial distal angle. Antennal acicle short, broad, generally subquadrate, outer spine not reaching beyond midlength of penultimate peduncular segment, anterior margin with 3 additional prominent spines. Antennal flagellum shorter than twice carapace length, articles each with pair of long ventral setae.

Left cheliped (Fig. 4B) with row of small spines on upper margin of dactyl and numerous spinules and flattened tubercles on outer surface. Outer surface of palm covered with circular, mushroom-shaped, flattened tubercles, upper and lower margins spinose and almost straight; proximal margin with 3 moderately stout short spines near lower angle and 4 subacute spines at mid-length, slightly curving onto outer face. Carpus with irregular double row of small spines on upper margin; outer surface with covering of spinules, more dense in lower half. Right cheliped missing.

Ambulatory legs with dactyls slightly curved, longer than unarmed propodi. Carpi of second pereopods each with row of small spines on dorsal margin; third with row of very small spinules on dorsal margin. [Henderson (1888) incorrectly reported these spines as being on the meri.]

Telson (Fig. 4C) with slender median cleft; left lobe with 4 moderately large spines on terminal margin, 1 more elongate spine at outer angle and 4 large spines on posterior 0.5 of lateral margin; right posterior lobe with 3 small and 3 larger spines on terminal margin, outer 2 actually extending onto rounded outer angle.

Color.—Not reported.

Habitat.—Coral mud.

Distribution.—Northern Australia; Andaman Sea; 11–61 m.

Discussion

That Tirmizi & Siddiqui (1981, 1982) mistook *Diogenes tirmiziae,* sp. nov., for Henderson's (1888) *D. guttatus* is not surprising. At that time, Henderson's taxon had not been reported since the original description except in the literature citations of Alcock (1905) and Gordan (1956). The armature of the left chela of *D. guttatus* was described by Henderson (1888:54) as "perfectly circular, drop-like and flattened"; however his (loc. cit., pl. 6, fig. 4) illustration of the chela was quite small and not very definitive. The spination of the palm of the left chela of *D. tirmiziae,* although not flattened, also can be described as circular and drop-like. More importantly, *D. guttatus* and *D. tirmiziae* share a rather distinctive type of antennal acicle, (i.e., Henderson 1888, pl. 6, fig. 4a; Tirmizi & Siddiqui 1982, fig. 30D), and it is undoubtedly this similarity that led Tirmizi & Siddiqui (1981, 1982) to believe that they were dealing with *D. guttatus.* A third species, also described on a single male, *D. dorotheae* Morgan & Forest, 1991, shares with *D. guttatus* and *D. tirmiziae* those characteristic, very truncated antennal acicles. Morgan & Forest differentiated *D. dorotheae* from *D. guttatus* by the circular, drop-like and flattened armature of the left cheliped of the latter species, as well as the presumed spinose dorsal margins of the meri of the ambulatory legs. As noted in our diagnosis of *D. guttatus,* and also pointed out by McLaughlin (2002b), it is the dorsal margins of the carpi of the ambulatory legs, not the meri, that are spinose. All three species share this character; however, unlike *D. guttatus* and *D. dorotheae, D. tirmiziae,* sp. nov., also has a row of spines on each propodus.

Morphological variability and sexual dimorphism in species of *Diogenes* have been reported frequently (e.g., Forest & Guinot 1956, Rahayu & Forest 1995, McLaughlin 2002a), and as can be seen in the species' description, *D. tirmiziae,* sp. nov., exhibits considerable variation in the strength and armature of the left cheliped. As the chelipeds of both *D. guttatus* and *D. dorotheae* are known only from their male holotypes, variation in these species cannot be assessed. However, despite the described differences in the structure of the tubercles in *D. guttatus* (mushroom-shaped and flattened) and *D. dorotheae* (short to long, acute to blunt, and cylindrical), the species share one character that is not found in *D.*

tirmiziae, i.e., 3 or 4 prominent acute spines near the lower proximal angle of the outer face of the left palm. The longer dactyls of the ambulatory legs and appreciably denser pilosity described for *D. dorotheae* also would distinguish this species from *D. tirmiziae,* as the mushroom-shaped tubercles of *D. guttatus* set it apart from all known species of *Diogenes.*

Morgan & Forest (1991) also differentiated *D. dorotheae* from *D. guttatus* by the bifid intercalary rostral process of their species; however, as was shown by McLaughlin (2002a) a bifid process is not a useful diagnostic character. Morgan & Forest (1991) noted another species that had been described on a single specimen collected in northwestern Australia, *D. granulatus* Miers, 1880. Siddiqui & Kazmi (2003) reported, on the basis of a remark by McLaughlin (pers. comm.), that there could be a remote chance that the species identified as *D. guttatus* from Pakistan might actually be referable to Miers' (1880) taxon. *Diogenes granulatus* was briefly described by Miers in a footnote to his discussion of "*Diogenes miles*" (not *D. miles* Fabricus, 1787, cf. McLaughlin & Holthuis 2001) but was never illustrated nor has it been knowingly collected again. Efforts to locate the holotype in the Natural History Museum collections presently have been unsuccessful (P. F. Clark, pers. comm.). However, Miers' (1880) related *D. granulatus* to *D. avarus* Heller, 1865, which suggests that the antennal acicles were of the usual triangular configuration seen in most species of *Diogenes.* Additionally, Miers' (1880) report that the ocular acicles of *D. granulatus* were "entire" and the fixed finger of the left chela was prominently deflected support our conclusion that the Pakistani species is not conspecific with *D. granulatus* any more than it is with *D. guttatus.*

Acknowledgments

We acknowledge, with thanks, the efforts of Paul F. Clark to locate the holotype of *D. granulatus* and for the loan of the holotype of *D. guttatus.* We also are very grateful to Prof. Dr. Quddusi B. Kazmi, Director, Marine Reference Collection and Resource Centre, University of Karachi, for providing research space and facilities in the Centre to the first author. This is, in part, a scientific contribution from the Shannon Point Marine Center, Western Washington University.

Literature Cited

Alcock, A. 1905. Anomura. Fasc. I. Pagurides.—Catalogue of the Indian decapod Crustacea in the collections of the Indian Museum 2:1–197. Indian Museum, Calcutta.

Fabricius, J. C. 1787. Mantissa insectorum sistens eorum species nuper detectas adjectis characteribus genericis, differentiis specificis, emendationibus, observationibus. 1:1–348. Hafniae.

Forest, J., & D. Guinot. 1956. Sur une collection de Crustacés Décapodes et Stomatopodes des mers tunisiennes.—Bulletin Station Océanographique Salammbô 53:24–44, figs. 1–3.

Gordan, J. 1956. A bibliography of pagurid crabs, exclusive of Alcock, 1905.—Bulletin of the American Museum of Natural History 108:253–352.

Heller, C. 1865. Crustaceen. *In* Reise der österreichischen Fregatte Novara um die Erde in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodors B. von Wüllerstorf-Urbair. Zoologischer Theil. 2(3):1–280. Kaiserlich-königlichen Hof-und Staatsdruckerei, Wien.

Henderson, J. R. 1888. Report on the Anomura collected by H.M.S. Challenger during the years 1873–76. Scientific Results of the Exploratory Voyage of HMS Challenger, (Zoology) 27:1–221. Her Majesty's Stationery Office, Edinburgh etc.

Martin, J. W., & G. E. Davis. 2001. An updated classification of the Recent Crustacea.—Natural History Museum of Los Angeles County, Science Series 39:1–124.

McLaughlin, P. A. 1997. Crustacea Decapoda: hermit crabs of the family Paguridae from the KARUBAR cruise in Indonesia. *In* A. Crosnier and P. Bouchet, eds., Résultats des Campagnes MUSORSTOM, 16.—Mémoires du Muséum national d'Histoire naturelle 172:433–572.

———. 2002a. *Diogenes pallescens* Whitelegge, *D. gardineri* Alcock and *D. serenei* Forest (Decapoda; Anomura; Diogenidae): morphological variants or distinct species?—Raffles Bulletin of Zoology 50:81–94.

———. 2002b. A review of the hermit crab (Decapoda: Anomura: Paguridea) fauna of southern Thailand, with particular emphasis on the Andaman Sea, and descriptions of three new species. *In* N. Bruce, B. Berggman and S. Bussarawit, eds., Proceedings of the International Workshop on the Crustacea of the Andaman Sea 29 November–20 December, 1998, Phuket Marine Biological Center.—Phuket Marine Biological Center Special Publication 23:385–460.

———, & P. F. Clark. 1997. A review of the *Diogenes* (Crustacea, Paguridea) hermit crabs collected by Bedford and Lanchester from Singapore, and from the 'Skeat' Expedition to the Malay Peninsula, with a description of a new species and notes on *Diogenes intermedius* De Man, 1892.—Bulletin of the Natural History Museum, London (Zoology) 63:33–49.

———, & L. B. Holthuis. 2001. In pursuit of J. F. W. Herbst's species of *Diogenes* (Anomura: Paguridea: Diogenidae).—Journal of Crustacean Biology 21:257–273.

Miers, E. J. 1880. On a collection of Crustacea from the Malaysian region.—Part III. Crustacea Anomura and Macrura (except Penaeidea).—Annals and Magazine of Natural History (5)5:370–384.

Morgan, G. J., & J. Forest. 1991. Seven new species of hermit crabs from northern and western Australia (Decapoda, Anomura, Diogenidae).—Bulletin du Muséum National d'Histoire Naturelle, (4)A12(3–4):649–689.

Rahayu, D. L., & J. Forest. 1995. Le genre *Diogenes* (Decapoda, Anomura, Diogenidae) en Indonésie, avec la description de six espèces nouvelles.—Bulletin du Muséum national d''Histoire naturelle [1994] (4)16(A):383–415.

Siddiqui, F. A., & Q. B. Kazmi. 2003. A checklist of marine anomurans (Crustacea: Decapoda) of Pakistan, northern Arabian Sea.—Memoirs of Museum Victoria 60:87–89.

Tirmizi, N. M., & F. A. Siddiqui. 1981. An illustrated key to the identification of northern Arabian Sea pagurids.—Institute of Marine Biology 1:1–31.

———, & ———. 1982. The marine fauna of Pakistan: 1 Hermit crabs (Crustacea, Anomura). University Grants Commission, Karachi, 103 pp.

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A new species of *Stenetrium* Haswell, 1881 (Crustacea: Peracarida: Isopoda: Asellota), from Navassa Island, Northern Caribbean Sea

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Abstract.—A new species of the isopod genus *Stenetrium* Haswell, 1881, is described from Navassa Island, Caribbean Sea. The new species, *S. kensleyi,* is compared to *S. serratum* Hansen, 1905, the only congener known from the western Atlantic following recent revisions of the Stenetriidae (Serov and Wilson, 1995, 1999; Bolstad and Kensley, 1999), and to some members of the recently proposed genus *Hansenium,* with which it shares several characters. The new species differs from *S. serratum* (and from other members of the genus) in its possession of an unusual male first pereopod, which has a greatly inflated dactylus, broadly triangular propodus, and a medial sharply triangular shark-fin-shaped tooth on the propodal cutting border.

In their comprehensive guide to isopods of the Caribbean Sea and adjacent regions of the northwestern Atlantic (Gulf of Mexico, Bahamas, and Bermuda), Kensley and Schotte (1989) reported two genera of the family Stenetriidae Hansen: *Stenetrium* Haswell, 1881, and *Stenobermuda* Schultz, 1979. The authors presented diagnoses, illustrations, and keys to these two genera and to the six species of *Stenetrium* (*S. bowmani* Kensley, 1984; *S. minocule* Menzies and Glynn, 1968; *S. patulipalma* Kensley, 1984; *S. serratum* Hansen, 1905; *S. spathulicarpus* Kensley, 1984; and *S. stebbingi* Richardson, 1902 [= *S. antillense* Hansen, 1905]) known at that time from the northwestern Atlantic. Since then, a seventh northwestern Atlantic species of *Stenetrium, S. caicosensis* Kensley and Heard, 1991, was described from the Turks and Caicos Islands. Additionally, Kensley (1994) designated a second northwestern Atlantic species of *Stenobermuda, S. iliffei,* a cave dwelling form that, like the type species *Stenobermuda acutirostrata* Schultz, 1979, came from Bermuda.

Serov and Wilson (1995) reviewed the taxonomic status of the more than 60 nominal species comprising the family Stenetriidae Hansen, 1905. As part of their study, they redescribed the type species, *Stenetrium armatum* Haswell, 1881, described the new species *S. adrianae,* and created four new genera to accommodate 23 species previously assigned to *Stenetrium.* Of the seven northwestern Atlantic species formerly assigned to *Stenetrium,* only *S. serratum* was recognized as a true member of that genus by Serov and Wilson (1995). The remaining stenetriid species from the northwestern Atlantic have been transferred to new genera (see Table 1) (and see Bolstad and Kensley, 1999, for a rediagnosis of Serov and Wilson's 1995 genus *Hansenium*). Thus, as currently understood (i.e., following Kensley and Schotte 1989; Kensley 1994; Serov and Wilson 1995, 1999; Bolstad and Kensley 1999) the family Stenetriidae contains 9 genera and approximately 67 species, 11 of which (in 6 genera) are currently known from the western Atlantic (Table 1).

Table 1.—Northwestern Atlantic species of the isopod family Stenetriidae and their current status following Serov and Wilson (1995, 1999) and Kensley and Bolstad (1999), listed in alphabetical order.

Former name	New name	Reference
Lexcenium poorei	Unchanged since description	Serov and Wilson, 1999
*Stenetrium antillense**	Transferred to *Hansenium*	Serov and Wilson, 1995
Stenetrium bowmani	Transferred to *Hansenium*	Serov and Wilson, 1995
Stenetrium caicoensis	Transferred to *Hansenium*	Serov and Wilson, 1995
Stenetrium kensleyi	Newly described, this study	
Stenetrium minocule	Transferred to *Liocoryphe*	Serov and Wilson, 1995
Stenetrium patulipalma	Transferred to *Mizothenar*	Serov and Wilson, 1995
Stenetrium serratum	Unchanged since description	Haswell, 1881
Stenetrium spathulicarpus	Transferred to *Hansenium*	Serov and Wilson, 1995
Stenetrium stebbingi	Transferred to *Hansenium*	Serov and Wilson, 1995
Stenobermuda acutirostrata	Unchanged since description	Schultz, 1979
Stenobermuda iliffei	Unchanged since description	Kensley, 1994

* Considered a junior synonym of *Stenetrium stebbingi* by Kensley (1982) but listed as a valid member of *Hansenium* by Serov and Wilson (1995).

As part of an ongoing biotic survey of the cryptic marine invertebrates of certain islands in the Caribbean (led by T. L. Zimmerman and J. W. Martin), we obtained numerous specimens, including adult males, of an undescribed asellote isopod referable to the genus *Stenetrium* Haswell, 1881, but also sharing some characters with the genus *Hansenium* as described by Serov and Wilson (1995) and Bolstad and Kensley (1999). The specimens came from waters surrounding Navassa Island, a United States Territory just off the southeastern coast of Cuba. Of the 18 species of *Stenetrium* recognized by Serov and Wilson (1995), the new species appears to have its closest affinities to *S. serratum,* the only other species of Stenetrium currently recognized (by Serov and Wilson 1995, but see also Remarks below) from the northwestern Atlantic. The species is also similar in some ways to *Stenetrium caicosensis,* a species that was treated as *Hansenium* (with spelling emended to *H. caicosense*) by Serov and Wilson (1995).

The description of the new species of *Stenetrium,* which is based solely on specimens collected from Navassa Island in the tropical Northwest Atlantic (northern Caribbean Sea), is the subject of this report. Unless otherwise indicated all of the material examined during this study was collected by R. Wetzer and G. Hendler. The specimens were fixed and preserved in 95% ethanol. Total length equals the distance from the tip of the rostrum to the posteriormost margin of the pleotelson. RW numbers refer to field collection stations of the third author; LACM numbers are catalog numbers in the Natural History Museum of Los Angeles County's collection of Crustacea.

***Stenetrium kensleyi,* new species**
Figs 1–4

Material examined.—Holotype (LACM CR 2000-017.2): 1 ovigerous female, Atlantic, Caribbean Sea, Navassa Island, Pinnacles, 18°24.463′N, 75°01.094′W, SCUBA, ~19 m, *Halimeda* washes, R/V Coral Reef II, 21 March 2000, RW00.070. Paratypes: LACM CR 2000-017.1, 2 adult males (most appendages present), 2 ovigerous females (lacking most appendages), 2 specimens (sex not determined), same collection data as holotype. LACM CR 2000-021.1, 4 females [2 females with oostegites and 2 females without oostegites; the latter 2 in poor condition]; 4 subadult males, Atlantic, Caribbean Sea, Navassa Island, NW Lulu Bay, 18°23.856′N, 75°01.220′W, SCUBA, *Halimeda* washes, R/V Coral Reef II, 19 March 2000, NIP-2000-13, RW00.049. LACM CR 2000-021.2, 1 subadult male, Atlantic, Caribbean Sea, Navassa Island NW Lulu Bay, 18°23.856′N, 75°01.220′W, SCUBA, *Halimeda* washes. R/V Coral Reef II, 19 March 2000, NIP-2000-13, RW00.049 (first left pereopod illustrated in fig. 3B). LACM CR 2000-020.1, 1 female without oostegites (most appendages intact), Atlantic, Caribbean Sea, Navassa Island, near Lulu Bay, 18°23.791′N 75°01.195′W, SCUBA, ~9 m, rock rubble wash, R/V Coral Reef II, 18 March 2000, coll. R. Wetzer and D. O'Foighel, RW00.044. LACM CR 2000-018.1, 1 adult male (most appendages missing), Atlantic, Caribbean Sea, Navassa Island, Tom's Rock, 18°23.655′N 75°01.094′W, SCUBA, rock and sponge washes, R/V Coral Reef II, 21 March 2000, RW00.074. LACM CR 2000-019.1, 4 adult males (most with appendages missing but with chelipeds intact), Atlantic, Caribbean Sea, Navassa Island, 18°23.655′N, 75°01.094′W, RW00.074 and RW00.051 (combined).

Diagnosis.—*Stenetrium* with short, wide, distally truncate rostrum. Cephalon with well developed and acute anterolateral and antennal spines subequal in length; anterolateral spine not quite reaching level of rostral tip; antennal spine slightly longer and extending anteriorly slightly beyond rostral tip. Eyes well pigmented, reniform. Pereonites 1–3 with sharply angled anterolateral margins (less so on pereonite 4). Pleotelson with lateral margins appearing serrate, with four movable spiniform setae and posterolateral tooth; posterior border gently rounded. Male first pereopod with dactyl distally inflated, terminally rounded, and longer than propodal width; propodus large, subtriangular, bearing 2 triangular teeth on distal border opposite dactyl, one at anteroventral border and one close to midlength of distal border; carpus not enlarged or elongate, unserrated. Uropodal exopod approximately equal in length to peduncle and 3/4 length of endopod.

Description of male.—Body (Fig. 1A, B). Total length 3.6 mm, approximately 3.5 times width, as measured across widest (6th) pereonite. Pereonites 1–3 sharply angled forward; pereonite 4 similar but less sharply angled; pereonites 5–7 directed posteriorly. All pereonites with at least one long lateral seta extending outward.

Pigmentation (Fig. 1A). Pattern somewhat similar to that described for *S. serratum* Hansen, 1905 (see Kensley and Schotte, 1989, fig. 46F). Head with pigmentation confined mostly to anterior third and between the eyes. Pereonite 1 with pigment in two narrow lateral bands running anterior to posterior, with central region and anterolateral corners unpigmented. Pereonite 4 mostly unpigmented. Pleotelson almost entirely pigmented except for horizontal unpigmented band at about midlength and for outer posterior and posterolateral margins. Other pereonites variously covered with reticulated pigmentation broken up by open areas, as shown.

Head (Fig. 1A, B). Eyes located dorsolaterally, reniform, well pigmented, composed of some 15–18 ommatidia. Anterolateral spines (anterolateral lobes) well developed, acute, extending forward almost as far as antennal spines, separated from antennal spines by rounded gap extending backward toward eye. Antennal spine acute, extending anteriorly to level of rostrum. Rostrum broad, distally truncate. Outer (lateral) border of anterolateral lobes each with 2 long setae and scattered shorter setae as illustrated.

Pleotelson (Fig. 1A, B). Base just wider than length; width measured at level of third lateral spine equal to length. Lateral margins with 4 movable spines (each with 1 long and 1 short seta on either side) and strong posterior tooth just anterior to posterolateral notch; posterolateral notch with single short seta. Posterior border of pleotelson (between notches) smoothly rounded,

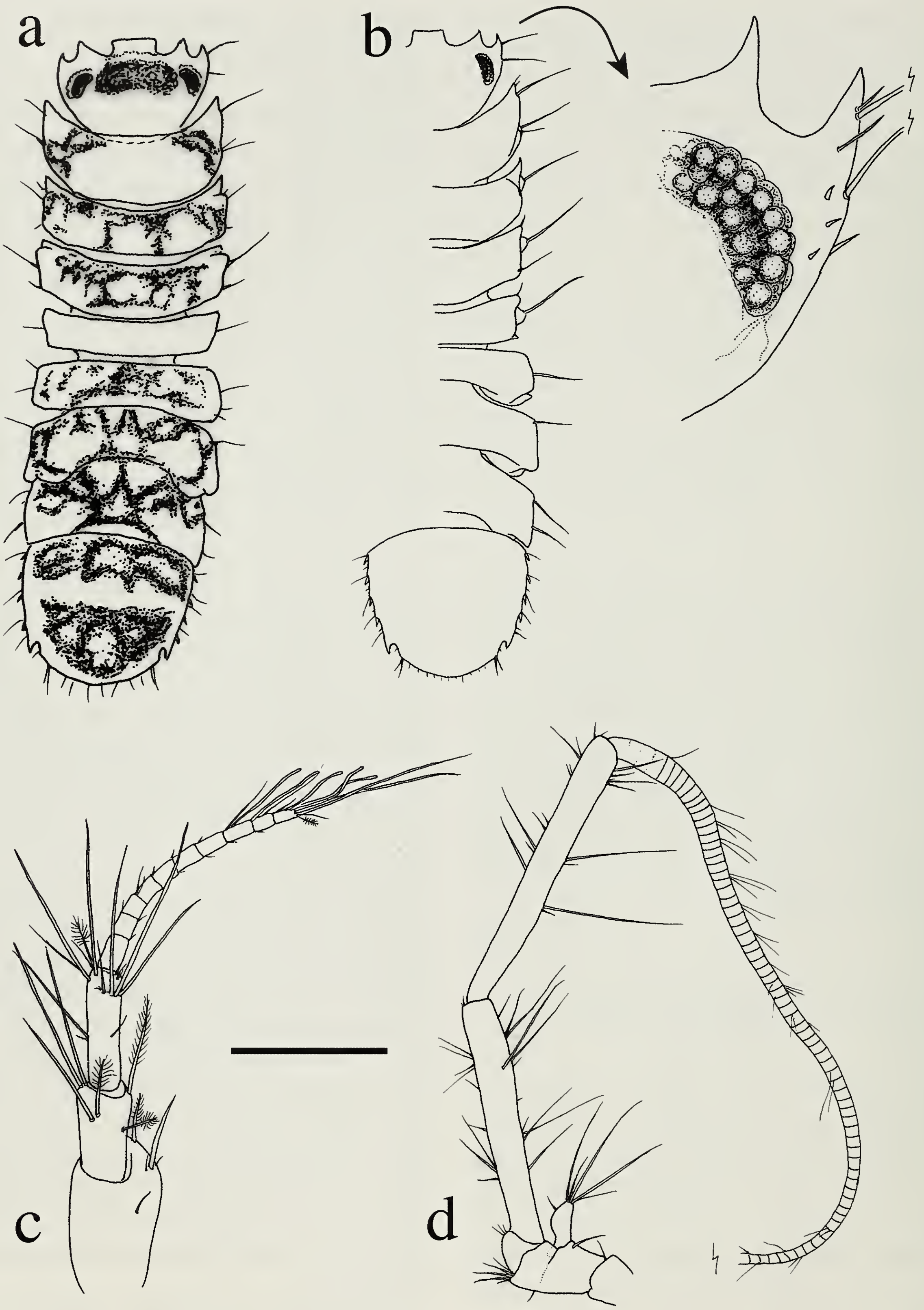

Figure 1. *Stenetrium kensleyi,* n. sp., adult male and female body from and antennae 1 and 2. A, adult female holotype (LACM CR 2000-017.2), dorsal aspect showing generalized pigmentation pattern; B, adult male (one of two male paratypes as part of LACM CR 2000-017.1), dorsal view of pleotelson, right half of pereonites and cephalon showing rostrum (chephalic appendages and uropods excluded) with enlargement showing distolateral aspect of cephalon with details of eye, anterior spines, and setation; C, antenna 1 of adult male (same specimen as B); D, antenna 2 of adult male (same specimen as B). Scale bar = 1 mm for A and B; 0.2 mm for C; 0.6 mm for D.

with scattered short setae flanked by pair of longer setae at either end of border.

Antenna 1 (Fig. 1C). Basal article broadest and extending anteriorly well beyond rostrum (rostrum reaching to about midlength of this article). Articles 1–3 with simple and plumose setae, with number of setae increasing from article 1 to 3. Flagellum with 10 articles, with distal 3 articles bearing 5 aesthetascs.

Antenna 2 (Fig. 1D). First article lacking lateral spine. Articles 2 and 3 side by side. Article 2 narrow. Article 3 wider distally than proximally and longer than combined articles 1 and 2, and bearing distal setose scale close to base of article; scale broadest at midlength and with 1 subterminal and 5 terminal setae. Article 4 about half length of article 3 and about 1/6 length of article 5. Articles 5 and 6 elongate, article 6 slightly longer than 5.

Mouthparts (Fig. 2A–E). Mandible (Fig. 2A, B; right mandible illustrated) with well developed molar and incisor processes; molar process with short, thick spines and curved spine-like setae; right incisor process with 4 strong distal teeth and approximately 8 stout, recurved, serrate setae. Mandibular palp (Fig. 2B) large, with 3 articles; first unarmed and slightly less than half length of second; second article longest and with 2 large, sinuous and minutely serrulate setae bordering field of 10 shorter stout setae; third article elongate, approximately two thirds as long as second, curved, thicker basally than distally, and bearing field of basal setae, row of short setae along ventral border, and gradually lengthening distal setae, as illustrated. Maxilla 1 (Fig. 2C) lateral lobe with 10 heavy serrate spines distally and scattered simple setae as shown, 2 aspects shown; medial lobe with 3 stout plumose setae and distal simple setae. Maxilla 2 (Fig. 2D) with lateral and middle lobes slender and subequal in length; medial lobe shorter and thicker, with stout, serrate setae on distal border and plumose and simple setae along medial border as shown; lateral and middle lobes each with 5 stout setae distally and row of 6–7 shorter, thinner setae just proximal to tip. Maxilliped (Fig. 2E) with long, straight-sided basis, 5-articulate palp, and elongate and distally tapering epipod with 6 short setae. Palp article 1 by far the shortest; articles 2 and 3 longer and wider than articles 4 and 5. Maxillipedal endite with 3 coupling hooks on mesial margin and 5 fan setae on distal margin.

Pereopod 1 (gnathopod) of terminal 3.6 mm male (Fig. 3A) extremely large, wide, subchelate. Dactyl distally swollen, widest at midlength, extending past anterolateral border of propodus and terminating in unequal pair of stout spines; setation as shown. Propodus broad, widest distally, subtriangular, with sharp anterolateral tooth and wide, triangular "sharkfin-shaped" tooth just proximal to midlength of distal border. Carpus and merus approximately equal in length; carpus lacking any extensions or projections and not serrate along distal border. Other articles and setation as shown. Subadult male (TL 3.2 mm) (Fig. 3B) with propodus subquadrate, dactyl acute distally. Propodus of female (Fig. 3C) lacking spines on anterolateral border.

Pereopods 2–7 (Fig. 4A–F) similar to each other. Dactylus with 2 stout, corneous distal "spines" (or heavily modified setae) giving the appearance of a "biunguiculate" tip, and 1 strong subterminal "accessory spine" on posterior margin. Propodus with large, blunt, distal "spine" nearly half as long as, and wider than, dactylus. Propodus and carpus elongate, each with 4 or 5 stout spines evenly spaced along ventral border; each with at least 1 plumose seta arising from distodorsal angle. Merus subtriangular, with long simple seta arising from distodorsal angle. Ischium with 1 to several plumose setae. Basis widest at midlength, with long seta arising from midlength projection.

Pleopods (Fig. 5A–C). Pleopod 1 (Fig. 5A) reduced, subrectangular, rami similar, with 2 small spines on medial border and with few setae on outer distal border. Ple-

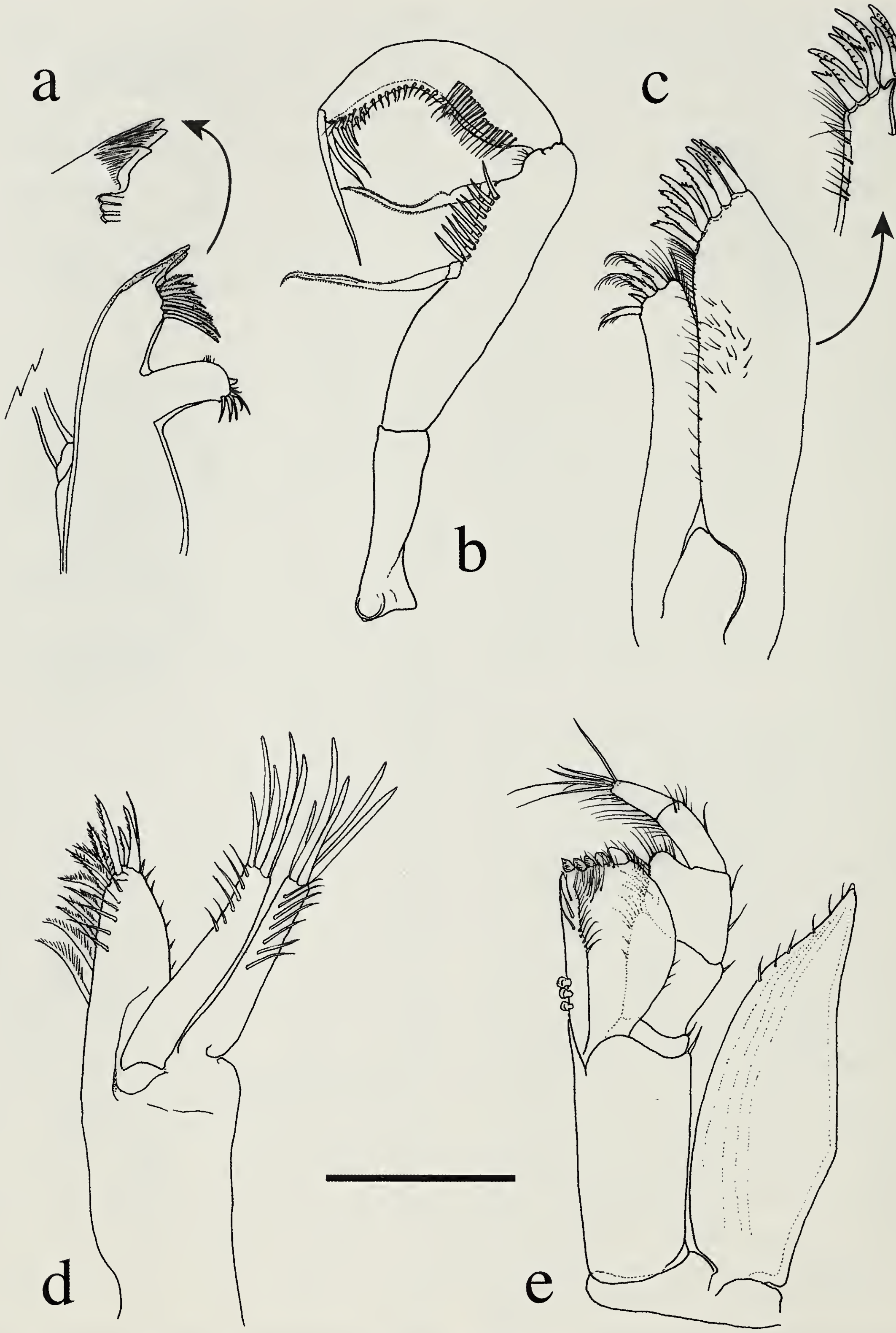

Figure 2. *Stenetrium kensleyi,* n. sp., mouthparts, adult male. All figures from a dissected male, one of four in LACM CR 2000-019.1). A, right mandible with enlargement of incisor process; B, mandibular palp; C, maxilla 1, outer aspect of lateral and medial lobes of adult male, and another aspect of lateral lobe; D, maxilla 2; E, inner face of maxilliped. Scale bar = 0.2 mm for A, E; 0.1 mm for B–D.

opod 2 (Fig. 5B) protopod subtriangular, widest at base, length 1.5 midpoint width. Exopod uniarticulate, blunt, length 1.6 width, positioned nearly apically on protopod, without setae. Endopod inserting 0.6 protopod length on medial margin; length 0.4 protopod length; proximal article groove length 0.4 article length. Appendix

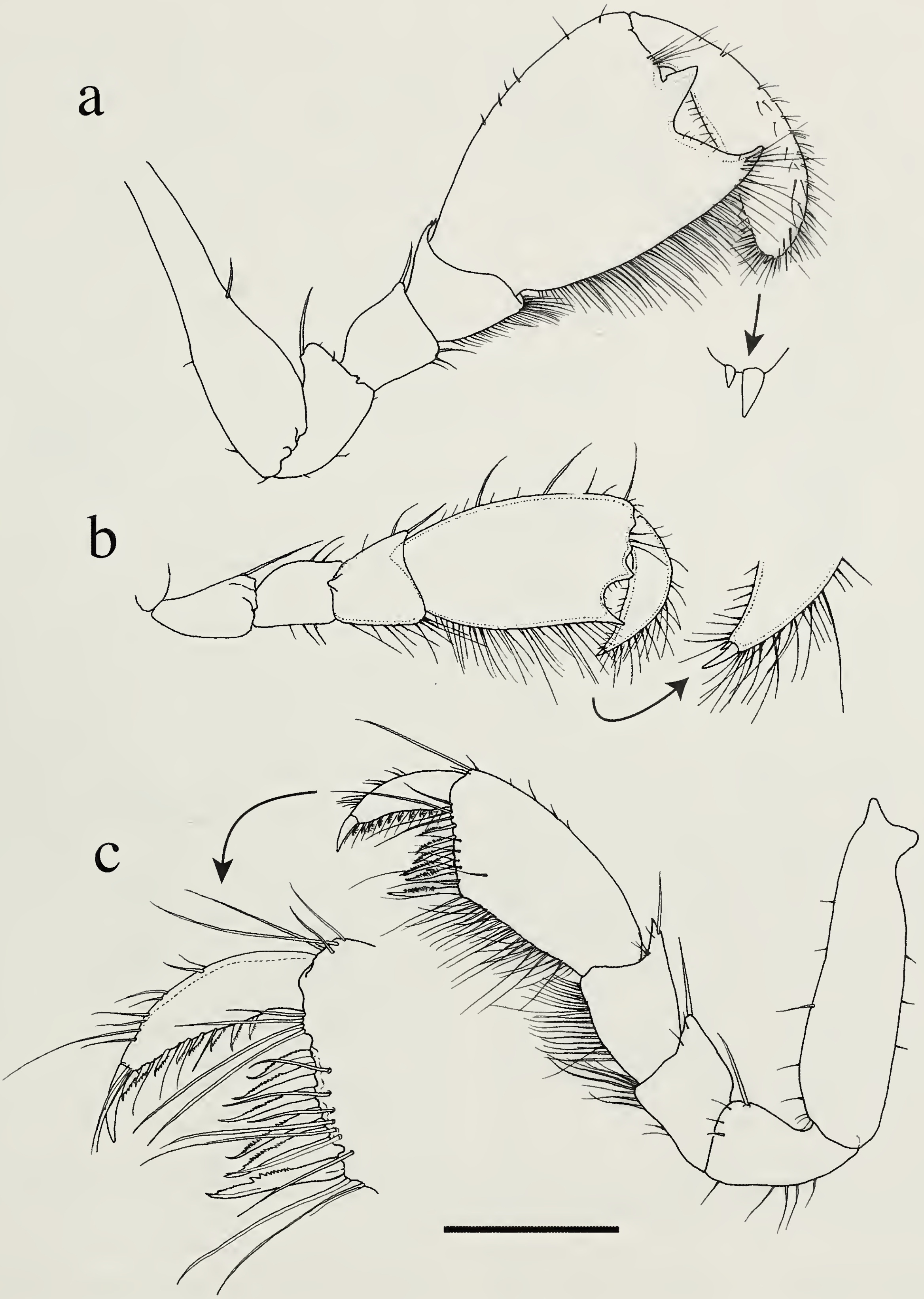

Figure 3. *Stenetrium kensleyi,* n. sp., male and female first pereopods. A, inner (mesial) surface of left pereopod 1 (gnathopod) of adult male paratype (from LACM CR 2000-017.1), TL 3.6 mm, inner aspect with enlarged view of dactylar tip; B, left pereopod 1, mesial aspect, of immature male paratype (LACM CR 2000-021.2), TL 3.2 mm, showing developing male gnathopod (with enlarged view of dactylar tip); C, inner (mesial) surface of left pereopod 1 (gnathopod) of adult female (paratype LACM CR 2000-020.1), TL 3.4 mm, inner aspect (with enlarged view of dactyl and distal part of propodus). Scale bar = 0.3 mm for A and C (excluding enlargements); 0.5 mm for B.

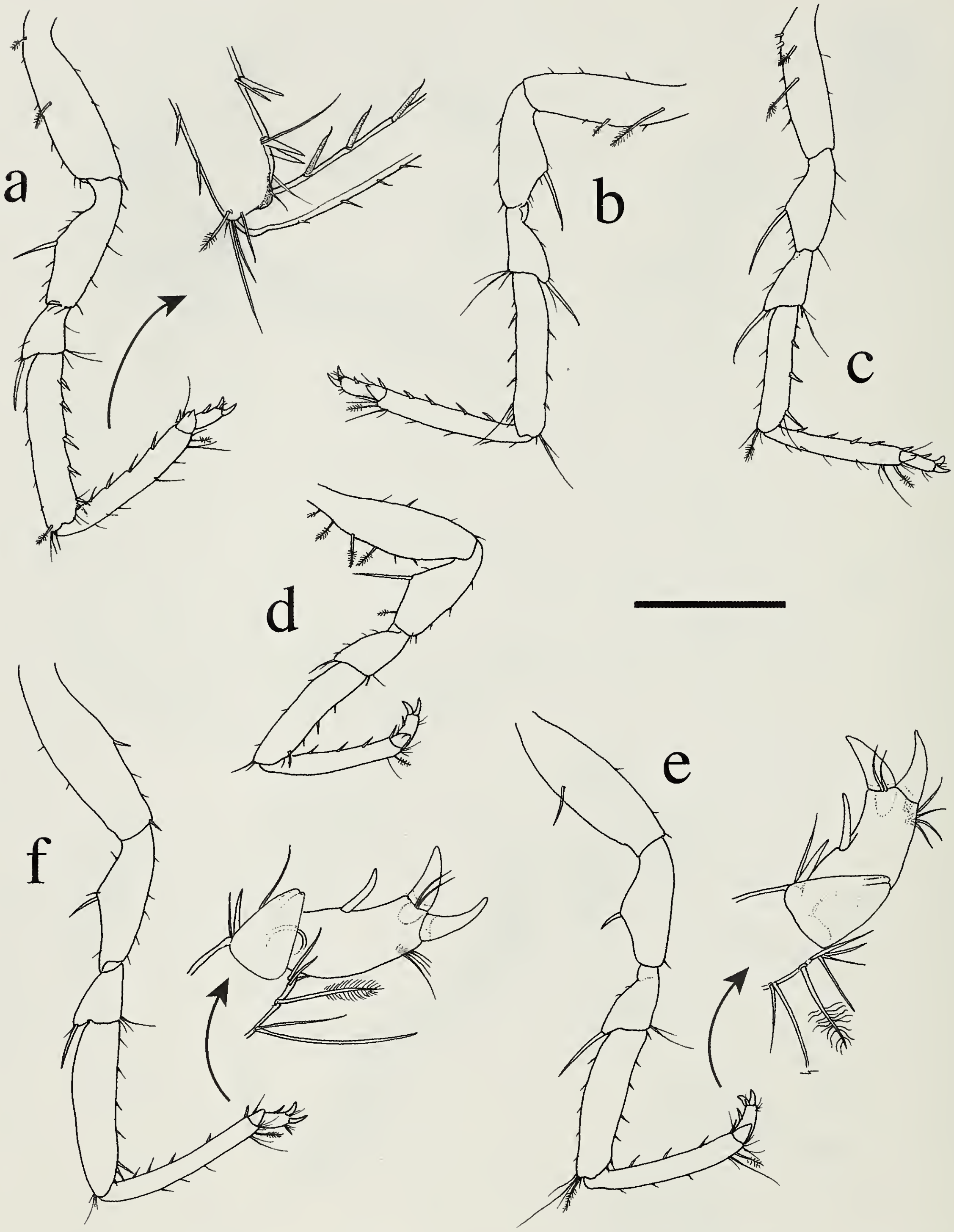

Figure 4. *Stenetrium kensleyi,* n. sp., pereopods of male (from LACM CR 2000-017.1). A–F, pereopods 2–7. Scale bar = 0.3 mm for all figures (excluding enlargements).

masculina length 1.5 endopod length, lacking setae, with 3 small recurved (dorsally-directed) barbs subapically and with sinuous groove on anterior surface; otherwise unornamented. Male pleopod 3 exopod length 1.1 width. Endopod length 2.0 width; length 0.7 exopod length; posteriorly subacute with 1 simple seta and 3 plumose setae on apex.

Uropod (Fig. 5D) with basis widest distally, with 1 long, slender seta on outer margin and 2 long setae along medial margin, plus 2 long setae on distal inner corner and scattered short setae. Inner ramus longer than outer, with 2 clusters of long, simple setae on medial border, 7 long terminal setae, and scattered plumose and simple setae along outer margin. Outer ramus approxi-

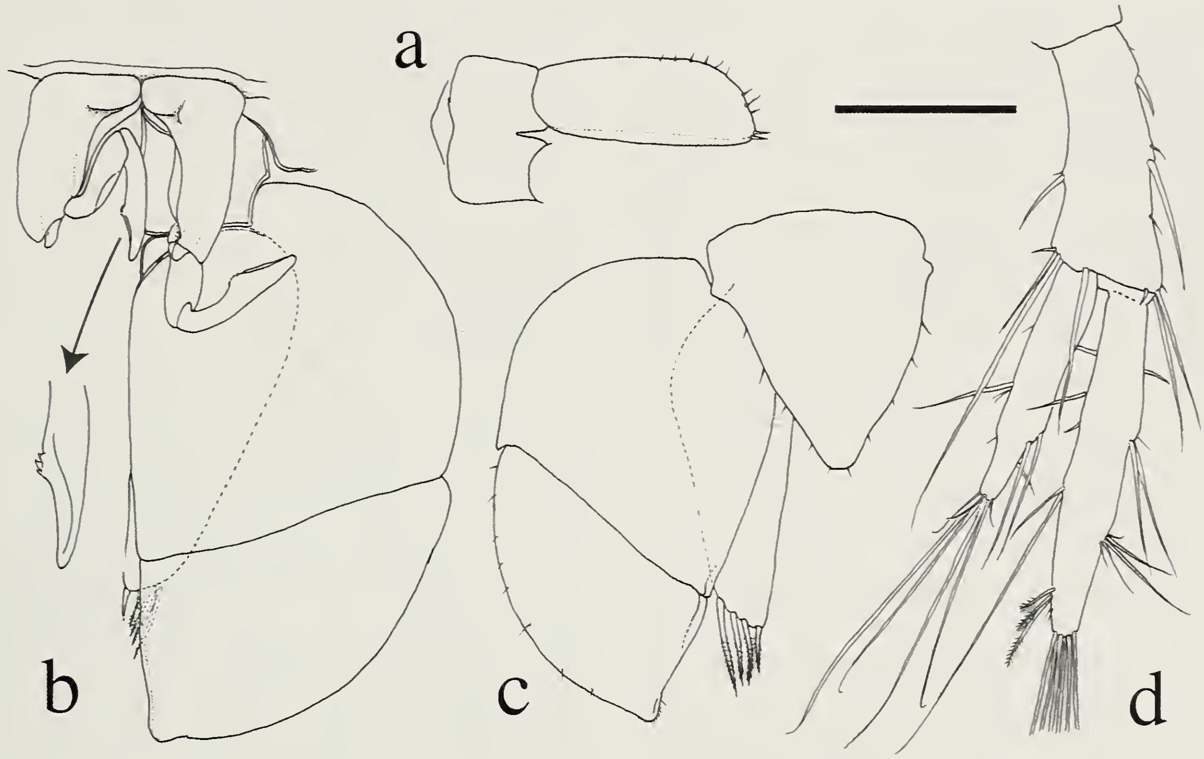

Figure 5. *Stenetrium kensleyi,* n. sp., pleopods and uropod. A. male first pleopod. B. male second pleopod: C. female second pleopod: D. uropod. A, B, and D from LACM CR 2000-017.1: C from LACM CR 2000-21.1. Scale bar = 0.3 mm.

mately 3/4 length of inner ramus and with long simple setae and scattered short setae as illustrated.

Adult female (Fig. 1A) with pigmentation and body similar to male, except for sexual dimorphism exhibited by smaller antenna 2, slightly different setation of uropods, and distinct differences in pereopod 1 (compare male in Fig. 3A to female in Fig. 3C) and in pleopods 1 and 2.

Pereopod 1 (Fig. 3C) with dactyl terminating in stout, sclerified spine, and with 8 serrate spines evenly spaced along ventral border; propodus approximately twice length of dactyl with 6 stout, serrate spines projecting from distal border opposite those of dactyl; ventral angle of propodus sharply angled at 2/3 length, marking change from stout serrate spines anteriorly to simple and plumose setae proximally; carpus heavily setose; other articles as illustrated.

Pleopod 2 (Fig. 5B) subtriangular, length 1.2 width. Distal tip blunt; 10 fine simple setae spaced evenly around lateral margins. Pleopod 3 exopod very broad, biarticulate; endopod length 0.7 exopod length, with 4 distal plumose setae.

Etymology. We take great pleasure in naming this species after Dr. Brian Kensley of the U.S. National Museum of Natural History for his numerous and significant contributions to our knowledge of Caribbean isopod crustaceans.

Remarks.—*Stenetrium kensleyi* appears most similar to *S. serratum* (see Kensley and Schotte, 1989:103, fig. 46), the only other species of the genus recognized by Serov and Wilson (1995) from the northwestern Atlantic. Both species share a similar pigmentation pattern, a distally truncate rostrum, and serrate-appearing lateral margins of the pleotelson. Additionally, eye morphology is similar (reniform and well pigmented) in both *S. kensleyi* and *S. serratum,* and also in *Stenetrium caicosensis* (now *Hansenium caicosense*; see Bolstad and Kensley, 1999). All three of these species also possess well-developed anterolateral and antennal spines on the head that are acute and anteriorly-directed, with a narrow and rounded gap separating them and extending backward almost to the eye. The species are readily distinguished by the male pereopod 1. The male pereopod 1 of *S. kensleyi* is marked by a dactyl that is distally inflated and wider at midlength than it is proximally or distally (somewhat true of *H. caicosense,* but different from the dactyl of *S. serratum*). The propodal cutting surface of this pereopod in *S. kensleyi* bears a single, medially positioned, widely triangular tooth that is notched at the base, in addition to having an acute and spine-like anterolateral border; it is also distally wide, giving the article a broadly triangular shape, unlike what is seen in mature male pereopods of other species of *Stenetrium* or species of *Hansenium.*

Concerning species of *Stenetrium* outside of the western Atlantic, the new species appears similar in some characters (the inflated dactylus of the first pereopod) to Barnard's (1940) brief description of *S. bartholomei* from the littoral of South Africa. However, as specimens of *S. kensleyi* were collected at a depth of approximately 20 meters in an area of high currents in which there are no ports (the Pinnacles off Navassa Island), the likelihood of these specimens belonging to some introduced species is essentially nonexistent.

The new species is in some ways intermediate between the currently accepted definitions of *Stenetrium* and *Hansenium* (following Serov and Wilson, 1995, and Bolstad and Kensley, 1999). Serov and Wilson (1995) defined *Hansenium* as having (in addition to other characters) the following features, all of which are found also in *S. kensleyi*: a rostrum that is "broad and apically flattened" and is "slightly longer than antennal spines," an antennular flagellum with 8–14 articles (*S. kensleyi* has 10), a reduced spine on antennal article 1 (this spine is lacking in *S. kensleyi*), pereonites 1–4 with angular margins (a character that is not mentioned in their diagnosis of *Stenetrium,* but which seems to be true of both genera and is true of *S. kensleyi*), and a pleotelson that bears prominent posterolateral spines and that has a smoothly rounded postanal region (characters that are true for several other former members of *Stenetrium*). These characters, taken alone, could be used to argue for placement of the new species within *Hansenium.* However, some of the characters that Serov and Wilson (1995) used to define *Hansenium* are not found in our new species (and also do not hold for some of the other species included by them in *Hansenium,* such as their *Hansenium caicosensis* and *H. bowmani,* both formerly treated as *Stenetrium*). These characters include a "head with reduced lateral and antennal spines," an elongated pleotelson, and, what is perhaps the most salient difference, a male first gnathopod with a carpus having the "lateral margin extended and serrate." This last character clearly is not the case in *S. kensleyi,* where the male first pereopod carpus is relatively simple and does not have an extended or serrate lateral margin. Bolstad and Kensley (1999) revised the diagnosis of *Hansenium* and maintained that the primary character separating the two genera was the expanded carpal lobe on the male first pereopod in *Hansenium,* leading us to place our new species firmly in *Stenetrium.* Yet such characters as the rectangular rostrum mentioned above are considered by Bolstad and Kensley (1999; table 1) to be characteristic of *Hansenium.* The finding of species such as *S. kensleyi* with characters that bridge the definitions of *Stenetrium* and *Hansenium* (other species with characters that do not fit well within *Hansenium* as currently defined are *Stenetrium bowmani* as described by Kensley (1984) and *Stenetrium caicosensis* described by Kensley and Heard (1991); in fact *S. caicosensis* is in some ways closer to *S. kensleyi* than is *S. serratum*) may be reason to reconsider the generic status of *Hansenium.* Clearly, in addition to the ever-present need for systematic work at the species level, additional studies clarifying the morphological characters that define and distinguish stenetriid genera are needed.

Acknowledgments

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Literature Cited

Barnard, K. H. 1940. Contributions to the crustacean fauna of South Africa. XII. Further additions to the Tanaidacea, Isopoda, and Amphipoda, together with keys for the identification of hitherto recorded marine and freshwater species.—Annals of the South African Museum 32:381–543.

Bolstad, K. S., and B. Kensley. 1999. Two new species of *Hansenium* (Crustacea: Isopoda: Asellota) from Madang, Papua New Guinea.—Proceedings of the Biological Society of Washington 112(1):164–174.

Hansen, H. J. 1905. On the morphology and classification of the Asellota group of crustaceans with descriptions of the genus *Stenetrium* Hasw. and its species.—Proceedings of the Zoological Society of London 1904 (2 supplement II):302–331.

Haswell, W. A. 1881. Some Australian marine Isopoda, part 1.—Proceedings of the Linnean Society of New South Wales 5:470–481.

Kensley, B. 1984. The Atlantic Barrier Reef ecosystem at Carrie Bow Cay, Belize, III: new marine Isopoda.—Smithsonian Contributions to Marine Sciences 24:1–81.

———. 1994. Records of shallow-water marine isopods from Bermuda with descriptions of four new species.—Journal of Crustacean Biology 14:319–336

———, and R. W. Heard. 1991. Studies on the Crustacea of the Turks and Caicos Islands, British West Indies I. Four new marine isopod crustaceans from the vicinity of Pine Cay.—Gulf Research Reports 8:237–246.

———, and M. Schotte. 1989. Guide to the marine isopod crustaceans of the Caribbean. Smithsonian Institution Press, Washington, D.C. 308 pp.

Menzies, R. J., and P. W. Glynn. 1968. The common marine isopod Crustacea of Puerto Rico.—Studies on the Fauna of Curaçao and other Caribbean Islands 27:1–133.

Richardson, H. 1902. The marine and terrestrial isopods of the Bermudas with descriptions of new genera and species.—Transactions of the Connecticut Academy of Arts and Sciences, New Haven 11:277–310.

Schultz, G. A. 1979. A new Asellota (Stenetriidae) and two, one new, Anthuridea (Anthuridae) from Bermuda (Crustacea, Isopoda).—Proceedings of the Biological Society of Washington 91: 904–911.

Serov, P. A., and G. D. F. Wilson. 1995. A review of the Stenetriidae (Crustacea: Isopoda: Asellota).—Records of the Australian Museum 47:39–82.

———, and ———. 1999. A revision of the Pseudojaniridae Wilson, with description of a new genus of Stenetriidae Hansen (Crustacea: Isopoda: Asellota).—Invertebrate Taxonomy 13: 67–116.

PROCEEDINGS OF THE BIOLOGICAL SOCIETY OF WASHINGTON
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Eocuma petrescui, a new species of bodotriid cumacean (Crustacea: Peracarida) from Malaysia

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Abstract.—The bodotriid cumacean, *Eocuma petrescui* new species, is described from western Malaysia. At least 12 congeners are known from marine waters proximate to the type locality. The new species appears to have its closest affinities to *Eocuma ferox* (Fischer, 1872), and *E. taprobanicum* (Calman, 1904).

The cumacean fauna of the Indian Ocean, including the shallower waters surrounding India, has been studied by a number of workers, notably Kurian (1954), and Radhadevi and Kurian (1989). Studies of the water in and around Malaysia, however, are limited, and only a few species have been described from the region (Petrescu 1997). During participation in the Fall 2000 voyage of Semester-at-Sea in Malaysian waters, we (IK) were involved in collection of an undescribed bodotriid cumacean belonging to the genus *Eocuma,* Marcusen, 1894. The description of this new species is the subject of this report. Of the 27 described species of *Eocuma,* 12 are reported in areas geographically proximate to Pulan Aman, Malaysia. Among these, *Eocuma longicorne* Calman, 1907, which has a type locality in the Red Sea, is the only congener that has been found in Malaysia (Stebbing 1913). While it bears some similarity to *E. petrescui* in the proportions of the uropods, and in the ventral projection of the basis of peraeopod 1, like the other 11 congeners of this region, it differs from the new species by a combination of characters. *Eocuma ferox* (Fischer, 1872), a taxon found in the Mediterranean and South China Seas, and *E. taprobanicum* (Calman, 1904), found off the coast of Sri Lanka and India, appear to have the greatest affinities to the new species.

Methods

Samples were collected with an epibenthic sled at a depth of 1–3 m in October 2000; specimens were preserved in 95% ethanol. Full body specimens were mounted in a mixture of glycerin and ethanol, and appendages were mounted on permanent preparations using CMCP-9, a low viscosity mountant. Drawings were prepared with a camera lucida on a Wild compound microscope.

Family Bodotriidae Scott, 1901
Subfamily Bodotriinae Scott, 1901

Eocuma Marcusen, 1894
Eocuma petrescui, new species
Figs. 1–3

Type material.—Holotype, ovigerous ♀, body length 6.5 mm, USNM 1008647, collected at Pulan Aman, Malaysia, (5°10′N, 100°5′E), depth 1.5 m, 21 Oct 2000. Paratypes, USNM 1008648, (1♂, 4♀♀) from same locality as holotype.

Diagnosis.—Carapace with lateral horns extending outwards, with marked lateral

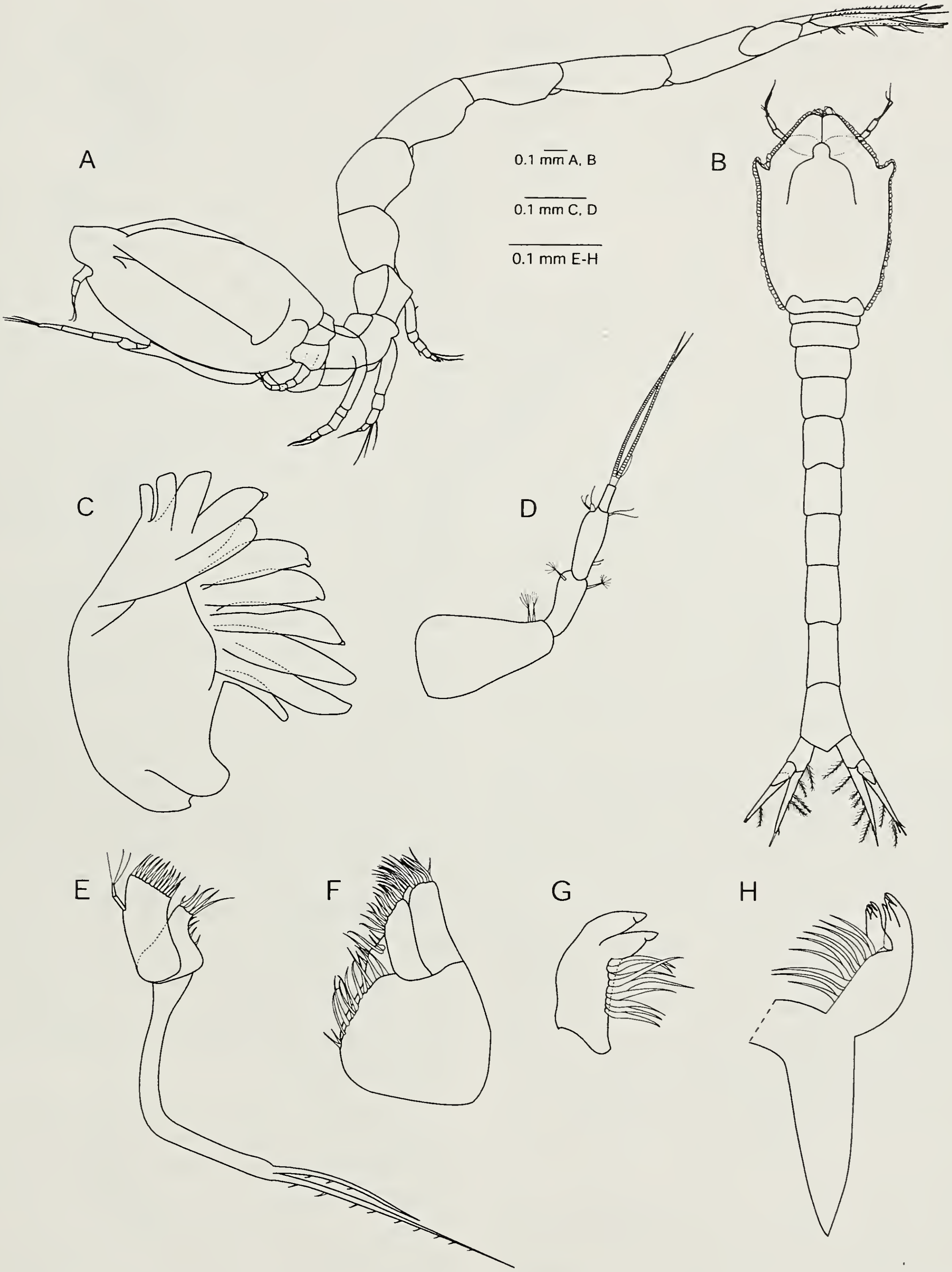

Fig. 1. *Eocuma petrescui*, new species. Paratype ♀ A, lateral view; B, dorsal view; C, branchial apparatus; D, antenna 1; E, maxilla 1; F, maxilla 2; G, left mandible, posterior view; H, right mandible, posterior view.

ridges; antennal notch narrow and deep; peraeopod 1 with ventral projection on basis; rami of uropods equal in length to pleonite 6. Male pleopods with developed internal process on the endopod.

Description.—Adult female, body length 3–6.5 mm; carapace longer than wide, ornamented (Fig. 1B) and textured (Fig. 3E); 1/4 of total body length, with marked lateral horns, antennal notch narrow and deep, lateral ridges leading into a posterior transverse ridge; carapace longer than peraeon and shorter than pleon (Figs. 1A, B). Frontal lobe extended anteriorly with eyelobe not pigmented; pseudorostral lobes extending well beyond eyelobe and meeting at midline; eyelobe 1/3 length of carapace with lenses not visible.

Peraeonite 1 not visible laterally, and only visible dorsally as it is seen under the carapace; peraeonites 2 to 5 with lateral ridges. Pleon longer than carapace and peraeon together, 2.5 times length of peraeon (Fig. 1B).

Antenna 1 (Fig. 1D) peduncle tri-articulated, proximal article robust, subequal in length to other two articles combined; second article shorter than third; first and second articles with setae bearing setules at their tips; third article with bifurcating setae distally; main flagellum with 1 article, with 2 aesthetascs at distal end; accessory flagellum uniarticulate, with 1 simple seta at tip.

Mandibles (Fig. 1G, H) with dorsal part to pars molaris naviculoid in shape; lacinia mobilis well developed; pars molaris and pars incisiva separated by a row of 9 setae armed with setules on distal portion.

Maxilla 1 (Fig. 1E) with two endites; broad endite with 12 simple setae and 1 annulated seta with 3 setules at distal tip emerging from outer margin; narrow endite with 4 simple setae; palp twice length of protopod bearing 2 setae with upwardly oriented setules; longest equal in length to palp.

Maxilla 2 (Fig. 1F) protopod with one article, longer than two lobes of the endite; endite longer than protopod; endite and protopod heavily setose at distal margin.

Maxilliped 1 (Fig. 2A) basis short and stout with two plumose setae merging from mid-area, with large endite extending beyond articulation of merus with carpus; ischium hidden under basis; carpus as long as propodus and dactylus together; armed with row of simple setae on inner margin and one plumose seta distally on outer margin; propodus with perpendicular row of 4 setae and 2 longer setae at distal margin medially; dactylus with 3 short simple setae; branchial apparatus containing 11 branchial elements (Fig. 1C).

Maxilliped 2 (Fig. 2B) basis dorsally robust, almost as long as rest of appendage; ischium very small, only visible on inner side of appendage when bent; basis and merus with long plumose seta on distal margin; merus slightly produced dorso-distally, merus shorter than carpus; carpus with row of five plumose setae on inner margin and one large plumose seta extending between articulation of merus and carpus; propodus distally expanded with row of setae on distal half of outer margin; dactylus with 2 terminal setae.

Maxilliped 3 (Fig. 2C) exopod fully developed, armed with numerous plumose setae; basis arcuate and longer than other articles together, produced distally well beyond articulation of ischium and merus, inner margin and tip of projection with long plumose setae; basis, ischium, merus, carpus, and propodus with small setae; ischium subequal in length to merus with row of plumose setae on inner margin; merus slightly projected dorso-distally, with plumose seta at tip of projection; carpus distally widened; propodus laterally widened with row of 4 setae on inner margin; dactylus subequal in length to propodus with 5 terminal setae.

Peraeopod 1 (Fig. 2D) exopod fully developed, with long plumose setae; basis of endopod subequal to other articles together, longer than peraeopod 2, with convex expansion on lower portion of inner wall, ventral projection at distal end reaching articulation of ischium and merus, with 1 small simple seta at tip of projection, basis and ischium with small setae; merus longer than ischium and subequal in length to carpus, propodus, and dactylus; propodus with 2 setae at distal margin; dactylus with 4 terminal setae and 3 subterminal setae.

Peraeopod 2 (Fig. 2E) uniramous with ischium missing; basis shorter than half

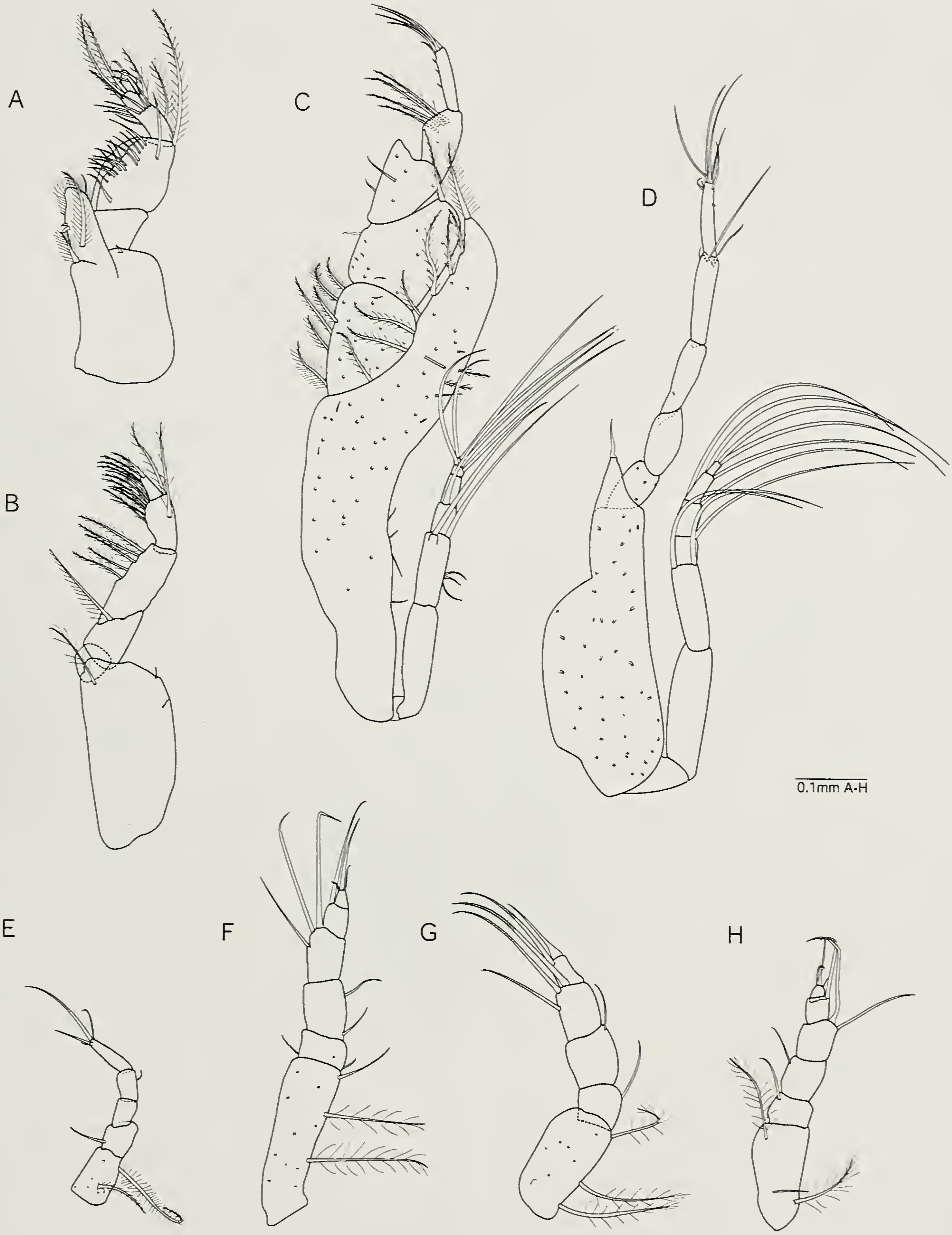

Fig. 2. *Eocuma petrescui*, new species. Paratype ♀ A, maxilliped 1; B, maxilliped 2; C, maxilliped 3; D–H, pereopod 1–5 (plumose exopod setae of maxilliped 3 and pereopod 1 are omitted).

length of appendage, subequal in length to dactylus, with 2 long plumose setae emerging from middle of basis, setae twice length of basis, basis with small setae; merus, carpus, and propodus subequal in length; merus subequal in width to basis, wider than other articles; dactylus with one long terminal simple seta and 2 shorter simple setae.

Peraeopod 3 (Fig. 2F) uniramous; basis equal in length to other articles together, shorter than length of peraeopod 2, with 2 long plumose setae, and small sensory setae; merus twice length of ischium; carpus subequal in length to merus with 1 long seta in the middle and 2 long setae at distal edge, all setae longer than propodus and dactylus together; propodus longer than dactylus, with long seta on distal edge; dactylus with 1 terminal and 2 shorter subterminal setae.

Peraeopod 4 (Fig. 2G) uniramous; basis with 3 long plumose setae, 2 in the proximal half and 1 on distal part of article, basis also with small setae; merus 1.5 times length of ischium; merus subequal in length to carpus, carpus with 2 annulated setae emerging from distal area portion; propodus subequal in length to ischium, with 1 long annulated seta at proximal portion, and one shorter annulated seta emerging from distal area of propodus; dactylus fused with its terminal, short, annulated seta.

Peraeopod 5 (Fig. 2H) uniramous; basis with one plumose seta on proximal end and another plumose seta at distal end; ischium with seta at distal end; merus with seta at distal end, merus twice length of ischium and subequal in length to carpus; carpus with 2 setae longer than propodus and dactylus on distal end; propodus with one long seta at distal end; dactylus short with setae emerging from distal tip.

Pleonite 6 subequal in length to pleonite 5 (Fig. 1B), moderately produced between uropods, subacute, subequal in length to rami, 2.5 times length of peduncle; uropod peduncle (Fig. 1B) with one plumose seta on inner margin; rami subequal in length; exopod bi-articulated, distal article twice length of proximal article, with 2 plumose setae on inner edge, and 2 truncated setae distally; endopod uniarticulate with 6 plumose setae in a row along inner margin; one thick, long truncated terminal seta.

Adult male paratype (Fig. 3A). Body length 5.9 mm. Carapace longer than wide, flattened and shorter when compared to female, also less bulbous in anterior area than female; one lateral ridge along middle portion of carapace joined posteriorly to a dorso-lateral ridge; no posterior transverse ridge as in female; antennal notch narrow and deep with acute anterolateral corner; peraeonite 1 visible in both lateral and dorsal views; abdominal segments thicker and more robust than in female; peraeon and pleon combined are twice length of carapace.

Antenna 1 (Fig. 3C) peduncle shorter than other 2 articles together; third article of antenna longer than second; accessory flagellum small with no setae or aesthetascs; proximal article of main flagellum with three short aesthetascs emerging from middle area; remainder of main flagellum broken.

Pleon with five pairs of pleopods; peduncle of pleopod (Fig. 3D) 1.5 as long as endopod with row of 8 setose setae along inner margin; endopod uniarticulate with 20 plumose setae, increasing in size towards middle, reaching twice length of endopod, endopod with internal process armed with 2 small simple setae at tip; exopod bi-articulated, distal article longer than proximal one, and with 18 plumose setae similar in arrangement to those on endopod.

Pleonites 5 and 6 (Fig. 3B) subequal in length; middle portion of pleonite 6 well produced between uropods, subacute.

Uropods (Fig. 3B) with rami subequal in length to pleonite 6, rami 2.5 times length of peduncle; peduncle with 3 setose setae on inner margin; rami subequal in length to each other; exopod bi-articulated, distal article twice length of proximal article, with 5 plumose setae on inner edge; exopod with 3 truncated terminal setae; endopod with thick truncated terminal seta.

Etymology.—This species is named in honor of Iorgu Petrescu, a crustacean taxonomist who has made numerous contributions to cumacean systematics, and has described other species found in Malaysia.

Remarks.—*Eocuma petrescui* is closely related morphologically to both *E. ferox* (Fischer, 1872), and *E. taprobanicum* (Calman, 1904). Differences among the three species are summarized in Table 1. Simi-

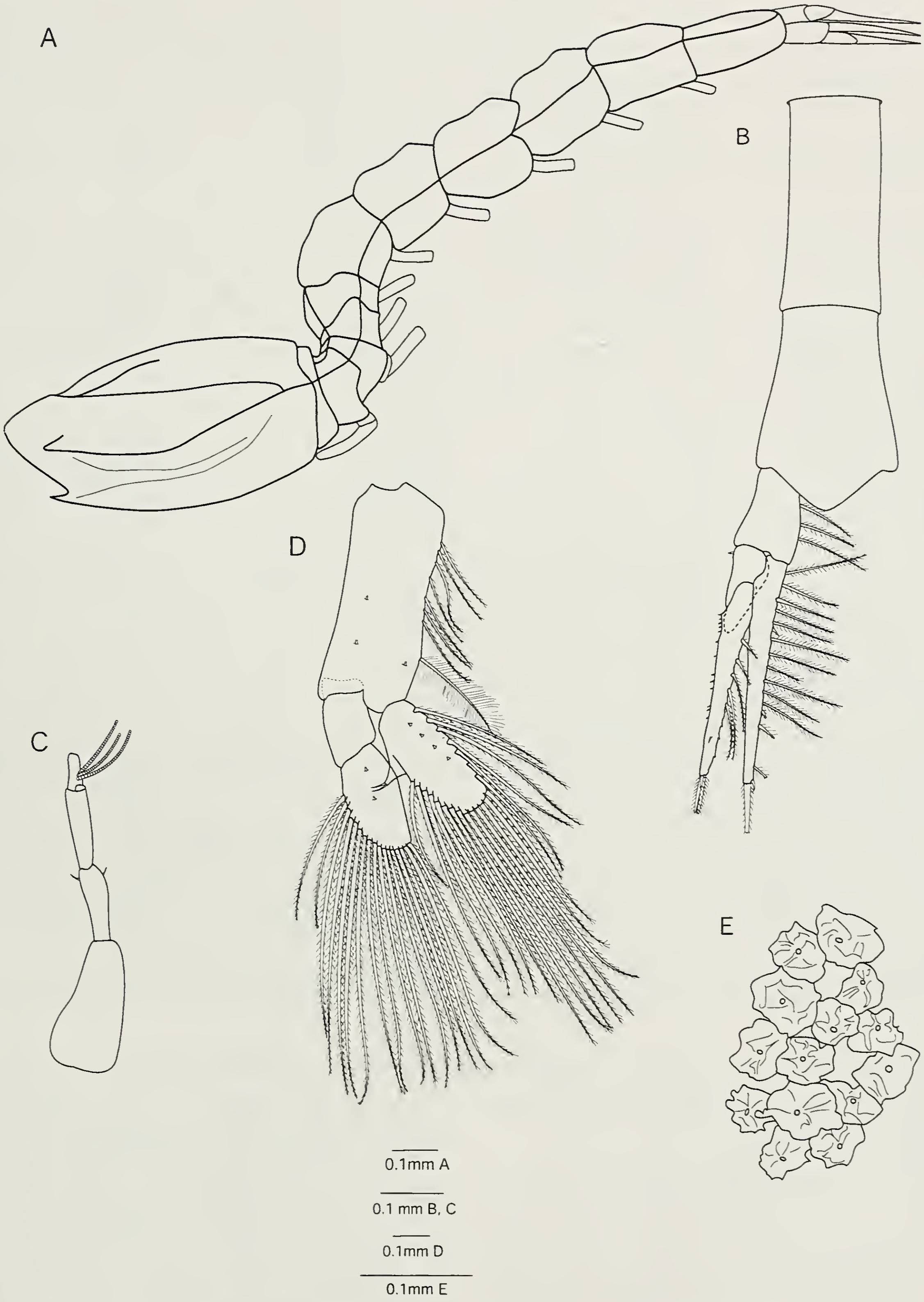

Fig. 3. *Eocuma petrescui,* new species. Paratype ♂ A, latero-ventral view, body length 5.9 mm: B, pleonites 5, 6 and uropods: C, antenna 1; D, pleopod: E, portion of textured carapace surface.

larities among all three species include (1) lateral horns on the carapace; (2) a hidden ischium in maxilliped 1; (3) a distal projection of basis and merus on maxilliped 3; (4) a distally expanded carpus and propodus on maxilliped 3; (5) row of setae on ventral side of maxilliped 3; (6) setae on margin of basis projection on maxilliped 3; (7) a convex projection on the basis of peraeopod 1; (8) an ischium missing on peraeopod 2; (9)

Table 1.—Morphological differences among *Eocuma petrescui,* new species, *E. ferox,* and *E. taprobanicum.*

Character	*E. petrescui* new species	*E. ferox* (Fischer, 1872)	*E. taprobanicum* (Calman, 1904)
Frontal lobe	1/3 size of carapace	1/3 size of carapace	1/4 size of carapace
Carapace shape when dorsal	smooth outline, same width from anterior to posterior ends	smooth outline, same width from anterior to posterior ends	rippled outline anteriorly, medial portion expanded
Carapace ridges	lateral ridge leading into posterior transverse ridge	no ridges present	lateral ridge leading into posterior transverse ridge
Antenna 1 main flagellum	uniarticulated	uniarticulated	biarticulated
Antenna 1 main flagellum	with 2 aesthetascs	with 2 aesthetascs	with 3 aesthetascs
Maxilliped 1 carpus and propodus	slim	robust	slim
Maxilliped 1 endite	large	large	small
Maxilliped 2 ischium	small	absent	small
Maxilliped 3 basis	arcuate	geniculate	geniculate
Maxilliped 3 basis shape at tip	acute	acute	rounded
Maxilliped 3	sensory setae present on basis	sensory setae present on basis	no sensory setae on basis
Maxilliped 3 relative size of ischium	small	small	large
Pereopod 1 projection on basis	ventral	distal	semi-ventral
Pereopod 1	sensory setae on basis	sensory setae on basis	no sensory setae on basis
Pereopod 1 carpus and propodus length	less than 1.5 times length of merus	less than 1.5 times length of merus	greater than 2.5 length of merus
Pereopod 2 projection on merus	absent	absent	absent
Pereopod 3 article proportions	similar	dissimilar	similar
Pleonites 5 and 6 length	equal	pleonite 5 longer	pleonite 5 longer
Pleonite 6 ending	pointed	rounded	flat
Uropods anal plate	not visible	not visible	visible

rami of the uropods equal in length to pleonite 6; and, (10) uropod endopod equal in length to exopod.

The third species most similar to *Eocuma petrescui* is *E. spinifera* Gamo, 1967, known from in Japan. It differs from *E. petrescui* by (1) larger and more protruding lateral horns; (2) a more bulbous posterior portion of the carapace when viewed dorsally; (3) a dorso-distal projection on the basis of maxilliped 3 that extends beyond the merus; (4) several long setae emerging from the distal end of propodus on peraeopod 1; (5) an extremely small almost rudimentary peraeopod 2; and (6) longer basis on all peraeopods when compared proportionally with the other articles of the appendage. *E. spinifera* has (1) similar markings on the carapace; (2) similar proportions of articles and segmented setae on the antenna 1 on the female; (3) three aesthetascs on the proximal article of main flagellum of antenna 1 on the male; (4) a very similar maxilliped 3 both in proportions, and in location and form of setae; and, (5) setae at the tip of projection on maxilliped 3 and projection on peraeopod 1.

The only other *Eocuma* species that was found in Malaysia is *E. longicorne* (Calman, 1905). It differs from *E. petrescui* in (1) shape of carapace both laterally and dorsally; (2) projection of merus on peraeopod 2; (3) relative proportions of articles on antenna 1; (4) bunch of aesthetascs on main flagellum of antenna 1; and, (5) the shape in which pleonite six ends. It is similar to *E. petrescui* by (1) markings on the carapace; (2) lateral ridge and placement of connected lateral horns; (3) peraeopod 1 proportions, ventral projection and convex projection on basis; and, (4) proportions of pleonite 6, peduncle and rami of uropods.

The other geographically proximate congeners are: *E. affine* Calman, 1904; *E. gorgasiae* Mühlenhardt-Siegel, 1996; *E. kempi* Kurian, 1954; *E. latum* Calman, 1907; *E. longicorne* (Calman, 1907); *E. sarsii* (Kossmann, 1880); *E. sanguineum* Kurian and Radhadevi, 1983; *E. stellifera* Calman, 1907; *E. striatum* Kurian and Radhadevi, 1983; *E. travancoricum* Kurian, 1951. These taxa differ from *Eocuma petrescui* by: (1) proportion of the frontal lobe length in relation to the carapace; (2) absence of similar lateral and posterior transverse ridges; (3) shape and proportions of the carapace, peraeon, and abdomen; (4) proportions of the articles on peraeopod 1; and (5) shape of terminal portion of pleonite six. The congeners bear some similarities to *E. petrescui* by: (1) cuticle of integument hexagonally reticulated, (2) semi-ventral projection on the tip of basis of peraeopod 1; and (3) a convex projection on the lower ventral side of peraeopod 1 basis.

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Literature Cited

Calman, W. T. 1904. On the classification of the Crustacean Malacostraca.—Annals of the Magazine of Natural History 13:144–158.

———. 1905. The Cumacea of the Siboga Expedition.—Siboga Expedition Monograph 36:1–23.

———. 1907. On new or rare Crustacea of the order Cumacea from the collection of the Copenhagen Museum, part I. The families Bodotriidae, Vaunthompsoniidae, and Leuconidae.—Transactions of the Zoological Society of London 18: 1–58.

Gamô, S. 1967. Studies on the Cumacea (Crustacea, Malacostraca) of Japan. Part I. Publications of the Seto Marine Biological Laboratory 17:175–182.

Fischer, P. 1872. Catalogue des Crustacés podophtalmaires et Cirripides du département de la Gironde.—Actes de la Société Linneenne de Bordeaux 28:22–24.

Kossmann, R. 1880. Zoologische Ergebnisse einer ausgeführten Reise in die Küstengebiete des Rothem Meeres 2:88–90.

Kurian, C. V. 1951. The Cumacea of Travancore.—Bulletin of the Central Research Institute, University of Travancore, ser. C 2:77–118.

———. 1954. Notes on Cumacea (Sympoda) in the Zoological Survey of India.—Records of the Indian Museum 52:275–312.

———, A. Radhadevi. 1983. A new species of Cumacea (Crustacea, Peracarida) from Vizhinjom, Kerala, India. In P. A. John ed., Selected papers on Crustacea.—Trivandrum: 149–153.

Marcusen, J. 1894. Uber ein neues Cumaceen genus *Eocuma*, Fam. Cumidae, aus Japan.—SB Gesellschaft Naturforschender Freunde Berlin 7: 170–171.

Mühlenhardt-Siegel, U. 1996. Cumacea (Crustacea) from the Red Sea and the Maldives (Indian Ocean) in the collection of the Zoological Museum, Hamburg, with the description of seven new species and new genus.—Beaufortia 46 (7):105–134.

Petrescu, I. 1997. Nannastacidae (Crustacea: Cumacea) from the Malayan shallow waters (South China Sea).—Beaufortia 47 (4):109–151.

Radhadevi, A., C. V. Kurian. 1989. A collection of Cumacea from the South West and south east coasts of India.—Records of the Zoological Survey of India, Occasional Paper, number 121.

Scott, T. 1900–1901. Notes on Scottish cumaceans.—Annals of Scottish Natural History: 215–224.

Stebbing, T. R. R. 1913. Cumacea (Sympoda).—Das Tierreich. R. Fiedlander and Son. 21 pp.

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Metandania tordi, a new stegocephalid (Crustacea: Peracarida: Amphipoda) species from the Southern Ocean

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Abstract.—A new stegocephalid (Amphipoda) species, *Metandania tordi* n.sp, is described, belonging to the subfamily Andaniexinae Berge & Vader 2001. The new species is the first record of the genus in the southern hemisphere. In addition, a morphological trait, previously not figured nor described within this family, is presented: a process proximally on the inner anterior surface of the fourth coxa. This locking-process is interpreted, and named accordingly, to enhance a relative stabilization of the third and fourth coxae. A brief comparison of the morphology of the fourth coxa between all five stegocephalid subfamilies is presented.

As part of an ongoing project aiming at a taxonomic revision of the Antarctic amphipod fauna (The Antarctic Amphipodologist Network), we were provided, from the collections of the Smithsonian Institution, with an extensive material of stegocephalids from the Southern Ocean. Among that material, was the first record of *Metandania* Stephensen, 1925 from the Southern Hemisphere, a genus previously only known from the North Atlantic. In addition to four other genera of the subfamily Andaniexinae Berge & Vader, 2001 (*Andaniexis* Stebbing, 1906, *Andaniotes* Stebbing, 1897, *Parandaniexis* Schellenberg, 1929 and *Stegosoladidus* Barnard & Karaman, 1987), this is the fifth genus within the subfamily to be recorded from the Southern Ocean.

Methods

This study is based upon material from the Smithsonian Institution. All dissected appendages were mounted in polyvinyl-lactophenol, stained with rose-bengal. These appendages were drawn using a Leica compound microscope equipped with a drawing-tube, while the habitus-drawings were made using a Leica dissecting microscope. Mature and immature females were distinguished from males by the presence of oostegites. The classification of setae and setae-groups follows that of Berge (2001a). All scales attached to the figures are 0.1 mm unless otherwise stated.

Specimens prepared for SEM, were first sonicated for 7 seconds in order to remove mucus and debris from their surface. Then they were dehydrated through a series of acetone, 10 minutes in each, ranging from 70% up to 100% acetone. Specimens were then dried in a critical point dryer, before mounted on a stub and coated with gold.

Pereopod 4 of the holotype was damaged during dissection and is thus not figured (but see description of the new species below). Uropods 1 and 2 are illustrated on the habitus drawing (Fig. 4) only.

Symbols: A1–2: Antenna 1–2; IP: Inner plate; L: Labium; LBR: Labrum; LMND:

Left mandible; MX1: Maxilla 1; MX2: Maxilla 2; MXP: Maxilliped; P1–7: Pereopods 1–7; PLP: palp; ST: Setal teeth on the first maxilla; T: Telson; U1–3: Uropods 1–3.

Results and Taxonomy

Locking-process on the fourth coxa: Found exclusively within the Andaniexinae, some of its genera possess a projection proximally on the inside of the fourth coxa (Fig. 1). This projection is found in the four genera *Andaniotes* Stebbing, 1897, *Glorandaniotes* Ledoyer, 1986 (but see also Berge & Vader 2003), *Metandania* Stephensen, 1925 and *Stegosoladidus* Barnard & Karaman, 1987, and is absent in the remaining three genera of the subfamily (see Table 1). Although its function has not been observed, it is interpreted to function as a locking-process between the third and the fourth coxa plates. In all stegocephalid genera, the coxae-shield, as formed by coxae 3 & 4, is hard and contiguous, whereas the first two coxae are, in many genera, more flexible and not contiguous. In e.g., *Andaniexis* Stebbing, 1906, coxae 1–4 do not form a continuous shield, and the first coxal plate is in addition very short. In e.g., *Andaniotes,* on the other hand, coxa 1 is long and deep with coxae 1–4 forming a hard and continuous shield. However, in both these genera, as in all other stegocephalid taxa, there is a conspicuous overlap between the third and the fourth coxae. This overlap is enhanced by the concave anterior margin of coxa four (covering almost the entire length of the coxa, see Fig. 1B), in which the posterior margin of coxa 3 fits in. As can be seen in Fig. 2, this concave anterior margin of coxa 4 is present in *Andaniexis lupus* Berge & Vader, 1997, but not, in contrast to *Andaniotes linearis* (Fig. 1), the specially derived "locking-process". Thus, it appears that the "locking-process" is an additional process on the already three-dimensional inner side of the coxal plate, enhancing a more stable and rigid coxal-shield. Figure 3 gives an overview of the corresponding traits in three of the other subfamilies (presence of the anterior concave margin, but absence of a "locking-process"). The condition within the last subfamily, the Parandaniinae Berge & Vader, 2001, is very much similar to that of *Andaniexis lupus* (Fig. 2).

Subfamily Andaniexinae Berge & Vader, 2001

Genus *Metandania* Stephensen, 1925

Metandania tordi, new species

Figs. 4–6

Holotype: Female, 8 mm. 55°00–03′S, 58°51–57′W, 4th of December 1962 on the Eltanin, cruise 6 station 350 (depth unknown). Collected with a Menzies Trawl.

Paratype: Male, 6 mm. 57°59′–58°00′S, 70°53′–71°00′W, 3rd of December 1962 on the Eltanin, cruise 5 station 311, depth 3911–4099 m. Collected with a Menzies Trawl.

Etymology: This species is named after the first author's son Tord Raddum Berge.

Diagnosis: *Metandania tordi* is separated from its congeners by the combination of 1) antennae 2 peduncle article 4 about as long as article 5, and 2) biarticulate outer ramus on the third uropod.

Description:

Head: Head retractable under pereonite 1. Rostrum rudimentary.

Antennae: Antenna 1 accessory flagellum shorter than flagellum article 1, uniarticulate. Antenna 2 peduncle article 3 short (Fig. 5 A2: only articles 3–5 of the peduncle figured), about as long as broad. Peduncle article 4 as long as article 5.

Epistome: Epistome laterally smooth. Epistomal plate (medial keel) produced and conspicuous.

Mouthparts: Mouthparts not elongate.

Mandibles with incisors transverse, partly toothed. Left lacinia mobilis present, strongly toothed and distally not produced.

Maxilla 1 palp articulation absent, distally with short robust setae. Outer plate distally rounded, ST in a 6/3 arrangement with

Fig. 1. *Andaniotes linearis* Barnard, 1932. Pereopod 4 with coxa, gill and oostegite: arrow indicating the locking-process on the inner anterior margin of the coxa. A: locking-process; B: anterior concave margin.

Table 1.—Overview of the morphology of coxa four among stegocephalid subfamilies, with special emphasis on the genera within the subfamily Andaniexinae. Classification follows that of Berge & Vader 2001.

	Coxae 1–4	Coxa 4 anterior margin	Locking-process
ANDANIEXINAE			
Andaniexis	not continuous	convex	absent
Andaniotes	continuous	convex	present
Glorandaniotes	continuous	convex	present
Metandania	continuous	convex	present
Mediterexis	not continuous	convex	absent
Paradaniexis	not continuous	convex	absent
Stegosoladidus	continuous	convex	present
ANDANIOPSINAE	not continuous	convex	absent
BATYSTEGOCEPHALINAE	continuous	weakly convex	absent
PARANDANIINAE	continuous	weakly convex	absent
STEGOCEPHALINAE	continuous	convex	absent

two parallel rows: First row with ST 1–5 present, ST 6 absent and ST7 present. Second row with ST A–C present. Inner plate with shoulder weakly developed, setae pappose.

Maxilla 2 outer plate not gaping and geniculate, setae distally straight. Inner plate with setae-rows A and B separated. Row B with the 3 first setae differentiated from the other setae. Row C present, row D absent.

Maxilliped palp 4-articulate, article 2 distally unproduced. Articles 1–3 with long plumose setae. Inner plate with inner corner weakly produced distally, 3 nodular setae present. Outer plate with inner and outer setae-row present, both with short simple setae. Distal setae-group absent.

Labrum about as long as broad, left lobe reduced.

Labium distally broad, distal finger absent.

Pereopods and coxae: Coxal plates and basis of the pereopods covered with short simple setae. Coxae 1–3 contiguous.

Pereopod 1 coxal plate about as deep as basis, basis anterior margin weakly expanded. Pereopod 1 propodus subovate, posteriorly without submarginal row of setae.

Pereopod 2 ischium not elongate, distal posterior margin with plumose setae. Propodus subrectangular.

Pereopod 3 basis anterior margin distally with short simple setae. Merus longer than carpus, anterior margin with short robust setae. Carpus subequal in length to propodus. Carpus and propodus anterior margins with short robust setae.

Pereopod 4 coxa locking-structure present. Basis without long setae, distally with plumose setae on anterior and posterior margins. Ischium with long plumose setae on distal posterior margin.

Pereopod 5 basis unexpanded, distal anterior and posterior margins with short simple setae. Merus longer than carpus, anterior margin with short robust setae. Carpus shorter than propodus. Carpus and propodus anterior margins with short robust setae.

Pereopod 6 basis posteriorly expanded, medially with a row of long plumose setae. Posterior margin of basis smooth.

Pereopod 7 conspicuously different from pereopod 6. Basis posteriorly serrate, medially with a row of short simple setae.

Oostegites and gills: Gills present on pereopods 2–7. Oostegites on pereopods 2–5.

Pleonites: Pleonites 1–3 dorsally smooth. Epimeral plate 3 weakly produced and rounded posteriorly, serrations absent.

Urosome: Articulation between urosomites 2 and 3 present. Uropod 1 rami with robust setae on outer and inner margin. Uropod 2 inner ramus with robust setae on outer and inner margin, outer ramus with robust setae on outer margin. Uropod 3 pe-

Fig. 2. *Andaniexis lupus* Berge & Vader, 1997. Pereopod 4 with coxa, gill and oostegite.

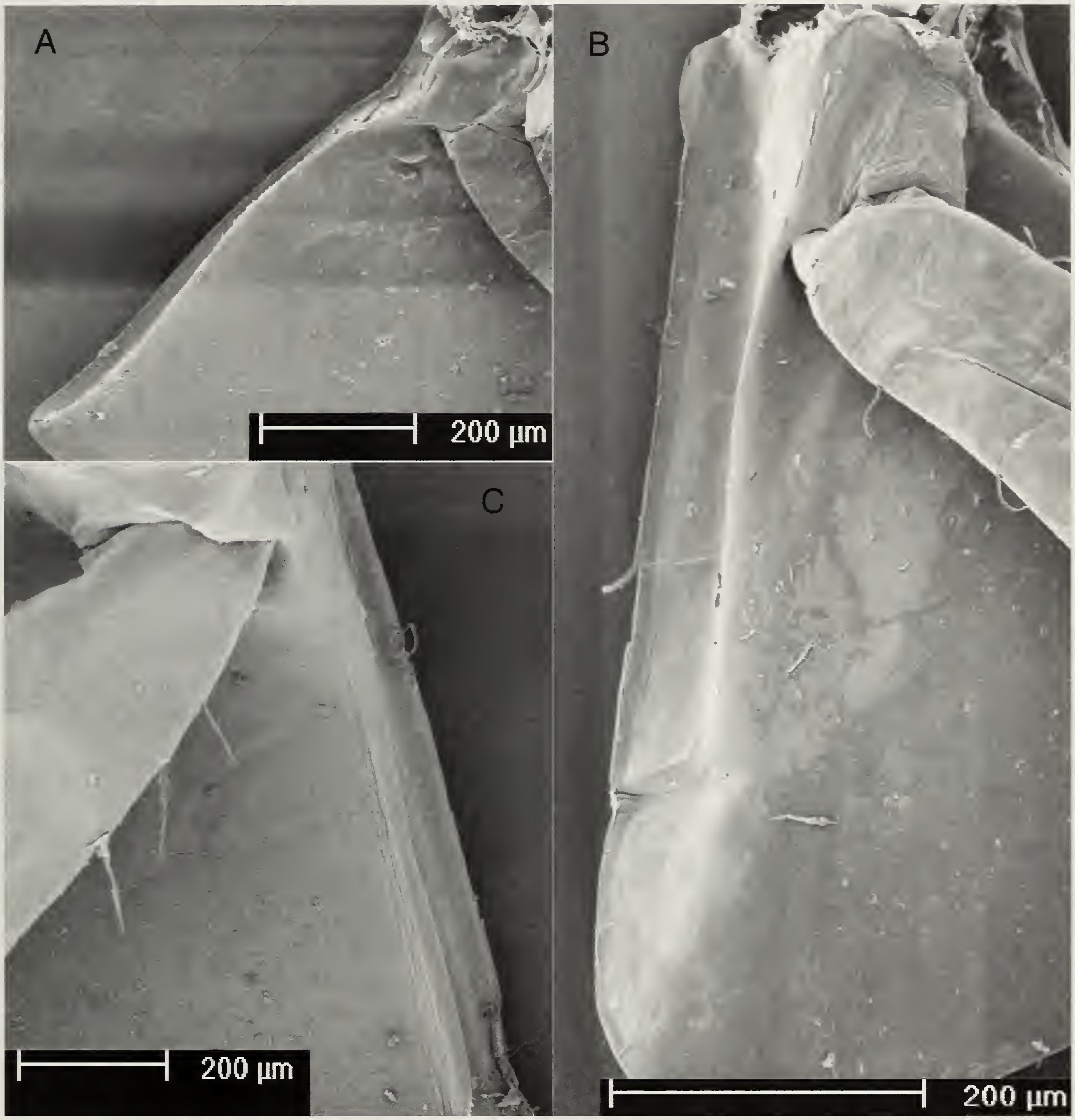

Fig. 3. A: *Tetradeion crassum* (Chilton, 1883), subfamily Stegocephalinae. Inner anterior margin of coxa 4; B: *Andaniopsis nordlandica* (Boeck, 1871), subfamily Andaniopsinae. Inner anterior margin of coxa 4; C: *Bathystegocephalus globosus* (Walker, 1909), subfamily Bathystegocephalinae. Inner anterior margin of coxa 4.

duncle longer than telson, outer ramus 2-articulate. Outer ramus with robust setae on outer margin, inner ramus with robust setae on outer and inner margins.

Telson cleft and rounded distally, submarginal setae on apex of each lobe present.

Males: No sexual dimorphism observed.

Remarks: This is the third species that is assigned to the genus *Metandania* since it was re-established as a valid taxon by Berge (2001b:825). Despite the taxonomical problems that still are associated (Berge 2001b:829) with its type species, *M. islandica,* (first of all there are reasons to doubt that the two recognized specimens in fact belong to the same species), the genus appears as a morphologically closely related group. Especially the morphology of the left mandible is a feature that links the three

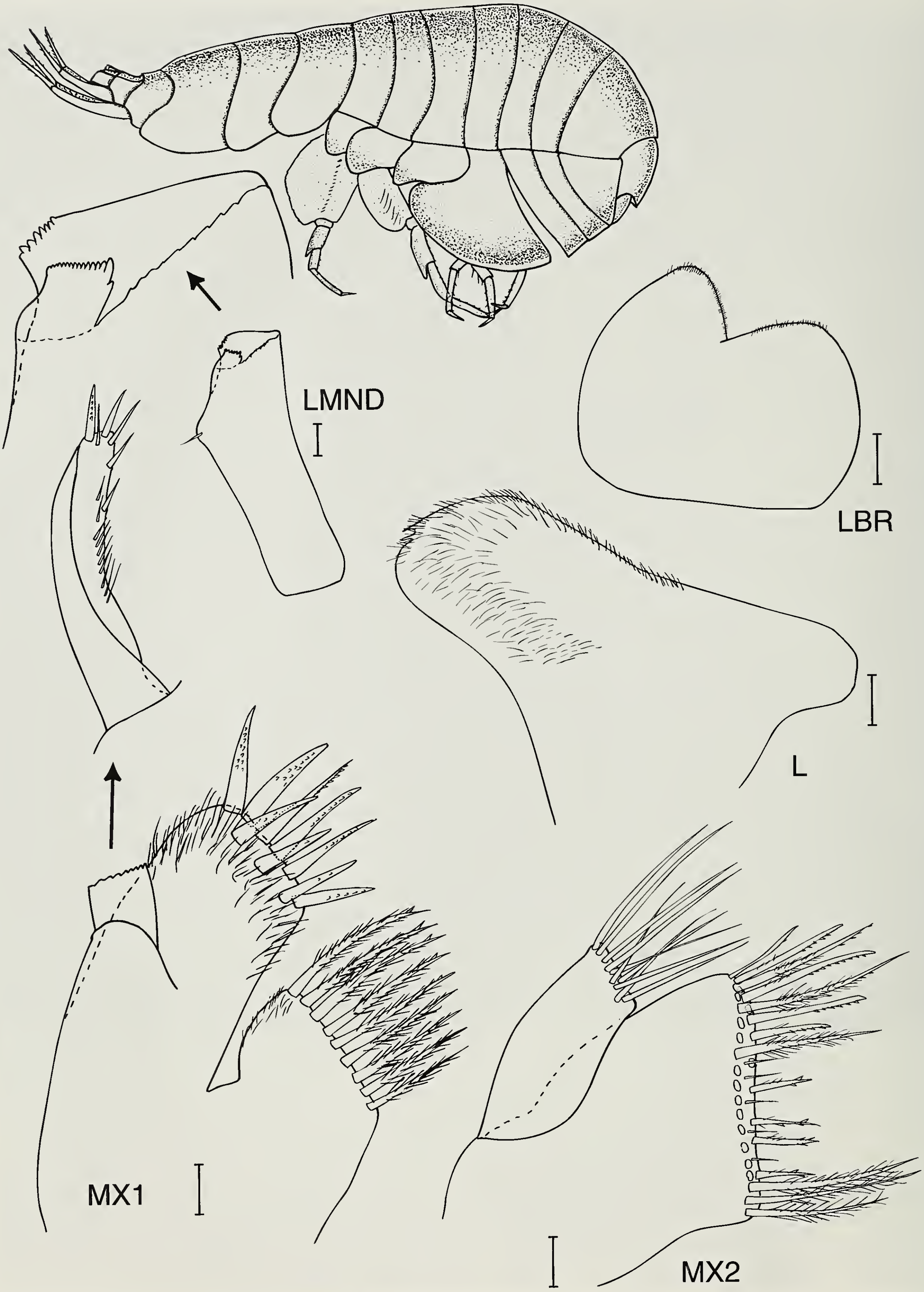

Fig. 4. *Metandania tordi* n.sp. Holotype.

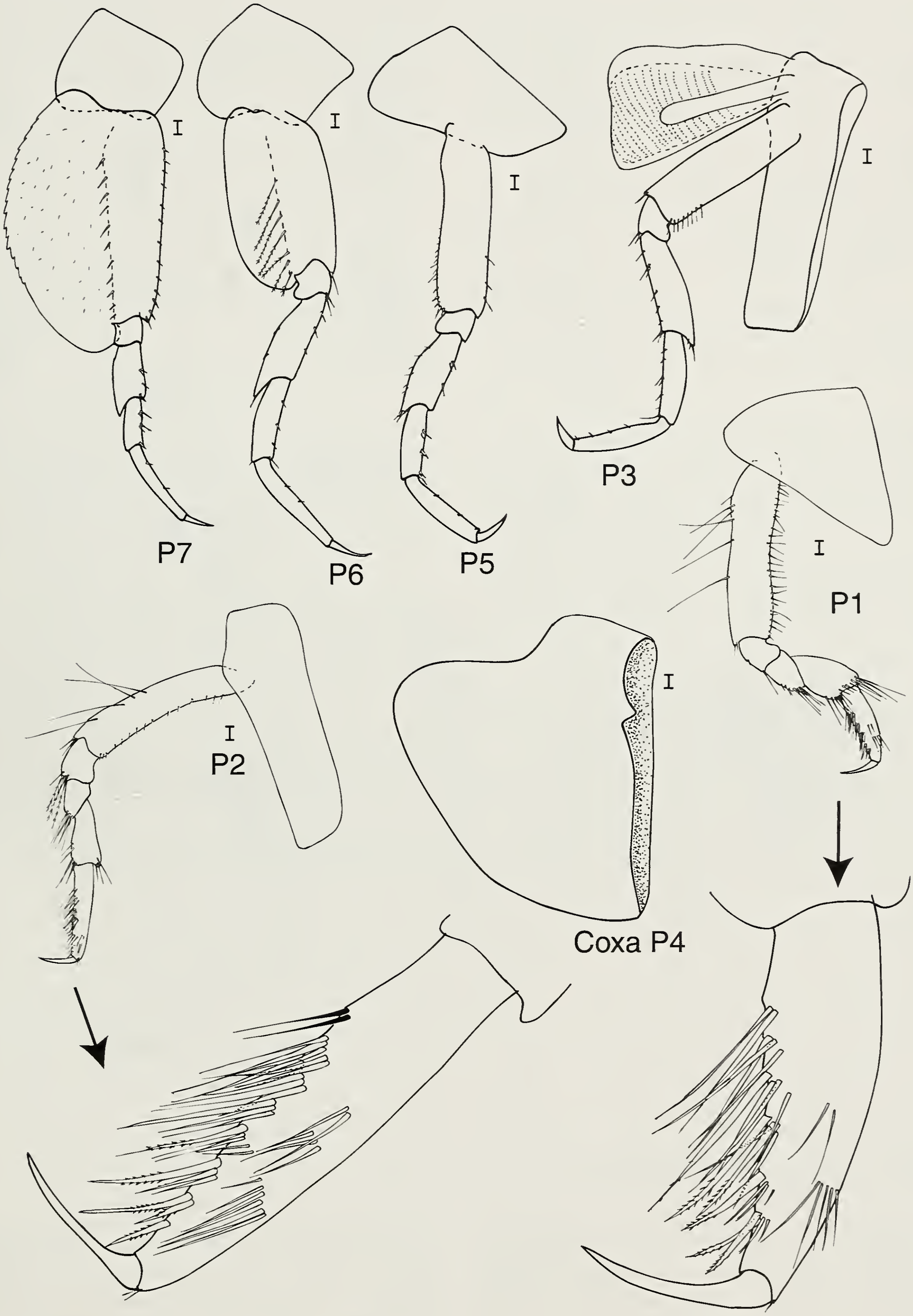

Fig. 5. *Metandania tordi* n.sp. Holotype.

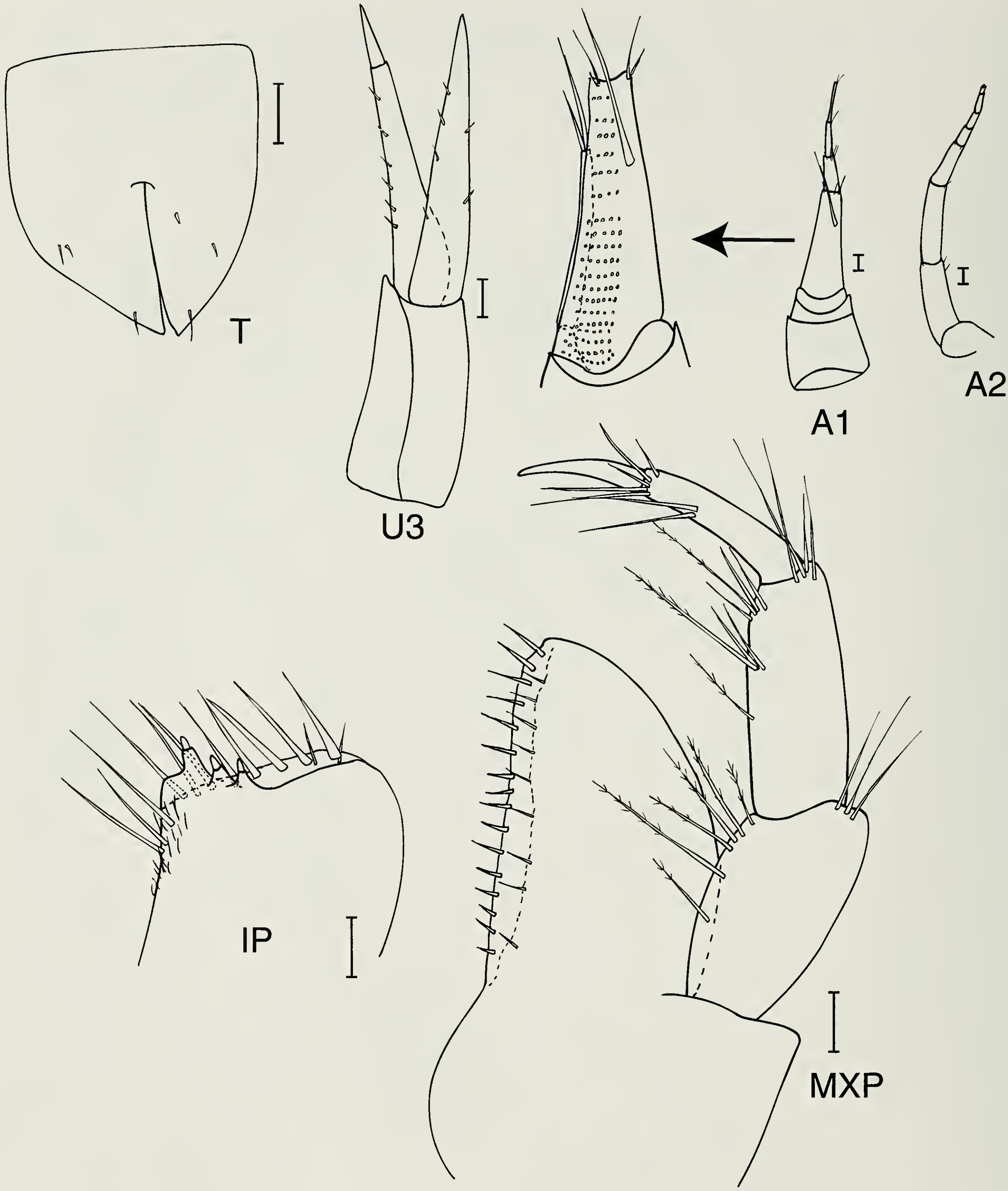

Fig. 6. *Metandania tordi* n.sp. Holotype.

recognized taxa together: the incisor is transverse and smooth, but toothed distally on the inner corner. Also the lacinia mobilis is toothed and much stronger than the typical character state otherwise found in the subfamily Andaniexinae. The present species is thus a typical member of its genus, possessing all the characteristics of the mandible as described above. Furthermore, it has a long and cleft telson, uni-articulate palp of the first maxilla and laterally smooth (vs. produced) epistome, all character states that are diagnostic for the genus.

Acknowledgments

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Literature Cited

Barnard, J. L., & G. S. Karaman. 1987. Revisions in classification of gammaridean Amphipoda (Crustacea) part 3.—Proceedings of the Biological Society of Washington 100:856–875.

Barnard, K. H. 1932. Amphipoda.—Discovery Reports 5:1–326.

Berge, J. 2001a. Revision of Stegosoladidus Barnard & Karaman, 1987 (Crustacea: Amphipoda: Stegocephalidae); redescription of two species and description of three new species.—Journal of Natural History 35:539–571.

———. 2001b. Description of two new species of Stegocephalidae (Crustacea: Amphipoda): Metandania wimi and Stegocephalina trymi.—Sarsia 86:213–220.

———, & W. Vader. 1997. Atlantic and Mediterranean species of the genus Andaniexis Stebbing (Amphipoda: Stegocephalidae).—Journal of Natural History 31:1429–1455.

———. 2001. Revision of the amphipod (Crustacea) family Stegocephalida.—Zoological Journal of the Linnean Society 133:531–592.

———. in press. Description of two new *Glorandaniotes* species (Crustacea: Peracarida: Amphipoda: Stegocephalidae: Andaniexinae).—Journal of Crustacean Biology 23(3):633–643.

Boeck, A. 1871. Crustacea Amphipoda borealia et arctica.—Videnskabs-Selskabets Forhandlinger for 1871, 83–280.

Chilton, C. 1883. Further additions to our knowledge of the New Zealand Crustacea.—Transactions and Proceedings of the New Zealand Institute 15:69–86.

Ledoyer, M. 1986. Crustacés Amphipodes Gammariens. Familles des Haustoriidae à Vitjazianidae.—Faune de Madagascar 59(2):599–1112.

Schellenberg, A. 1929. Abyssale und Pelagische Gammariden.—Bulletin of the Museum of Comparativ Zoology LXIX (9):193–201.

Stebbing, T. R. R. 1897. Amphipoda from the Copenhagen Museum and other sources.—Transactions of the Linnean Society of London Zoology 7:25–45.

———. 1906. Amphipoda I. Gammaridea.—Das Tierreich 21:806 pp.

Stephensen, K. 1925. Crustacea Malacostraca. VI. (Amphipoda. II.).—The Danish Ingolf-Expedition 3(9):101–178.

Walker, A. O. 1909. Amphipoda Gammaridea from the Indian Ocean, British East Africa, and the Red Sea.—Transactions of the Linnean Society of London Zoology 12:323–344.

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A new species of *Stygonitocrella* (Crustacea: Copepoda: Ameiridae), the first report of the genus in North America

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Abstract.—A new species of ameirid harpacticoid copepod, *Stygonitocrella sequoyahi,* was collected in streambeds in Arkansas and Oklahoma, U.S.A., and is described herein. The new taxon shares with its congeners the 1-segmented endopodite of leg 4, but differs in having much longer caudal rami, as well as in the major armament of the swimming legs. Other species of *Stygonitocrella* are known from freshwater hypogean habitats in Europe, Central Asia, Argentina, and Cuba. This is the first record of a member of the genus from North America. No type species has ever been designated for the genus *Stygonitocrella.* In order to make the genus name available, we designate *Stygonitocrella montana* (Noodt) as the type species, and provide a diagnosis for the genus.

Collections from the hyporheic zones of streams in the Ozark region of Arkansas and Oklahoma, south-central U.S.A., resulted in the discovery of a previously undescribed species assignable to *Stygonitocrella,* a genus proposed by Petkovski (1976). The ameirid harpacticoid copepods which have been assigned to this genus have been reported from freshwater hypogean habitats in Europe, Central Asia, the Ryukyus, Argentina, and Cuba. The species described herein constitutes the first record of the genus from North America. We describe the species and provide information on its habitat.

Eleven freshwater subterranean species of the family Ameiridae are presently included in *Stygonitocrella.* Petkovski (1976) revised the genus *Nitocrella* Chappuis, 1924, and proposed the erection of a new genus *Stygonitocrella* for species with much-reduced segmentation of the endopodites of swimming legs 2–4, i.e., with combinations of 2,2,1; 2,1,1; or 1,1,1 segments in the endopodites of legs 2–4 respectively. As Petkovski (1976) noted, all the species then known have short conical caudal rami, about 1–2 times longer than wide. The few species described since also share this feature. The species are, as originally assigned by their authors: *Nitocrella dubia* Chappuis, 1937, from Spain; *Nitocrella karamani* Petkovski, 1959, from Yugoslavia (now Macedonia, near Skopje); *Nitocrella montana* Noodt, 1965, from Argentina; *Nitocrella ljovuschkini* Borutsky, 1967, from Transcaucasia; *Nitocrella colchica* Borutsky & Mikhailova-Neikova, 1970, from West Georgia; *Nitocrella tianschanica* Borutsky, 1972, from Kirghizstan; *Nitocrella orghidani* Petkovski, 1973, from Cuba; *Nitocrella pseudotianschanica* Štěrba, 1973, from Afghanistan; *Nitocrella djirgalanica* Borutsky, 1978, from Kirghizstan; *Stygonitocrella guadalfensis* Rouch, 1985, from Spain; and *Stygonitocrella petkovskii*

Pesce, 1985, from Lesbos, Greece. Another species, *Nitocrella insularis* Miura, 1962, from the Ryukyu Islands was included in *Stygonitocrella* by Petkovski (1976), but was transferred from *Stygonitocrella* to a new genus *Neonitocrella* by Lee & Huys (2002).

Petkovski (1976) did not designate a type species for the genus *Stygonitocrella,* nor has any subsequent investigator done so. Since definite type fixation by original designation or indication is a mandatory requirement for the availability of generic names published after 1930 (ICZN 1999 Art. 13.3), it follows that the name *Stygonitocrella* is unavailable. In order to maintain nomenclatural stability, we propose to re-establish *Stygonitocrella* as a new name, taking the date and authorship of the present paper. A similar action was taken by Galassi et al. (1999) in the case of *Nitocrellopsis,* another genus defined by Petkovski (1976), which now takes the authorship Galassi, De Laurentiis & Dole-Olivier, 1999.

Unfortunately, of the species originally included by Petkovski in the genus, the type material of several (*S. dubia, S. karamani, S. orghidani*) no longer exists. To satisfy the criteria both of available and accessible material and an accurate published description, we propose *S. montana* as the type species, and provide a diagnosis for the genus. Since species-group names must be published in combination with a generic name, but the latter need not be valid or even available (ICZN 1999 Art. 11.9.3.1), the unavailability of Petkovski's (1976) generic name has no implications for the species of *Stygonitocrella* described since 1976, other than that they will be treated as new combinations.

Methods

Samples were collected from wells driven into the stream substrates. Hyporheic samples, pumped from the wells with a hand pump, were concentrated with a 63 μm mesh net and preserved in 5% formalin. Detailed information on the sampling method and habitat parameters in Sager Creek and Baron Fork was provided by Hunt & Stanley (2000). Station data and information on the hydrology and water chemistry of all the streams were presented by Hunt (1999). Sorting, facilitated by the addition of rose bengal stain, was done using an Olympus dissecting microscope. For morphological examination, specimens were transferred to glycerin and then to lactic acid. All the specimens were extremely fragile, and the appendages broke easily during dissection. To compensate for this fragility, the habitus and larger appendages were drawn from whole specimens in lactic acid under supported cover glasses. Mouthparts were drawn and details of all appendages were verified and in some cases redrawn after the specimens were dissected and permanently mounted in CMC-10® (Masters Chemical Co., Wood Dale, Illinois, U.S.A.) with a little chlorazol black E stain added. Drawings were made using a Wild M30® compound microscope fitted with a drawing tube, at magnifications of 600× or 1000×. Details were verified using a Leica DMLB® microscope equipped with phase-contrast and differential interference contrast illumination. The specimens were deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Order Harpacticoida

Family Ameiridae Monard, 1927

Genus ***Stygonitocrella,*** new genus

Diagnosis.—Ameiridae. Antennule of female 8-segmented, segment 1 not elongated. Antennule of male geniculate. Antenna with basis and 1-segmented exopodite bearing 2 or 3 setae. Medial spine on leg 1 basipodite modified in male. Basipodites of legs 1–4 all with lateral (outer) spine or seta. Exopodites of legs 1–4 and endopodite of leg 1 3-segmented. Endopodites of legs 2–4 with 2,2,1; 2,1,1; or 1,1,1 segments respectively, or leg 4 endopodite reduced to tiny nub without seta. Baseoendopodite and exopodite of leg 5, if present, either distinct or fused. Caudal ramus short, about 1–1.5 times longer than wide, or long and cylindrical. Lacking eye and pigment.

Type species.—*Stygonitocrella montana* (Noodt, 1965), new combination.

Additional species.—*Stygonitocrella colchica* (Borutsky & Mikhailova-Neikova, 1970), new combination; *S. dubia* (Chappuis, 1937), new combination; *S. djirgalanica* (Borutsky, 1978), new combination; *S. guadalfensis* (Rouch, 1985), new combination; *S. karamani* (Petkovski, 1959), new combination; *S. ljovuschkini* (Borutsky, 1967), new combination; *S. petkovskii* (Pesce, 1985), new combination; *S. pseudotianschanica* (Štěrba, 1973), new combination; *S. tianschanica* (Borutsky, 1972), new combination; and *S. sequoyahi,* new species.

Species incertae sedis.—*Stygonitocrella orghidani* (Petkovski, 1973), new combination.

Stygonitocrella sequoyahi, new species
Figs. 1–4

Material examined.—Holotype ♀, dissected on slide (USNM 288040); allotype ♂, dissected on slide (USNM 288041); paratypes: 1 ♀, dissected on slide, and 1 ♀ and 4 copepodids (USNM 288042), preserved in 70% ethanol, all from depths of 5–20 and 60–75 cm at 2 stations in streambed of Sager Creek, Benton Co., Arkansas, about 36°12′N, 94°35′W, 29 Jul 1997, collector G. W. Hunt. Additional paratypes, all ethanol-preserved: 1 ♀, 2 ♂♂, and 4 copepodids (USNM 288043), from 30–45 cm depth in streambed of Snake Creek, Cherokee Co., Oklahoma, about 36°09′N, 95°08′W, 27 Jun 1996, collectors G. W. Hunt and E. H. Stanley; 8 ♀♀, 5 ♂♂, and 5 copepodids (USNM 288044), from several depths combined in streambed of Baron Fork, Cherokee Co., Oklahoma, about 35°55′N, 95°51′W, 2 Jan 1997, collector G. W. Hunt.

Female.—Length of holotype (measured from anterior margin of cephalosome to apex of caudal ramus and excluding caudal setae) 0.56 mm; range of lengths of paratypes from 0.444–0.548 mm, median length 0.470 mm ($n = 11$). Habitus (Fig. 1A, B, drawn extended in lactic acid) slender, prosome dorsoventrally compressed. Intercalary membranes broad, i.e., body quite flexible. Prosome ornamented only with scattered hairs (setules). Cephalic shield (Fig. 1A, C) with irregularly round dorsal integumental window. Pedigers 2–4 each with 1 round integumental window on each side. Genital double-somite (Fig. 1A,D), both original somites completely fused, with no trace of previous separation. Genital field (Fig. 1D) short, copulatory pore located at anterior 1/4 of genital double-somite. Leg 6 (Fig. 1D) consisting of tiny plate bearing 1 hairlike seta. Genital double-somite and next urosomite each with lateroventral row of tiny spinules near posterior border; following urosomite with lateral row of similar spinules near posterior border. Anal somite (Fig. 1A, D, E) with few rows of tiny spinules near anteroventral border, and larger spinules along posterior border. Anal operculum (Fig. 1E) crescentic, reaching approximately to posterior end of anal somite, bordered with tiny teeth. Caudal ramus (Fig. 1A, D, E) about 5 times longer than wide, with 6 main setae, tiny accessory seta next to anterior lateral (outer) seta, and few small spines at bases of posterior lateral, dorsal, and medialmost (innermost) terminal setae. Dorsal seta longer than ramus, doubly articulated at base. Medialmost terminal seta shorter than lateralmost terminal seta, and with slightly enlarged base. Medialmost terminal seta about as long as urosome, without breaking plane.

Rostrum (Fig. 1C) short, broad, and continuous with cephalic shield.

Antennule (Figs. 1A, 2A) longer than cephalosome, 8-segmented. Segments (indicated by Roman numerals) with numbers of setae (indicated by Arabic numerals) and aesthetascs (ae) as follows: I (1), II (6), III (6), IV (3 + ae), V (1), VI (2), VII (3), VIII

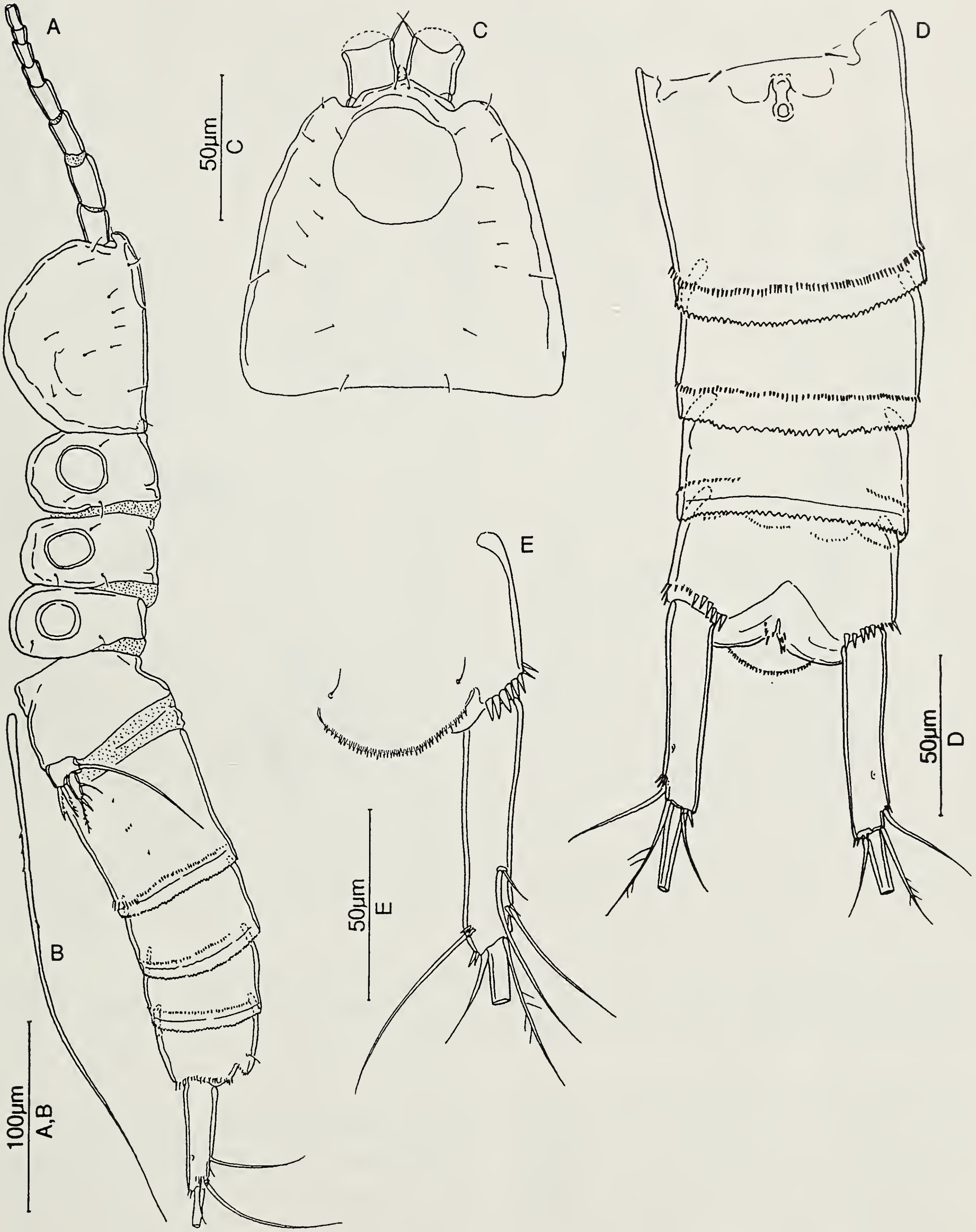

Fig. 1. *Stygonitocrella sequoyahi,* new species, female, holotype (USNM 288040). A, Habitus, left lateral; B, Middle terminal caudal seta; C, Cephalosome, dorsal; D, Urosome (somite bearing leg 5 omitted), ventral; E, Anal somite and right caudal ramus, dorsal.

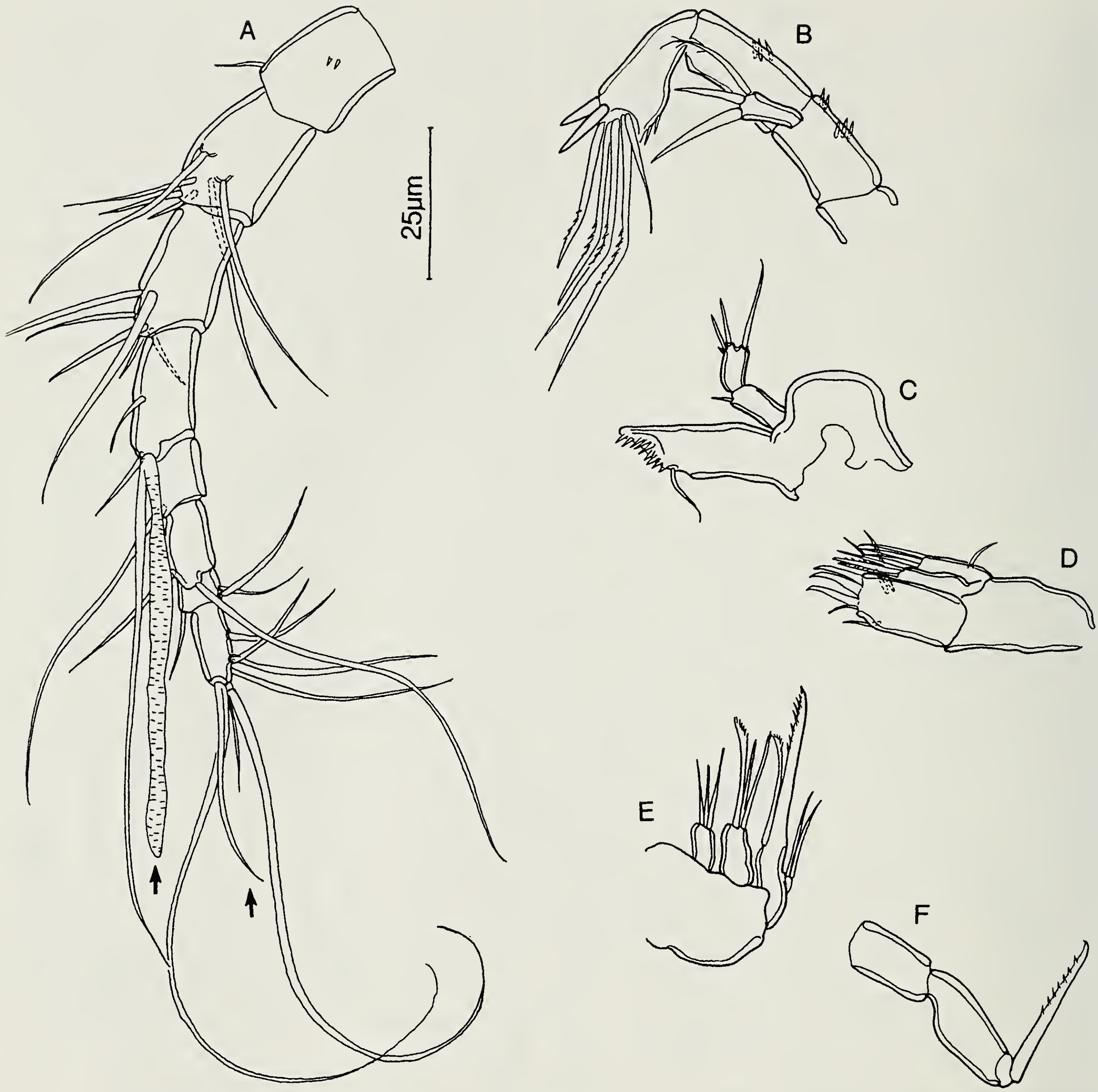

Fig. 2. *Stygonitocrella sequoyahi*, new species, female; A, B, holotype (USNM 288040), C–F, dissected female paratype (USNM 288042). A, Antennule (aesthetascs indicated by arrows); B, Antenna; C, Mandible; D, Maxillule; E, Maxilla; F, Maxilliped. All figures to same scale.

(7 + ae). Aesthetasc of segment IV long and wide, aesthetasc of segment VIII slender (aesthetascs indicated by arrows in Fig. 2A).

Antenna (Fig. 2B) with basis; suture between basis and endopodite complete on both sides. Antennal exopodite 1-segmented, bearing 1 setiform and 2 spiniform elements. Segment 1 of endopodite with few spinules along inner margin; segment 2 with few spinules, 2 socketed spines, and 5 terminal setae, 4 of these setae geniculate.

Mandible (Fig. 2C) with 2-segmented palp, proximal segment with 1, distal segment with 3 setae and 1 tiny spinule.

Maxillule (Fig. 2D), precoxal arthrite with 3 terminal spines and 2 lateral and 2 surface setae. Coxa and basis each with 3 terminal setae. Exopodite represented by tiny nodule bearing 1 seta.

Maxilla (Fig. 2E), syncoxa with 2 endites bearing 3 setae each, 1 seta on distal endite modified with brushlike tip. Allobasis extended into strong claw bearing 1 modified seta; endopod 1-segmented, bearing 2 setae.

Fig. 3. *Stygonitocrella sequoyahi,* new species, female; A–D, holotype (USNM 288040), E, dissected paratype (USNM 288042). A, Leg 1; B, Leg 2; C, Leg 3; D, Leg 4; E, Leg 4 endopodite; F, Leg 5. All figures to same scale.

Maxilliped (Fig. 2F) prehensile, basis and endopodal segment without ornamentation, terminal claw long, slender, and serrate.

Legs 1–4 (Fig. 3A–E), exopodites of all legs and endopodite of leg 1 3-segmented. Endopodites of legs 2 and 3, 2-segmented, endopodite of leg 4, 1-segmented. Couplers (intercoxal sclerites) broad, without ornamentation. Leg 1 basipodite with small spine on anterior surface of distomedial (inner) corner. Leg 1 exopodite segment 2 with lateral (outer) spine. Medial setae of legs 1–4 exopodite 2, leg 3 endopodite 1, leg 4 exopodite 3, and terminal seta of leg 4 endopodite spiniform. Formula for chaetotaxy as follows:

	Exopodite	Endopodite
Leg 1	0.1.022	1.0.030
Leg 2	0.1.022	1.010
Leg 3	0.1.021	1.010
Leg 4	0.1.121	010

Leg 5 (Fig. 3F) with 2 short spiniform setae on medial expansion of baseoendopodite; outer basal seta long and slender. Exopodite ovoid, with 2 terminal and 2 lateral setae, middle 2 setae shorter and slightly thicker than others. No ornamentation visible on surface of leg.

Male.—Length of allotype 0.460 mm, lengths of paratypes from 0.432–0.552 mm (median = 0.466 mm, $n = 7$). Habitus similar to female except for normal sexual dimorphism in genital segments and geniculate antennules. Urosomites 3–5 (Fig. 4A) each with continuous lateroventral row of tiny spinules near posterior border. Anal somite and anal operculum (Fig. 4B) as in female. Caudal ramus (Fig. 4A, B) about 5.7 times longer than wide; caudal setae as in female, except dorsal seta with 3 basal segments.

Antennule (Fig. 4C, D) geniculate, 9-segmented, segment 5 appearing to be composed of 2 partly fused segments. Broad aesthetasc present on segment 5 and narrow aesthetasc on segment 9 (aesthetascs indicated by arrows in Fig. 4C). Number of elements on each segment as follows: I (0), II (7), III (6), IV (1), V (6 + ae), VI (2), VII (1 + spinous process), VIII (3), IX (6 + ae).

Antenna as in female, except exopodite (Fig. 4E) with 3 slender setae.

Mandible, maxillule, maxilla, and maxilliped as in female.

Legs 1–4 (Fig. 4F–J) with same segmentation and major armament as in female. Leg 1 basipodite with modified spine on mediodistal corner (Fig. 4F, G). Some setae different from corresponding setae of female: particularly in legs 2 and 3, terminal setae of endopodites stouter and more spiniform, and medial setae of exopodite segment 2 and terminal setae of exopodite 3 thinner and more thickly plumed.

Leg 5 (Fig. 4A) with baseoendopodites partly fused at median line, each bearing 2 spiniform setae. Exopodite ovoid, with 2 medial, 1 terminal, and 1 lateral setae plus lateral hairlike setule.

Leg 6 (Fig. 4A) consisting of wide plate bearing 1 seta on free border.

Type locality.—Sager Creek, Benton County, Arkansas, U.S.A., about 36°12′N, 94°35′W.

Etymology.—The species name honors the great educator and inventor of the Cherokee Indian alphabet, Sequoyah (George Gist).

Discussion and comparisons.—According to our diagnosis, which is based mainly on the concept of Petkovski (1976), members of the genus *Stygonitocrella* are separable from other ameirids mainly by the reduction in numbers of segments of legs 2–4, and particularly by the 1-segmented endopodite of leg 4. However, features of some of the species indicate that the genus as presently composed may well be polyphyletic. For instance, most species for which both sexes are known do not differ in setation of legs 1–4 between the sexes, but *S. tianschanica* does, according to the description by Borutsky (1972). Unlike its congeners, *S. orghidani* has the leg 5 exopodite and baseoendopodite fused, bearing only the lateral baseoendopodite seta in both sexes. According to Borutsky (1978), the leg 5 is lacking in both sexes of *S. djirgalanica.* We doubt whether *S. tianschanica, S. orghidani,* or *S. djirgalanica* are appropriately included in *Stygonitocrella.*

The systematic relationships among the species that are presently assigned to *Stygonitocrella* cannot be resolved on the basis of the information available in the published descriptions. As Fiers & Iliffe (2000) noted, many of the present generic groupings in the family Ameiridae are merely a practical division of the diversity seen in this widely distributed and speciose family. Lee & Huys (2002) discussed the confused taxonomic subdivisions within the freshwater Ameiridae. They strongly criticized the practice of inferring relationships in derived lineages based on leg segmentation, which has led to the establishment of genera such as *Stygonitocrella,* which they characterized as "unnatural". Lee & Huys (2002) also provided a table of known characters of appendages of members of the related genera *Stygonitocrella, Inermipes* Lee & Huys, 2002, *Neonitocrella,* and *Psammonitocrella* Rouch, 1992. Although they considered that the members of *Stygonitocrella* can be grouped into several discrete

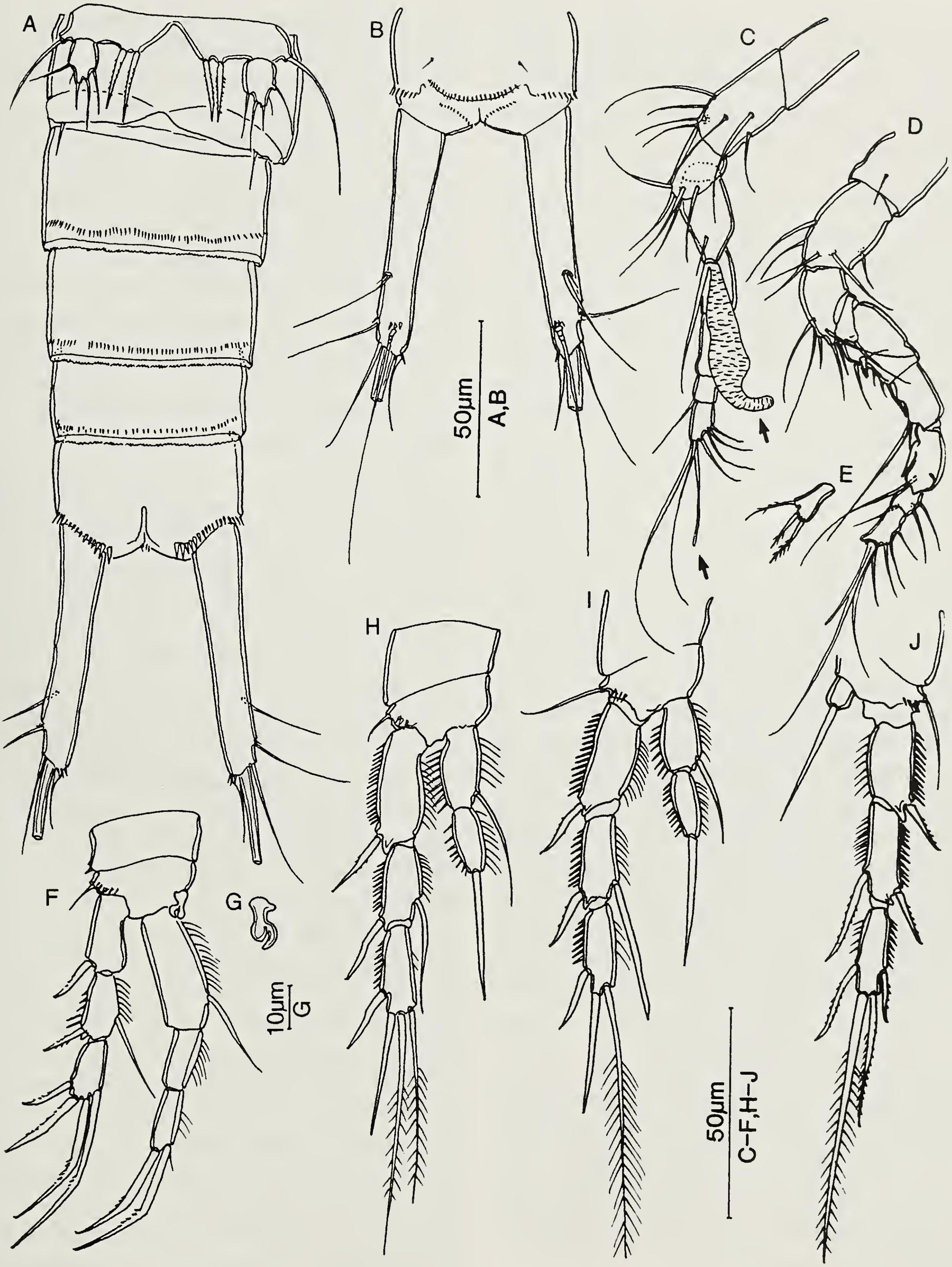

Fig. 4. *Stygonitocrella sequoyahi,* new species, male allotype (USNM 288041). A, Urosome, ventral; B, Anal somite and caudal rami, dorsal; C, Antennule, medial; D, Antennule, lateral; E, Antennal exopodite; F, Right leg 1; G, Spine on distomedial corner of left leg 1 basipodite (enlarged); H, Leg 2; I, Leg 3; J, Leg 4.

lineages, each with a typical leg setation pattern and a restricted geographical distribution, they emphasized that formal recognition of these lineages is presently impossible because of the lack of detail provided by most descriptions and the fact that many of them are based on few specimens or only one sex. As in the case of another ameirid genus, *Nitocrellopsis,* which was discussed by Fiers & Iliffe (2000), type material for several species of *Stygonitocrella* does not exist, and most of the original descriptions lack critical information on the morphology of mouthparts, body somites, or even the exact setation of some legs (reviewed by Lee & Huys 2002). For instance, although Lee & Huys (2002) noted that in the case of *S. orghidani* there is no evidence that it is related to any other species now included in *Stygonitocrella,* because of the summary nature of its description they were able only to relegate it to a position of incertae sedis in the genus.

The characters of presence or absence of sexual dimorphism in leg setation, and fusion or lack of fusion of the leg 5 baseoendopodite and exopodite would seem to be important in the systematics of the ameirids. A general revision of the Ameiridae is necessary to provide perspective on the systematic value of such characters (cf., discussions by Lang 1965 and Galassi 2001). In certain instances, they may be useful; Lee & Huys (2002) included the reduced leg 5 of both sexes of *Stygonitocrella insularis* in the array of characters used to support their proposal to separate it into a new genus *Neonitocrella*; and also pointed to the extremely reduced fifth legs of *S. orghidani* as one of two unusual characters indicating that the species is improperly allocated to *Stygonitocrella.*

Some of the problems in systematics of freshwater ameirids have been resolved on the basis of recently gathered information. Galassi et al. (1999) provided a diagnosis and designated a type species for *Nitocrellopsis,* another genus originally proposed by Petkovski (1976). In that case, Galassi et al. (1999) were able to examine type material of four species of *Nitocrellopsis,* and corrected errors in several of the published descriptions. Lee & Huys (2002) removed *S. insularis* to the new genus *Neonitocrella.* Like Lee & Huys (2002), we expect that the genus *Stygonitocrella* will be rearranged into more logical groups when and if a revision based on sufficient material becomes possible. For now it seems best to maintain the simple and general concept of *Stygonitocrella* as proposed by Petkovski (1976), pending recollection and redescription of several of the species that are presently assigned to this genus.

The only synapomorphy in the genus *Stygonitocrella* is the 1-segmented endopodite of leg 4, which is of course present in *S. sequoyahi.* Certain other features of *S. sequoyahi,* in particular the 2-segmented endopodites and the unusual and also probably plesiomorphic setae on segment 1 of the endopodites of legs 2 and 3, are less reduced than in most congeneric species. The latter feature is apparently shared only with the male of *S. tianschanica.* The long cylindrical caudal rami of *S. sequoyahi* are quite different from all the other known species of *Stygonitocrella,* which have short conical caudal rami.

The only harpacticoid species in North America which somewhat resemble *S. sequoyahi* are the two members of the genus *Psammonitocrella, P. boultoni* and *P. longifurcata,* which were described by Rouch (1992) from the hyporheic zone of a stream in Arizona, U.S.A. Both are vermiform species, with the endopodites of the swimming legs reduced as in *Stygonitocrella,* and also resemble *S. sequoyahi* in having long, widely set, cylindrical caudal rami. They differ from most species of *Stygonitocrella* except *S. orghidani* in having the leg 5 exopodite fused to the baseoendopodite; and from all other known ameirid species in having the medial spine of the leg 1 basipodite not transformed in the male. Martinez Arbizu & Moura (1994) considered that the presence of an untransformed leg 1 spine in the males indicates that *Psammonitocrella* does not belong in the family Ameiridae, and suggested that this genus is more closely related to the Parastenocarididae. Lee & Huys (2002) proposed to reallocate *Psammonitocrella* to the Ameiridae, based on their opinion that the structure of leg 5, the presence of separate genital and first abdominal segments in the adult female, and the absence of a sexually dimorphic medial basal spine in leg 1 are paedomorphic features, the last being an autapomorphy in the genus.

Integumental windows are osmoregulatory structures that are now known to occur in several families and genera of copepods living in freshwater and estuarine environments (Reid 1994, Hosfeld & Schminke 1997). This is the first report of their presence in a species of *Stygonitocrella.* In *S. sequoyahi* these windows are extremely difficult to see unless specimens have been cleared in lactic acid for several days.

The three streams in which this species was collected are located in the western part of the Ozark Mountain region in northeastern Oklahoma and northwestern Arkansas. The streams are fed by springs and have bed sediments consisting of chert and limestone gravels (Hunt & Stanley 2000). All the streams lie within the drainage basin of the Arkansas River, a tributary of the Mississippi. All the specimens of *S. sequoyahi* appeared in samples pumped from depths of 5 to 75 cm deep in the streambeds. This hyporheic habitat is typical for the genus.

Continental ameirids are considered marine relicts, which remained in their present locations following the withdrawal of ancient seas; for general discussions see Lang (1948) and Galassi (2001). The location of *S. sequoyahi* in the Ozarks, although not that of the two species of *Psammonitocrella* in Arizona, lies within the boundaries of the great North American inland sea, which receded in the early Paleocene (Bănărescu 1992). Fiers & Iliffe (2000) noted that the distribution of the genus *Nitocrellopsis* resembles the Tethyan distribution pattern of several other crustacean groups which have three general centers of distribution in south-central North America, the Caribbean, and the circum-Mediterranean region. Although the locations of *S. sequoyahi* and congeneric species from Cuba, Spain, Greece, West Georgia, Macedonia, and Transcaucasia fall within this pattern, those from Afghanistan, Kirghizstan, and Argentina obviously do not. This incongruency of the distributions of members of the genus *Stygonitocrella,* in addition to the hints of polyphyly provided by the morphological characters, suggests that the extreme reductions in the swimming legs may well have arisen independently several times.

Acknowledgments

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Literature Cited

Bănărescu, P. 1992. Zoogeography of Fresh Waters, vol. 2. Distribution and Dispersal of Freshwater Animals in North America and Eurasia. AULA-Verlag, Wiesbaden, pp. 519–1091.

Borutsky, E. V. 1967. Biospeleologica Sovietica 32. On the genus *Nitocrella* Chappuis (Copepoda, Harpacticoida).—Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody, Otdel Biologichesky, New Series 72(3):32–39 (in Russian; English abstract).

———. 1972. Copepoda Harpacticoida from subterranean water of the shore of Lake Issyk-kul and southern Kisilkum.—Trudy Zoologicheskogo Instituta, Leningrad 51:98–119 (in Russian).

———. 1978. Copepoda-Harpacticoida from subterranean waters of Tian-shan.—Sbornik Trudov

Zoologicheskogo Muzeya MGU 16:66–91 (in Russian).

———, & M. Mikhailova-Neikova. 1970. Copepoda Harpacticoida of caves in West Georgia, Azerbaijan and Central Asia.—Zoologichesky Zhurnal 49:1334–1341 (in Russian; English abstract).

Chappuis, P. A. 1924. Descriptions préliminaires de copépodes nouveaux de Serbie.—Buletinul Societăţii de Ştiinte din Cluj, Romania 2:27–45.

———. 1937. Subterrane Harpacticoiden aus Nord-Spanien.—Buletinul Societăţii de Ştiinte din Cluj, Romania 8:556–571.

Fiers, F., & T. M. Iliffe. 2000. *Nitocrellopsis texana* n. sp. from central TX (U.S.A.) and *N. ahaggarensis* n. sp. from the central Algerian Sahara (Copepoda, Harpacticoida).—Hydrobiologia 418:81–97.

Galassi, D. M. P. 2001. Groundwater copepods: diversity patterns over ecological and evolutionary scales.—Hydrobiologia 453/454:227–253.

———, P. De Laurentiis, & M.-J. Dole-Olivier. 1999. *Nitocrellopsis rouchi* sp. n., a new ameirid harpacticoid from phreatic waters in France (Copepoda: Harpacticoida: Ameiridae).—Hydrobiologia 412:177–189.

Hosfeld, B., & H. K. Schminke. 1997. The ultrastructure of ionocytes from osmoregulatory integumental windows of *Parastenocaris vicesima* (Crustacea, Copepoda, Harpacticoida).—Archiv für Hydrobiologie 139:389–400.

Hunt, G. W. 1999. The ecology of hyporheic invertebrates in Oklahoma and Arkansas streams. Unpublished Ph.D. dissertation, Oklahoma State University, Stillwater, 167 pp.

———, & E. H. Stanley. 2000. An evaluation of alternative procedures using the Bou-Rouch method for sampling hyporheic invertebrates.—Canadian Journal of Fisheries and Aquatic Sciences 57:1545–1550.

International Commission on Zoological Nomenclature, 1999. International code of zoological nomenclature, fourth edition. The International Trust for Zoological Nomenclature, The Natural History Museum, London, 306 pp.

Lang, K. 1948. Monographie der Harpacticiden. Vols. 1, 2, Nordiska Bokhandeln, Stockholm, 1662 pp.

———. 1965. Copepoda Harpacticoidea from the California Pacific coast.—Kunglige Svenska Vetenskapsakademiens Handlingar, Fjärde Serien, 10(2):1–560 + pls. 1–6.

Lee, W., & R. Huys. 2002. A new genus of groundwater Ameiridae (Copepoda, Harpacticoida) from boreholes in Western Australia and the artificial status of *Stygonitocrella* Petkovski, 1976.—Bulletin of the Natural History Museum, London (Zoology) 68:39–50.

Martínez Arbizu, P., & G. Moura. 1994. The phylogenetic position of the Cylindropsyllinae Sars (Copepoda, Harpacticoida) and the systematic status of the Leptopontiinae Lang.—Zoologische Beiträge, New Series 35:55–77.

Miura, Y. 1962. Subterranean harpacticoid copepods of the Amami Group of the Ryukyu Islands.—Annotationes Zoologicae Japonenses 35:95–105.

Monard, A. 1927. Synopsis universalis generum Harpacticoidarum.—Zoologische Jahrbucher, Abteilung für Systematik 54(1–2):139–176.

Noodt, W. 1965. Crustacea subterranea aus Argentinien.—Beiträge zur Neotropischen Fauna 4:84–129.

Pesce, G. L. 1985. Stygobiological researches in subterranean waters of Lesbos (Greece) and description of *Stygonitocrella petkovskii* n. sp.—Fragmenta Balcanica 12(12/273):125–139.

Petkovski, T. K. 1959. Neue und bemerkenswerte Harpacticoide Ruderfußkrebse (Crust. Cop.) aus den Grundgewässern Jugoslaviens.—Acta Musei Macedonici Scientiarum Naturalium, Skopje 6(5/57):101–119.

———. 1973. Subterrane Süßwasser-Harpacticoida von Kuba (Vorläufige Mitteilung).—Résultats des Expéditions Biospéologiques Cubano-Roumaines à Cuba 1:125–141.

———. 1976. Drei neue *Nitocrella*-Arten von Kuba, zugleich eine Revision des Genus *Nitocrella* Chappuis (s. restr.) (Crustacea, Copepoda, Ameiridae).—Acta Musei Macedonici Scientiarum Naturalium 15(1/126):1–26.

Reid, J. W. 1994. *Murunducaris juneae,* new genus, new species (Copepoda: Harpacticoida: Parastenocarididae) from a wet campo in central Brazil.—Journal of Crustacean Biology 14:771–781.

Rouch, R. 1985. Une nouvelle *Stygonitocrella* (Copepoda, Harpacticoidea) des eaux souterraines d'Andalousie, Espagne.—Stygologia 1:118–127.

———. 1992. Un nouveau genre d'Ameiridae (Copepoda, Harpacticoida) dans le milieu hyporhéique d'un cours d'eau de l'Arizona.—Stygologia 7:149–157.

Štěrba, O. 1973. Die neuen Harpacticidenarten der Gattung *Nitocrella* (Crustacea, Copepoda) aus Afghanistan.—Zoologischer Anzeiger 190:333–342.

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Four new solitary entoprocts (Entoprocta: Loxosomatidae) from Okinawa Island, The Ryukyu Archipelago, Japan

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Abstract.—Four new solitary entoprocts are described from Okinawa Island, the Ryukyu Archipelago, Japan. Based on the foot structures and the budding modes, three of them are assigned to the genus *Loxosomella* Mortensen, 1911 (*L. stomatophora,* new species; *L. lecythifera,* new species; and *L. intragemmata,* new species) and the other to the genus *Loxocorone* Iseto, 2002 (*L. dicotyledonis,* new species). They were found on glass slides or a glass bottle collected from a shallow reef flat, and thus, they are not commensal, unlike most of the other species hitherto described from other localities.

To date, a total of approximately 170 species are recognized in the phylum Entoprocta, of which about 120 species are solitary and the remainder are colonial. It is believed that a great number of unknown species are yet to be described for this phylum (Nielsen 1989, Wasson 2002), and thus, taxonomic study, describing new species, is still a principal subject for its biology and is essential to document its diversity. The solitary entoprocts (= the family Loxosomatidae Hincks, 1880) are currently classified into five genera based on foot structures and budding modes (Iseto 2002). Species of the genus *Loxosoma* Keferstein, 1863 have a disk-shaped foot, a sucking disc by which the animals can attach to and detach from substratum. Species of *Loxosomella* Mortensen, 1911 and *Loxocorone* Iseto, 2002 have, at least in the bud stage, an antero-posteriorly elongated foot with a foot gland and a foot groove that enables the animal to glide over the substratum. However, the two genera are distinguished by differences in their budding mode. The buds of the former genus attach to the body of the parent by the posterior tip of the foot, in contrast to the buds of the latter genus that attach to the parent by the back of the stalk or the calyx. The genus *Loxomitra* Nielsen, 1964 resembles the genus *Loxocorone* in the budding mode; the buds attach to the parent by the back of the stalk. The buds of this genus, however, lack the foot groove and have a pair of small lateral expansion termed "terminal wings" (Nielsen 1989) at the tip of the stalk. The genus *Loxomespilon* Bobin & Prenant, 1953 is a monotypic genus; the sole component species of this genus, *L. perezi,* lacks a definite foot and stalk and attaches to the substratum, the body surface of the host polychaetes, by an attaching organ at the basal end of the calyx.

Solitary entoprocts have been reported from tropical areas to polar regions, from shallow to deep (> 500 m) waters. However, in most regions reports are still scarce, except in Europe where this animal group has been surveyed most intensively (Prenant & Bobin 1956, Nielsen 1989). Recently, three *Loxosomella* (*L. aloxiata, L. lappa, L. monocera*), two *Loxomitra* (*L. mizugamaensis, L. tetraorganon*), and one *Loxocorone* (*L. allax*) were described from coral reef shores of the Okinawa Islands, the middle part of the Ryukyu Archipelago, Japan (Iseto 2001, 2002). Since the entoproct fauna of this area has still not been studied sufficiently, extended surveys are expected

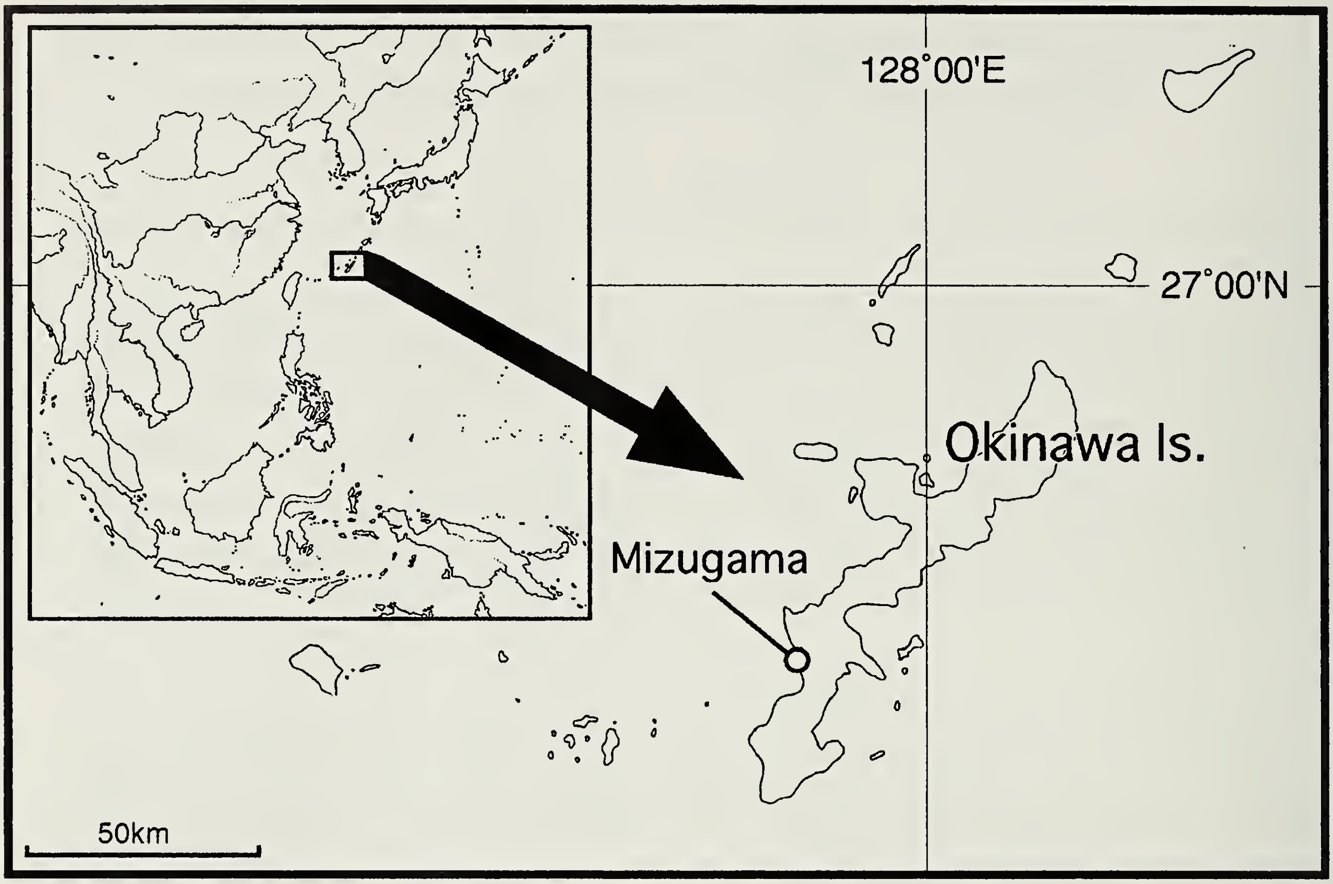

Fig. 1. Map of Okinawa Island and its vicinity, showing geographic location of Mizugama, the type locality of the species described in this study.

to yield numerous unknown entoprocts. Four new solitary entoprocts were collected from Okinawa Island and are described here.

Sampling of solitary entoprocts was carried out at a shallow reef flat in Mizugama (26°21′N, 127°45′E), on the west coast of Okinawa Island, the Ryukyu Archipelago, Japan (Fig. 1). Glass slides were placed at a shady point at a depth of about 1 m and collected after two or four months. On one occasion, a glass bottle was collected. The epifauna on these objects was examined under a binocular stereomicroscope. Some of the entoprocts found from these objects were transferred to petri dishes and cultured in order to obtain the liberated buds or adult individuals that budded from the original individuals. Culturing, narcotization and fixation followed those of Iseto (2001). Drawings were prepared on the basis of fixed specimens, using a light microscope equipped with a camera lucida. Type specimens are deposited in the National Science Museum, Tokyo (NSMT).

Family Loxosomatidae Hincks, 1880
Genus *Loxosomella* Mortensen, 1911

Loxosomella stomatophora, new species
Figs. 2, 3

Type material.—Holotype: adult (NSMT-Ka 52) settled on a glass slide submerged on the reef flat for two months at a depth of about 1 m in Mizugama, Okinawa Island, Japan, collected on 30 Aug 2001. Paratypes: 50 adults (NSMT-Ka 53) collected with the holotype. 19 adults (NSMT-Ka 54) settled on a glass slide submerged at the type locality for two months, collected on 25 Apr 2001.

Etymology.—Specific name *stomatophora* derived from Greek *stoma* = mouth + latinized greek suffix *phorus* = bearing, carrying, in allusion to the resemblance of the roundish body, in abfrontal view, to

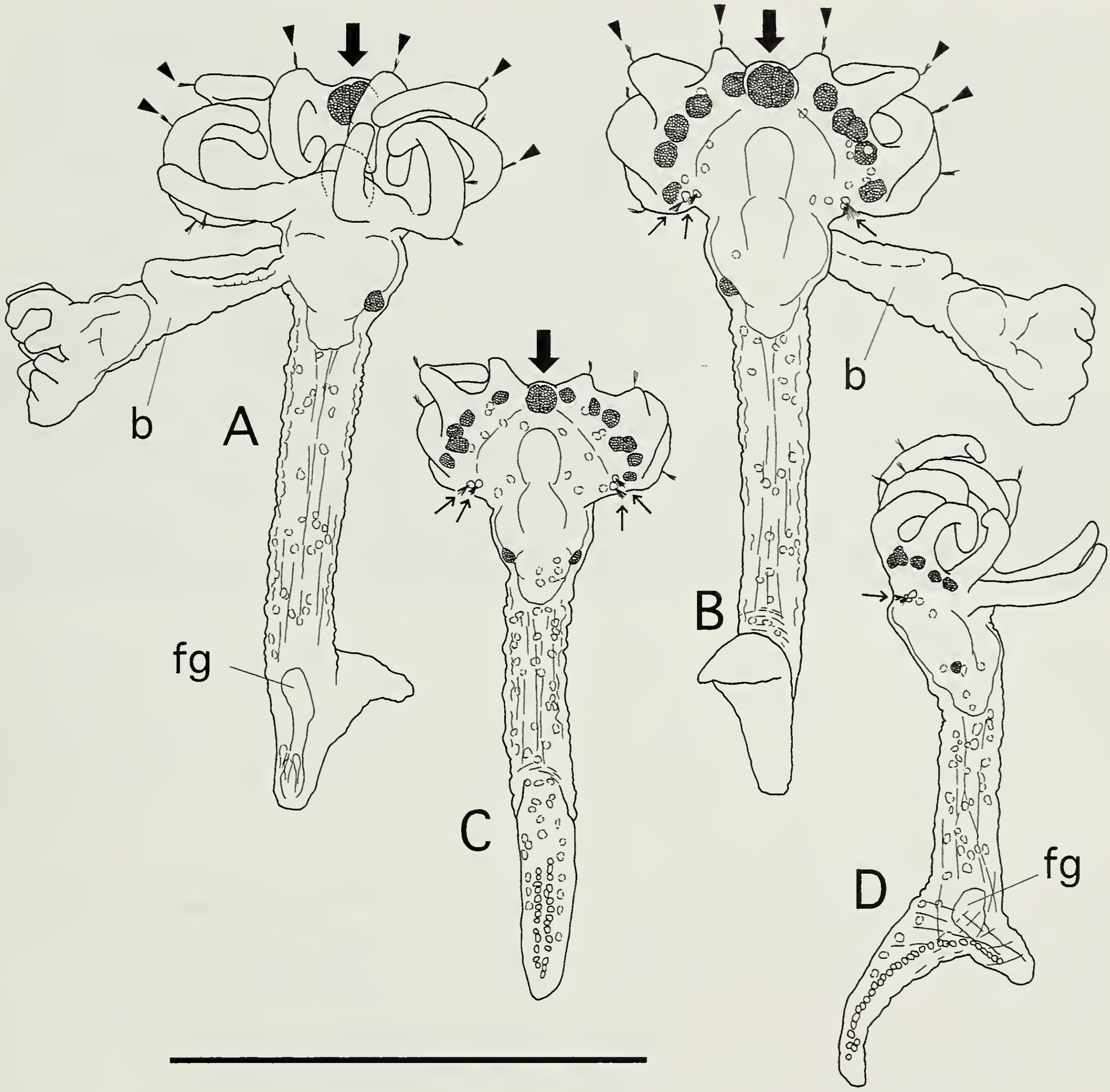

Fig. 2. Drawings of *Loxosomella stomatophora*, new species. A, B, holotype (NSMT-Ka 52) with large bud (b) in frontal and abfrontal views, respectively. C, D, paratype (NSMT-Ka 53) in abfrontal and lateral views, respectively. Thick arrows, characteristic roundish organ consisting of two large granular cells. Thin arrows, ciliary bundles at both lateral sides of the calyx. Arrowheads, ciliary bundles at outer side of tentacles. fg, foot gland. Scale bar = 500 μm.

plant stomata; both are roundish structures consisting of two cells. Used as an adjective.

Description.—Total length (from basal attachment position of foot to upper-most level of tentacular membrane) 330 to 780 μm. Tentacle number 10 in all specimens. Ciliary bundle present at outer side of each tentacle (arrowheads in Fig. 2). Two ciliary bundles present at each lateral side of calyx at level of upper side of stomach (thin arrows in Fig. 2; Fig. 3D). A peculiar roundish organ consisting of two large granular cells, 30 to 50 μm in diameter, present at margin of tentacular crown between two abfrontal tentacles (thick arrows in Figs. 2, 3; Fig. 3B, C). Granular cells of 15 to 25 μm in diameter present at margin of tentacular crown (thin arrows in Fig. 3A; Fig. 3E) and, in most specimens, at each lateral side of stomach. Stalk as long as or a little longer than calyx. Foot with foot gland and foot groove present both in bud and adult. Oral-most pair of tentacles bend outward

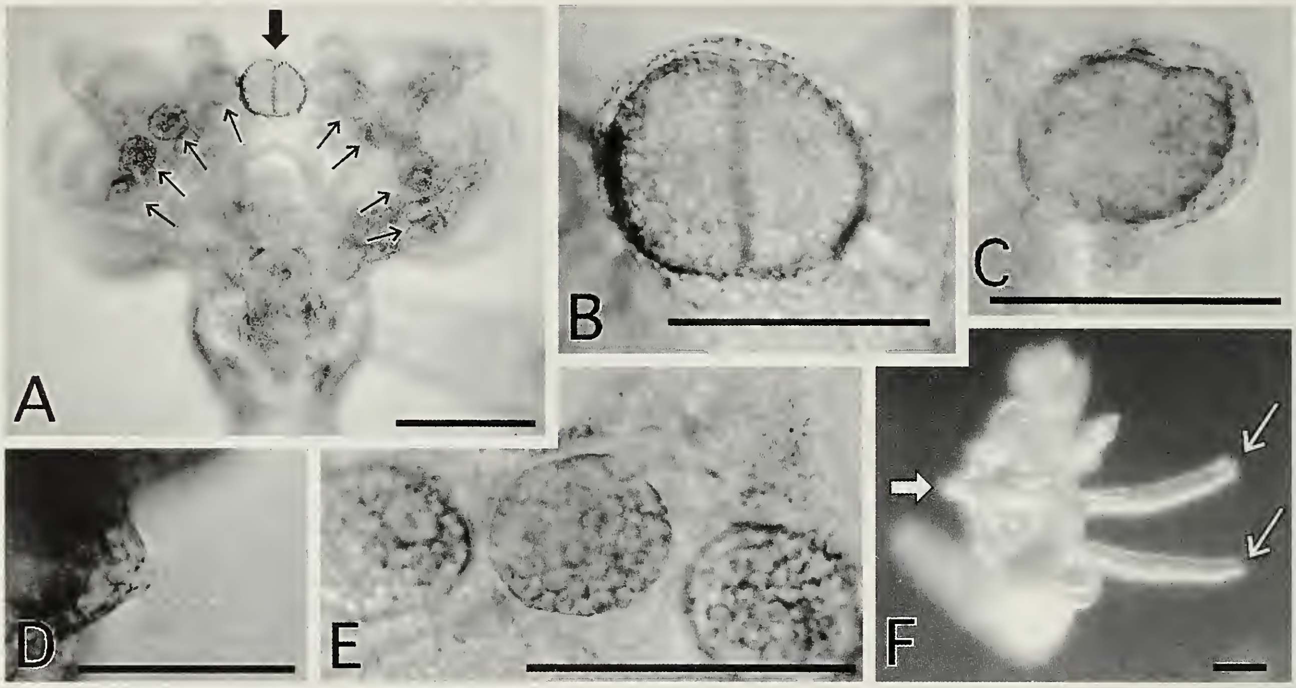

Fig. 3. Photographs of *Loxosomella stomatophora,* new species. A, abfrontal view of calyx of holotype (NSMT-Ka 52). Thick arrow indicates characteristic roundish organ. Granular cells at margin of calyx indicated with thin arrows. B, enlargement of roundish organ in A. C, left-side view of he roundish organ (paratype: NSMT-Ka 53). D, ciliary bundle at lateral side of calyx (paratype: NSMT-Ka 53). E, enlargement of granular cells at margin of calyx in A. F, upper view of living specimen. Note that frontal two tentacles (thin arrows) are extended frontally. The roundish organ indicated with thick arrow. Scale bars: A, F = 100 μm; B–E = 50 μm.

relative to other tentacles in expanded living specimens (Fig. 3F) but are often arranged as the other tentacles in fixed specimens.

Reproduction.—Buds emerge from the laterofrontal areas of the calyx at the level with the upper half of the stomach, attached by the foot tips. A maximum of four buds were observed simultaneously on a single parent. Sexual reproduction has not been observed.

Discussion.—The most characteristic feature of *Loxosomella stomatophora* lies in its possession of a peculiar roundish organ at the abfrontal margin of the tentacular crown. *Loxosomella vivipara* Nielsen, 1966 is also reported to have a specialized organ at the same position as *L. stomatophora* (Nielsen 1966, Emschermann 1993). The organ in *L. vivipara* is, however, found only in some individuals, and its form varies among individuals. In some individuals, it is a hollow cup-shaped structure with a plug of secretion and consists of 7 to 16 cells (Nielsen 1966), and in others it is a more conspicuous bell-shaped structure consisting of more than 25 cells (Emschermann 1993). The roundish organ of *L. stomatophora* is, however, composed of only two cells, showing only little variation among all the individuals examined in this study. *Loxosomella vivipara* is also distinct from *L. stomatophora* in having lateral wings on the calyx and conspicuous lateral pockets at the stomach (Nielsen 1966). Moreover, the tentacle number, which is invariably 10 in *L. stomatophora,* is 12 to 16 in *L. vivipara.*

Loxosomella lecythifera, new species
Figs. 4, 5

Type material.—Holotype: adult (NSMT-Ka 55) found on a glass bottle collected at the reef flat in Mizugama, Okinawa Island, Japan on 25 Oct 2000. Paratypes: Two adults (NSMT-Ka 56) collected with the holotype. 52 adults (NSMT-Ka

57), 473 adults (NSMT-Ka 58), and 41 adults (NSMT-Ka 59) settled on glass slides submerged on the type locality for two months, collected on 28 Mar 2001, 29 Jul 2001, and 29 Sep 2001, respectively. An adult (NSMT-Ka 60) having larvae in its calyx, collected with NSMT-Ka 58. A liberated bud (NSMT-Ka 61) budded from the holotype. A liberated bud (NSMT-Ka 62) budded from an adult collected with the holotype. Three liberated buds (NSMT-Ka 63) budded from adults settled on glass slides submerged on the type locality for two months, collected on 30 Jan 2001.

Etymology.—Specific name *lecythifera* from Latin *lecythus* = bottle or flask + suffix *-fer, -fera, -ferum* to bear or have, in allusion to the bottle-shaped appendages of the species. Used as an adjective.

Description.—Adult: Total length (from basal tip of stalk to uppermost part of tentacular membrane) up to 1650 μm. Tentacle number 14 to 22. Stalk one and a half to two times longer than calyx. Adult without foot. A pair of lateral sense organs present at level of upper side of stomach (thick arrows in Figs. 4A–C, 4E, 5A; Fig. 5C). Four to seven bottle-shaped appendages, 40 to 55 μm in length, present at abfrontal side of calyx at levels above the lateral sense organ (thick arrows in Figs. 4A–C, 4E, 5A; Fig. 5B, E). Many cylindrical appendages of 20 to 30 μm long present at calyx and stalk (Fig. 5D). Whole body, except tentacular crown, often covered with detritus. Liberated bud: Total length (from posterior tip of foot to anterior-most point of tentacular membrane between two abfrontal tentacles) 560 to 770 μm. Tentacle number 14 to 16. Stalk very short. Foot with foot gland and foot groove present. A pair of lateral sense organs present (thick arrows in Figs. 4D, 5F). Two to five bottle-shaped appendages comparable to those in adult specimens present (thin arrows in Figs. 4D, 5F).

Reproduction.—Buds emerge from the laterofrontal areas of the calyx at the level of the upper side of the stomach, attached by tips of their feet. A maximum of six buds were observed simultaneously on a single parent. An embryo was found in the calyx of an individual (NSMT-Ka 60, Fig. 5G) collected in July. The size of the embryo is approximately 100 μm in diameter.

Discussion.—The distinguishing feature of *Loxosomella lecythifera* lies in its possession of several bottle-shaped appendages. Some *Loxosomella* species are reported to have appendages of more irregular shape, but bottle-shaped appendages have not previously been reported from the congeners. *Loxosomella hispida* Marcus & Marcus, 1968 resembles *L. lecythifera* in having appendages at the calyx and stalk, having a maximum of six buds, and having more than 20 tentacles (Marcus & Marcus 1968). However, the large appendages referred to as sense organs, at the middle level of the stomach in *L. hispida* (Marcus & Marcus 1968; fig. 11) do not resemble any appendage of *L. lecythifera.*

Loxosomella intragemmata, new species
Figs. 6, 7

Type material.—Holotype: adult (NSMT-Ka 64) settled on a glass slide submerged on the reef flat for two months at a depth of about 1 m in Mizugama, Okinawa Island, Japan, collected on 29 Dec 2000. Paratypes: Seven adults (NSMT-Ka 65) collected with the holotype; 81 adults (NSMT-Ka 66), 389 adults (NSMT-Ka 67), and 25 adults (NSMT-Ka 68) settled on glass slides submerged on the type locality for two months, collected on 28 Feb 2001, 29 Jul 2001, and 29 Nov 2001, respectively. Five adults (NSMT-Ka 69) having larvae in their calyx, collected with NSMT-Ka 67. Three liberated buds (NSMT-Ka 70) budded from adults collected with the holotype.

Etymology.—Specific name *intragemata* from Latin *intra* = within + *gemmatus,* with buds, from *gemma* = bud, in allusion to the bottle-shaped appendages of the species. Used as an adjective.

Description.—Adult: Total length (from basal tip of stalk to uppermost part of ten-

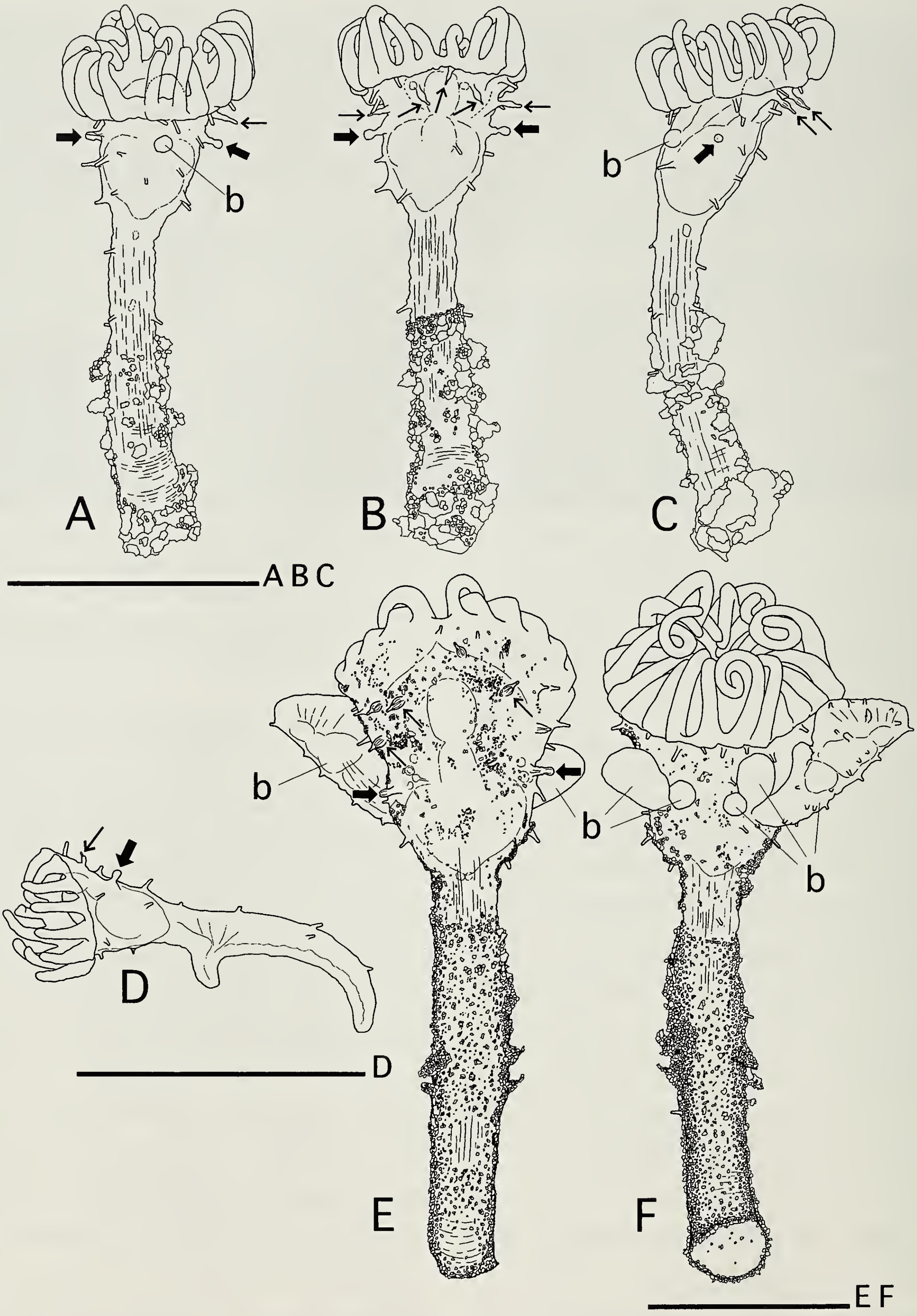

Fig. 4. Drawings of *Loxosomella lecythifera*, new species. A–C, adult holotype (NSMT-Ka 55) with small bud (b) in frontal, abfrontal, and lateral views, respectively. D, lateral view of liberated bud (paratype, NSMT-Ka 61) budded from holotype. E, F, large adult specimen (paratype, NSMT-Ka 57) with five buds (b) in abfrontal and frontal views, respectively. Thick arrows, lateral sense organs. Thin arrows, some of bottle-shaped appendages. Scale bars = 500 μm.

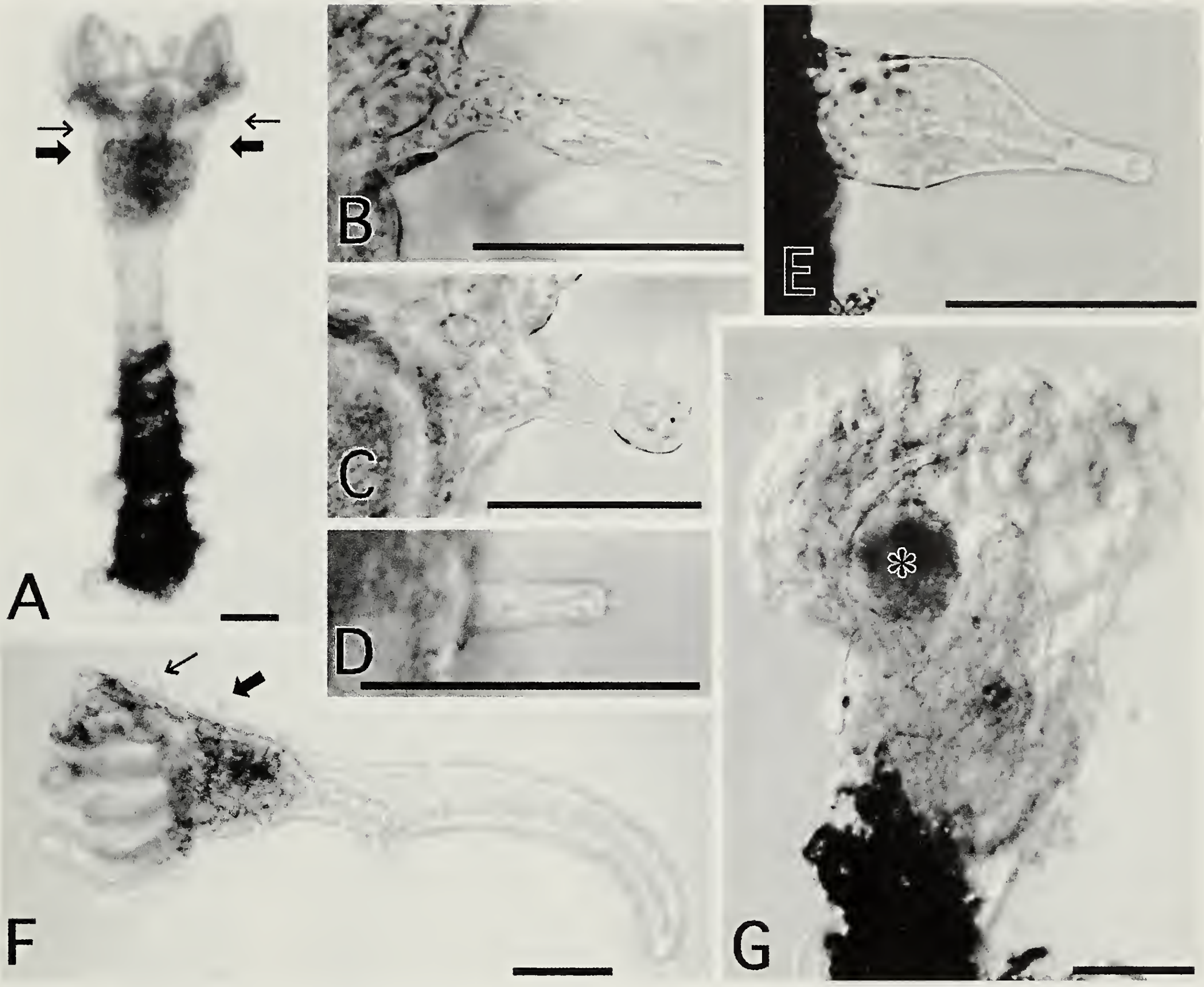

Fig. 5. Photographs of *Loxosomella lecythifera,* new species. A–D, adult holotype (NSMT-Ka 55). A, abfrontal view of whole body. B, characteristic bottle-shaped appendage. C, lateral sense organ. D, cylindrical appendage at calyx. E, bottle-shaped appendage of large paratype specimen (NSMT-Ka 57). F, left side view of liberated bud (paratype, NSNT-Ka 61). G, latero-abfrontal view of calyx of paratype (NSMT-Ka 60) brooding larva (asterisk) in its calyx. Thick arrows, lateral sense organs. Thin arrows, bottle-shaped appendages. Scale bars: A, F, G = 100 μm in; B–E = 50 μm.

tacular membrane) up to 1260 μm. Tentacle number 10 to 15. Stalk two to three times longer than calyx. Adult without foot. A pair of lateral sense organs present (arrows in Fig. 6). Liberated bud: Total length (from posterior tip of foot to anterior-most point of tentacular membrane between two abfrontal tentacles) 420 to 480 μm. Tentacle number 10. Foot with foot gland and foot groove present. A pair of lateral sense organs present (arrows in Figs. 6D, 7C).

Reproduction.—Buds emerge internally at the laterofrontal areas of the calyx at the level with the upper half of the stomach. When the spherical small buds become elongate, the buds begin to protrude from the parent's body (Fig. 7B). Buds attached by the tips of their feet. A maximum of three buds were observed simultaneously on a single parent. Embryos (up to four) were found in the calyx of five individuals (NSMT-Ka 69, Fig. 7D) collected in July. The size of the embryos are up to 120 μm.

Discussion.—The most remarkable feature of *Loxosomella intragemmata* is that the buds are formed internally in contrast to most other solitary species in which the buds emerge from the outer surface of the parent. Similar internal budding was reported for *L. bocki* Franzén, 1966 found on

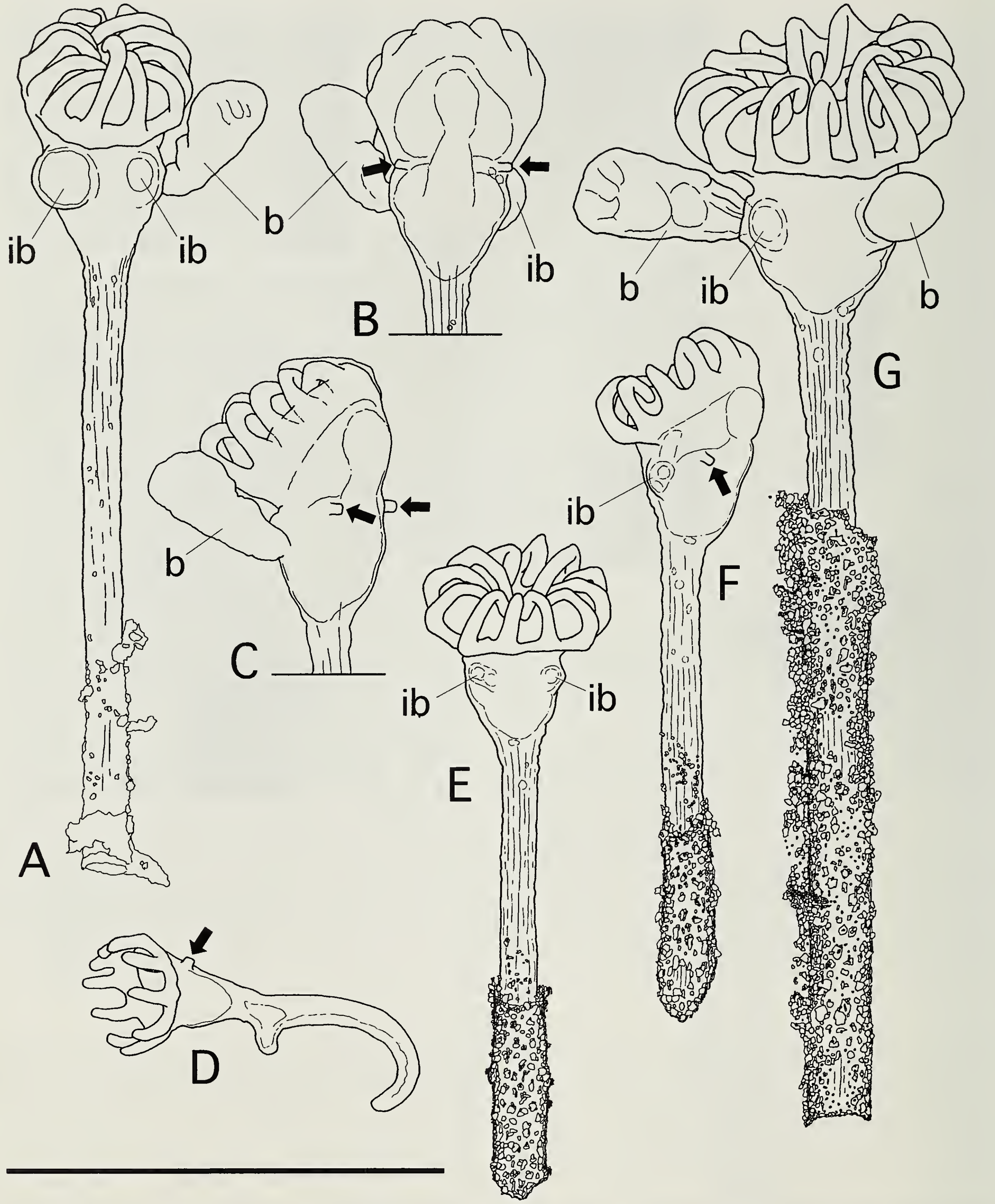

Fig. 6. Drawings of *Loxosomella intragemmata,* new species. A–C, adult holotype (NSMT-Ka 64) with two internal buds and bud protruding from its pocket at calyx, in frontal, abfrontal, and lateral views, respectively. D, left side view of liberated bud (paratype, NSMT-Ka 70). E, F, small adult specimen (paratype, NSMT-Ka 67) with internal buds in early stage, in frontal and lateral views, respectively. G, large paratype specimen in frontal view. Arrows, lateral sense organs. b, protruding bud. ib, internal bud. Scale bar = 500 μm.

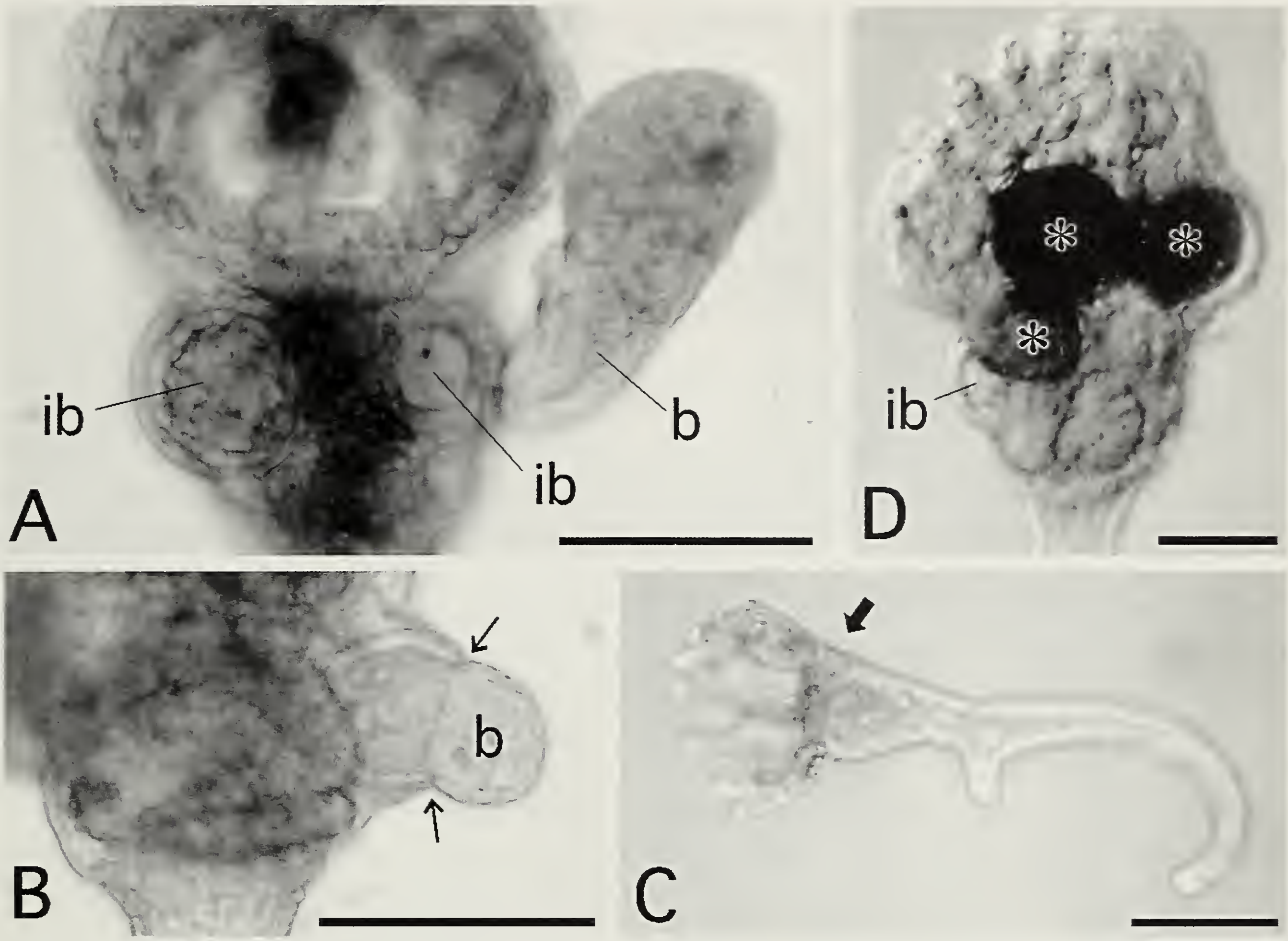

Fig. 7. Photographs of *Loxosomella intragemmata*, new species. A, frontal view of calyx of holotype (NSMT-Ka 64) with two internal buds (ib) and protruding bud (b). B, frontal view of lower half of calyx of paratype (NSMT-Ka 65) showing bud which has just begun to protrude from parent body (b). Arrows indicate opening of pocket from which bud protrudes. C, left side view of liberated bud (paratype, NSMT-Ka 70). Arrow indicates lateral sense organ. D, latero-abfrontal view of calyx of paratype specimen (NSMT-Ka 69) with internal bud (ib) and three larvae (asterisks). Scale bars = 100 μm.

a sponge collected at the Gilbert Islands. *Loxosomella bocki* is, however, distinct from *L. intragemmata* in retaining the foot in the adult stage, having a short (slightly shorter than the calyx) stalk, and lacking the lateral sense organ at the calyx (Franzén 1966). The internal buds, in both species, may occur from deep epitherial pockets, a pair of depressions at the laterofrontal area of the calyx (Franzén 1966). Budding from less deep pockets was reported from some congeneric species such as *L. raja* (Schmidt, 1876), *L. pes* (Schmidt, 1876), *L. antis* Krylova, 1985, and *L. cricketae* Nielsen, 1966. However, these pockets have outer openings unlike those of the above two species, which appear completely covered by the epidermis.

Genus *Loxocorone* Iseto, 2002

***Loxocorone dicotyledonis*, new species**
Figs. 8, 9

Type material.—Holotype: adult (NSMT-Ka 71) settled on a glass slide submerged on the reef flat for four months at a depth of about 1 m in Mizugama, Okinawa Island, Japan, collected on 5 Jul 2000. Paratypes: 138 adults (NSMT-Ka 72) derived by budding from three adults found on a slide submerged at the type locality for two months, collected on 11 Apr 1999. An adult (NSMT-Ka 73) derived by budding with NSMT-Ka 72.

Etymology.—Specific name *dicotyoedonis,* Latinized Greek *di* = two + *cotyledon* = seed leaf of a plant + suffix *-is,* = resemblance, in allusion to the laterally elongated tentacular crown resembling the seedling of a dicotyledonous plant. Used as an adjective.

Description.—Total length (from basal attachment position of foot to upper-most level of tentacular membrane) 380 to 900 μm. Number of tentacles 18 to 28. Tentacles alternately directed laterally and frontally. Both lateral sides of the tentacular crown expand laterally making the tentacular crown bilobed rather than circular. Stalk as long as calyx. Foot with foot gland and foot groove present both in bud and adult. Foot gland long (about 300 μm), reaching to the middle level of the stalk. Lateral sense organs absent. Glandular cells of about 20 μm in diameter scattered in calyx (arrowheads in Fig. 9C; Fig. 9D, E), tentacles, stalk (arrows in Fig. 9F; Fig. 9G), and foot (Fig. 9H). These glandular cells often have external secretion (arrows in Fig. 9E, G, H).

Reproduction.—Buds emerge from the frontal areas of the calyx at the level of the upper side of the stomach, attached to their parent's calyx by the back of the upper part of the stalk. A maximum of two buds were observed simultaneously on a single parent. Nevertheless, only one bud grew large at a time. Large buds have the same proportion as the adults but are smaller and have a lower tentacle number than the adults. When the bud has grown large enough to detach, the parent bends its stalk frontally. Then, the foot of the bud attaches to the substratum and the bud detaches from the parent. *Loxocorone dicotyledonis* showed active asexual propagation under laboratory culture fed with microalgae. The 138 paratype specimens (NSMT-Ka 72) were derived from only three individuals after 40-days culture. Sexual reproduction has not been observed.

Discussion.—The bilobed shape of the tentacular crown is the distinguishing feature of *Loxocorone dicotyledonis.* The deviation of the shape of the tentacular crown from the normal circular shape is also observed in some other loxosomatids (e.g., *Loxosoma nung* Nielsen, 1996). In those species, however, the deviation is not as conspicuous as in *Loxocorone dicotyledonis.* The characteristic arrangement of the tentacles that are alternately directed laterally and frontally was also reported in *Loxocorone allax* Iseto, 2002. However, the two species are easily distinguishable because in *L. allax* the foot degenerates in the adult stage unlike *L. dicotyledonis* in which all individuals retain the foot throughout the life. The shape of the bud is also considerably different in the two species. Unlike the bud of the present species that has a definite stalk and foot-shaped foot, that of *L. allax* lacks stalk and has a long, cylindrical foot the length of which reaches one and half times as long as its calyx.

Another noteworthy feature of *Loxocorone dicotyledonis* lies in its possession of the glandular cells with external secretion at abfrontal side of the calyx, tentacle, stalk, and foot. Among these glandular cells, two distinct cell types seem to be distinguishable. The cells at calyx and tentacles are spherical, secreting vague mucous material (arrows in Fig. 9E), whereas the cells at stalk and foot are more irregular, secreting more clearly outlined substance (arrows in Fig. 9G, H).

General Discussion

Most of the solitary entoprocts hitherto described were found on host animals such as polychaetes, bryozoans, sipunculans and sponges (summarized in Nielsen 1964, Soule & Soule 1965). All of the ten species recorded in the Ryukyu Archipelago, however, had settled on glass slides or a glass bottle, and thus, do not depend on host animals (Iseto 2001, 2002, present study). Some of these species are also found on

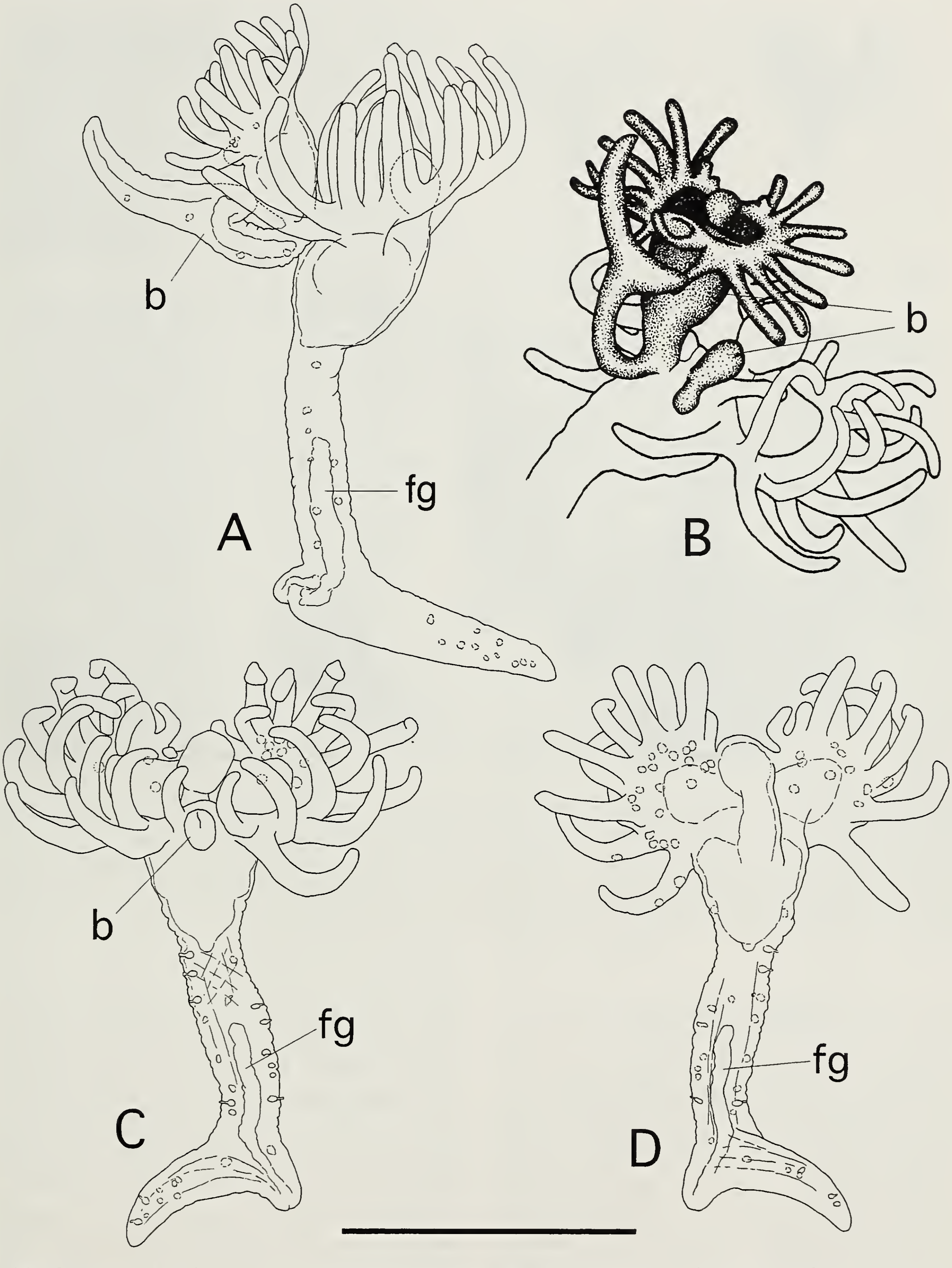

Fig. 8. Drawings of *Loxocorone dicotyledonis,* new species. A, lateral view of holotype (NSMT-Ka 71) with a large bud. B, calyx of a paratype (NSMT-Ka 72) with a large and a small bud (shaded). C, D, paratype (NSMT-Ka 73) with a small bud, in frontal and abfrontal views, respectively. b, bud. fg, foot gland. Scale bar = 500 μm.

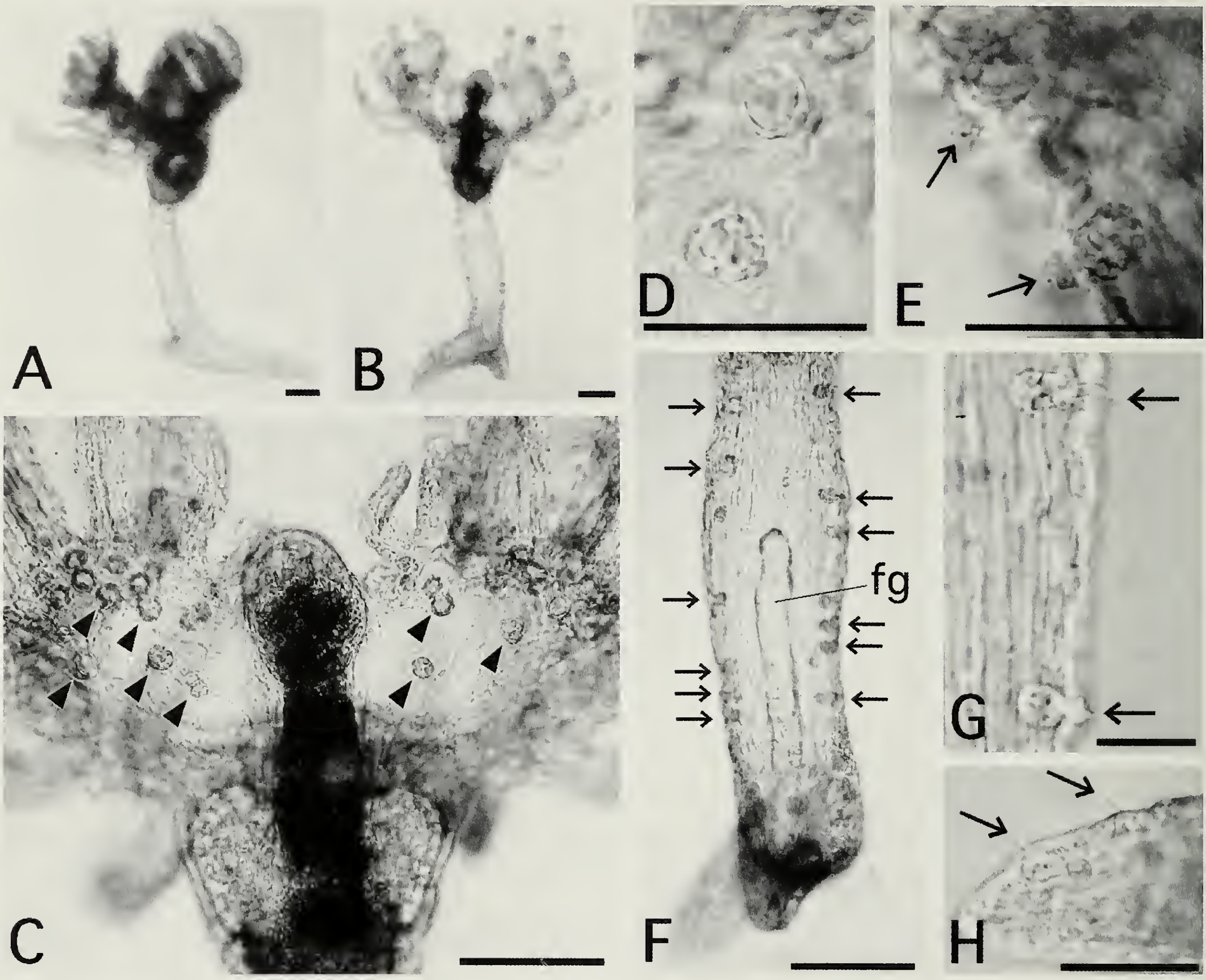

Fig. 9. Photographs of *Loxocorone dicotyledonis*, new species. A, lateral view of holotype (NSMT-Ka 64) with large bud. B–H, paratype (NSMT-Ka 72). B, frontal view. C, abfrontal view of the calyx. Arrowheads indicate glandular cells. D, E, enlargement of glandular cells at calyx in surface view and lateral views, respectively. Arrows indicate external secretion. F, frontal view of lower half of animal. Arrows indicate glandular cells at lateral sides of stalk. fg, foot gland. G, enlargement of glandular cells at stalk. H, posterior tip of foot. Arrows in G and H indicate external secretion of glandular cells. Scale bars: A–C, F = 100 μm; D, E, G, H = 50 μm.

dead coral fragments and shell remains collected from reef flats, and thus, non-living substrata are undoubtedly their natural habitat. Although commensal species may possibly be discovered from this area in future studies, non-living substrata seem to be a common habitat for the solitary entoprocts of this area. The studies in the Ryukyu Archipelago aroused the question of whether solitary entoprocts are an animal group that is commensal in general, as noted in many publications (Hyman 1951, Ruppert & Barnes 1994, Nielsen 2001). As well as the ten species from the Ryukyu Archipelago, *Loxosomella olei* du Bois-Reymond-Marcus, 1957 and *Loxosoma isolata* Salvini-Plawen, 1968 were found only on non-living substrata. Furthermore, some species were found on several animals of different phyla and also on non-living substrata (cf. Nielsen 1964), suggesting that a host animal is not essential for these entoprocts.

Nielsen (1964) insisted that the solitary entoprocts are "energy commensals" that depend on the host-made water current to obtain food particles. The basis of his argument was that commensal species are mostly situated at points where water currents are made by the hosts. However, the ten species found from the Ryukyus live without host animals. Despite this, they do not seem to have any adapted characteristics to make stronger water currents than the commensal species. This indicates that most commensal species can also produce sufficient water currents by themselves. Non-commensal species were often found at small cleavage points of stones, which may offer protection from larger animals; the densely aligned glass slides used in my studies may have provided a similar condition. My observation suggests that the habitat preference of solitary entoprocts is to avoid predators. The body surface of the host animals or inner side of host tubes also help solitary entoprocts to avoid predators, although it is still probable that short-tentacled species depend on the host-produced water current.

To my knowledge, there is no report on long-term laboratory culture of solitary entoprocts. In this study, however, vigorous budding in several generations was induced on *Loxocorone dicotyledonis* cultured in petri dishes (ca. 50 ml). They were fed surplus amount of microalgae, *Nannochloropsis* (Marine Chlorella 100, Marine-bio Co., Japan), and the seawater was exchanged after about 30 minutes. The microalgae and excrements that accumulated under the dishes were cleaned up several times a week using a thin wood stick. I did not try long-term culture for the other three species described in this study, but the buds that were already present at the collection time were grown and released within a week. Among the six other species that I previously reported from the same region, *Loxomitra mizugamaensis* Iseto, 2002, *L. tetraorganon* Iseto, 2002 and *Loxocorone allax* Iseto, 2002 proliferated similarly to *Loxocorone dicotyledonis* by the same culture method. For *Loxosomella monocera* Iseto, 2001, the culture was successful, but the budding and growth rate was very slow, suggesting that the culture method was not adequate for this species. For *L. aloxiata* Iseto, 2001, budding could be induced but the newly liberated buds never successfully fixed on substrata and failed to reach the normal adult form. At present, it is not understood why some species are tolerant to the culture condition and others are not. *Loxosomella lappa* Iseto, 2001 was found attached to a glass plate that had been kept in a bucket with seawater and coral rubble on which the original individual(s) were attached. In this case, diet was not supplied, but the animals proliferated with contaminated detritus. The seawater was not exchanged and the bucket was left for about one month with air supply. This is the second culture method I have tried and also an easy collecting method for inconspicuous species that are difficult to find directly from the original, complicated substrata.

In my surveys in the Ryukyu Archipelago, most of the non-commensal entoprocts were found on glass slides used as settlement panels. Ryland & Austin (1960) found two solitary species, *Loxomitra kefersteinii* (Claparède, 1867) and *Loxosomella antedonis* Mortensen, 1911 on plastic settlement panels. Settling panels seem to be an effective way to collect non-commensal solitary entoprocts. Adaptation of this method may reveal a rich entoproct fauna without host animals in areas outside the Ryukyu Archipelago, including areas from which only commensal species have been reported in the past studies.

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Literature Cited

Bobin, G., & M. Prenant. 1953. Deux Loxosomes nouveaux de Roscoff.—Archives de Zoologie Expérimentale et Générale 91:25–35.

Claparède, E. 1867. Miscellanées zoologiques, V. Sur le Loxosoma kefersteinii V. sp., Bryozoaire mou du golfe de Naples.—Annales Sciences Naturelles, Ser. 5, Zoologie et Paléontologie 8: 28–30, pl 6.

Emschermann, P. 1993. Lime-twig glands: a unique invention of an Antarctic entoproct.—Biological Bulletin 185:97–108.

Franzén, Č. 1966. A new Loxosomatid from the Pacific (Gilbert Islands) with a note on internal budding in Entoprocta.—Arkiv för Zoologi, Ser. 2 19:381–390 + pl. 1.

Hincks, T. 1880. A History of the British Marine Polyzoa. Van Voorst, London, 601 pp + 83 pls.

Hyman, L. H. 1951. Acanthocephala, Aschelminthes, and Entoprocta. The pseudocoelomate Bilateria. The Invertebrates, vol. 3. McGraw-Hill, New York, 572 pp.

Iseto, T. 2001. Three new *Loxosomella* (Entoprocta: Loxosomatidae) from coral reef shore in Okinawa, Ryukyu Archipelago, Japan.—Zoological Science 18:879–887.

———. 2002. *Loxocorone,* a new genus of the family Loxosomatidae (Entoprocta: Solitaria), with descriptions of two new *Loxomitra* (sensu stricto) and a new *Loxocorone* from Okinawa, the Ryukyu Archipelago, Japan.—Zoological Science 19:359–367.

Keferstein, W. 1863. Untersuchungen über niedere Seethiere. VIII: Ueber *Loxosoma singulare* gen. et sp. n., den Schmarotzer einer Annelide.—Zeitschrift für Wissenschaftliche Zoologie 12: 131–132 + pl. 11.

Krylova, E. M. 1985. Two new species of the genus *Loxosomella* (Kamptozoa, Loxosomatidae) from the White Sea.—Zoologicheskii Zhurnal 64:1262–1264.

Marcus, E. du B.-R. 1957. Neue Entoprocten aus der Gegend von Santos.—Zoologischer Anzeiger 159:68–75.

———, & E. Marcus. 1968. Neue brasilianische Loxosomen.—Zoologische Beiträge 14:203–212.

Mortensen, T. 1911. A new species of Entoprocta, *Loxosomella antedonis,* from North-east Greenland.—Meddelelser om Grønland 45:399–406, pl 26.

Nielsen, C. 1964. Studies on Danish Entoprocta.—Ophelia 1:1–76.

———. 1966. On the life-cycle of some Loxosomatidae (Entoprocta).—Ophelia 3:221–247.

———. 1989. Entoprocts.—Synopses of British Fauna, New Series 41:1–131.

———. 1996. Three new species of *Loxosoma* (Entoprocta) from Phuket, Thailand, with a review of the genus.—Zoologica Scripta 25:61–75.

———. 2001. Animal Evolution, 2nd ed. Oxford University Press, New York, 563 pp.

Prenant, M., & G. Bobin. 1956. Bryozoaires. Première Partie. Entoproctes, Phylactolèmes, Cténostomes.—Faune de France 60:1–398.

Ruppert, E. E., & R. D. Barnes. 1994. Invertebrate Zoology, 6th ed. Saunders College Publishers, Philadelphia, 1056 pp.

Ryland, J. S., & A. P. Austin. 1960. Three species of Kamptozoa new to Britain.—Proceedings of the Zoological Society of London 133:423–433.

Salvini-Plawen, L. v. 1968. Neue Formen im marinen Mesopsammon: Kamptozoa und Aculifera.—Annalen des Naturhistorichen Museums in Wien 72:231–272 + pls. 1–9.

Schmidt, O. 1876. Die Gattung *Loxosoma.*—Archiv für mikroskopische Anatomie 12:1–14.

Soule, D. F., & J. D. Soule. 1965. Two new species of *Loxosomella,* Entoprocta, epizoic on Crustacea.—Occasional Papers of the Allan Hancock Foundation 29:1–19.

Wasson, K. (2002) A review of the invertebrate phylum Kamptozoa (Entoprocta) and synopsis of kamptozoan diversity in Australia and New Zealand.—Transactions of the Royal Society of South Australia 126:1–20.

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