





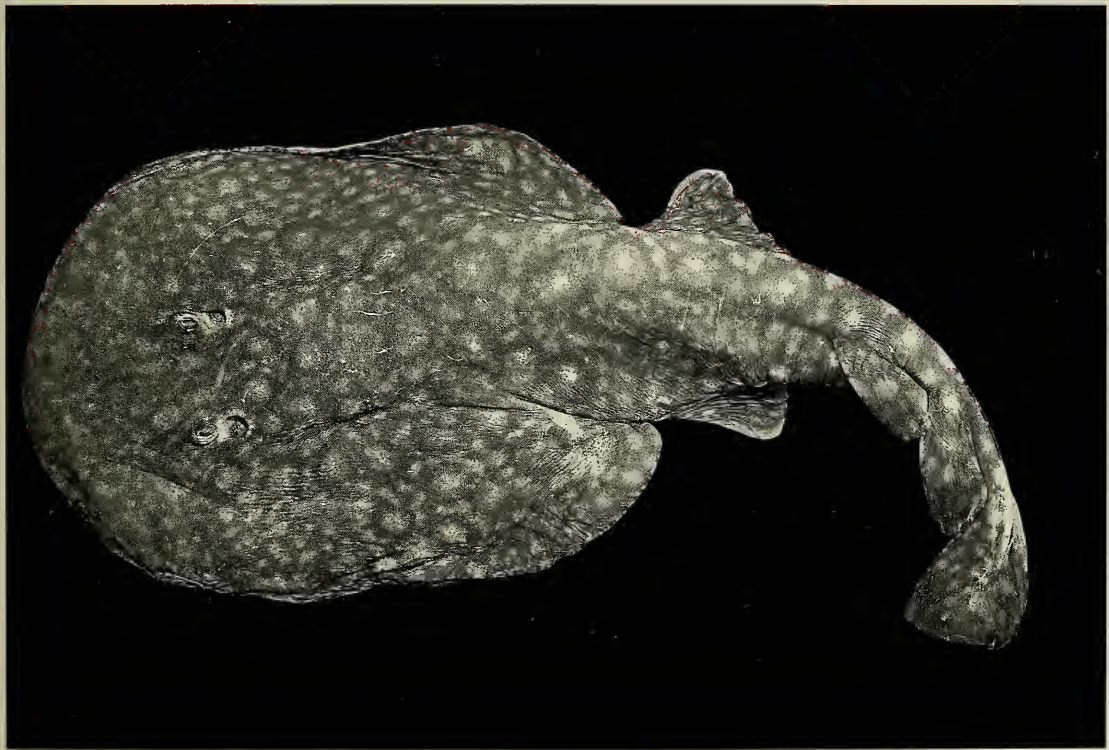




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**A new species of electric ray, *Narcine leoparda*, from the tropical eastern Pacific Ocean (Chondrichthyes: Torpediniformes: Narcinidae)**

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*Abstract.*—A new species of electric ray, *Narcine leoparda*, is described from 17 specimens collected from four localities off the southern Pacific coast of Colombia, in shallow waters up to 35 m in depth. *Narcine leoparda* is distinguished from all other species of *Narcine* by its unique dorsal color pattern, composed of numerous small white to creamy-white spots and/or ocelli that are also present on dorsal and caudal fins, over a brown to reddish-brown background. Other characters that in combination further distinguish this new species include broadly rounded tooth bands that are sub-equal in width, tail length shorter than or sub-equal to disc width or length, spiracles devoid of external papillae, lateral tail fold originating under first dorsal fin base, and second dorsal fin usually slightly greater than first in both height and length of base. *Narcine leoparda* is similar in overall aspect and proportional measurements to *N. vermiculatus*, also from the tropical eastern Pacific (Gulf of California south to Costa Rica), but dorsal coloration easily distinguishes individuals of all sizes of both species, which do not co-occur. *Narcine leoparda* is the third valid species of *Narcine* from the eastern Pacific Ocean.

Species of the electric ray genus *Narcine* Henle, 1834 are small to medium-sized batoids that are more diverse in the tropical Indo-west Pacific region, where at least 15 valid species are known to occur (Carvalho et al. 2000). In contrast, only two previously described species of *Narcine* are here accepted as valid from the eastern Pacific Ocean: *Narcine entemedor* Jordan & Starks, 1895 and *Narcine vermiculatus* Breder, 1928. *Narcine entemedor* has erroneously been considered a junior synonym of *N. brasiliensis* (= *N. bancroftii*) by many recent authors (Bussing & López S. 1994, Castro-Aguirre & Pérez 1996), who have followed the otherwise excellent revision of Bigelow & Schroeder (1953) (cf. Beebe & Tee-Van 1941, McEachran 1995). *Narcine schmitti* Hildebrand, 1948, described from a single specimen from the Gulf of California, has previously been considered to be a valid species as well (Bigelow & Schroe-

der 1953, Castro-Aguirre & Pérez 1996), but was synonymized with *N. vermiculatus* by Carvalho (1999a), who revised the genus. A third and very distinctive species of *Narcine* has been collected from shallow waters off the Pacific coast of southern Colombia, and is described below as a new species.

#### Methods

Measurements on the holotype and 12 paratypes were taken with electronic calipers in a straight line, point-to-point to the nearest tenth of a millimeter. Large specimens requiring measurements of 150 mm or more were measured with the aid of a steel ruler or tape measure, and are expressed to the nearest millimeter. All measurements are presented in Table 1, and are expressed as proportions of total length, following Carvalho (1999a). Measurements of

electric rays are subject to discrepancy due to preservational variations, and should be interpreted with caution if specimens appear damaged or distorted (Fechhelm & McEachran 1984, Carvalho 1999b). Measurements are as follows: total length (TL, from tip of snout to posteriormost tip at mid-caudal height; in millimeters, independent variable from which all proportional values are derived); disc width (DW, across widest aspect of disc, usually close to level of third gill openings); disc length (DL, from anterior snout region to greatest disc length, lateral to pectoral axil); preorbital snout length (PBS, from in between anterior level of eyes to anterior margin of snout); preoral snout length (POS, from top of lower tooth band to anterior margin of snout); prenasal snout length (PNS, from in between anterior level of nostrils to anterior snout margin); snout to greatest disc width (SDW, from anterior snout to level of greatest disc width, measured over mid-disc); interorbital distance (IOD, straight distance between inner margins of orbits); eye length (EL, between anterior and posterior margins of eye); interspiracular distance (ISD, between inner margins of spiracles); spiracle length (SPL, greatest antero-posterior distance through spiracle); spiracle width (SPW, greatest lateral extent of spiracle); mouth width (MW, distance between mouth corners, measured between junction of upper and lower labial cartilages on each side of jaws); upper tooth band width (UTB, width of exposed upper tooth band in between posterior margin of lips [formed by the upper labial cartilages], close to mouth opening); lower tooth band width (LTB, width of exposed lower tooth band at anterior margin of lips [formed by the lower labial cartilages], close to mouth opening); nasal curtain width (NCW, width of nasal curtain at greatest width below nostrils); nasal curtain length (NCL, length of nasal curtain from level of anterior margin of nostrils to posterior-most point at midline of nasal curtain); distance between nostrils (DBN, between inner margins of nos-

trils); distance between first gill openings (FGO, between inner margins of first pair of gill openings); distance between last gill openings (LGO, between inner margins of last pair of gill openings); branchial basket length (BBL, between first and last gill openings); pelvic fin length (PFL, length of pelvic fin from insertion to posterior-most point, measured ventrally); pelvic fin width (PFW, distance between outer-most corners of pelvic fins, from tip to tip, measured ventrally); anterior margin of pelvic fin (AMP, greatest extent from insertion to outer-most corner of pelvic fin); posterior margin of pelvic fin (PMP, greatest extent from outer-most corner to posterior-most point of pelvic fin); tail width (TW, extent across base of tail at greatest width, measured dorsally); height of first dorsal fin (HFD, distance from greatest height at apex to mid-base of first dorsal fin); length of first dorsal fin (LFD, greatest length of base of first dorsal fin); height of second dorsal fin (HSD, distance from greatest height at apex to mid-base of second dorsal fin); length of second dorsal fin (LSD, greatest length of base of second dorsal fin); length of dorsal lobe of caudal fin (LDC, distance from origin on dorsal caudal peduncle to posterior-most tip of caudal fin); length of ventral lobe of caudal fin (LVC, distance from origin on ventral caudal peduncle to posterior-most tip of caudal fin); height of dorsal lobe of caudal fin (HDC, measured vertically from uppermost tip of caudal fin apex to base of dorsal lobe on tail); height of ventral lobe of caudal fin (HVC, measured vertically from lower-most tip of caudal fin to base of ventral lobe on tail); height of caudal fin (HC, greatest distance between dorsal and caudal fin margins, does not equal HDC + HVC); distance between dorsal fins (DBD, distance between posterior tip of first dorsal fin base and anterior tip of second dorsal fin base); distance between second dorsal and caudal fins (SDC, from posterior tip of second dorsal fin to dorsal origin of caudal peduncle); snout to cloaca length (SCL, distance between anterior snout margin to or-



igin of cloaca); cloaca to caudal fin length (CLC, distance from posterior tip of cloaca to posterior margin of caudal fin, equals tail length); snout to first dorsal fin length (SFD, distance from anterior margin of snout to origin of first dorsal fin); electric organ length (EOL, from anterior margin to posterior margin of electric organ, measured ventrally); electric organ width (EOW, greatest width of electric organ at its mid-length, close to level of third gill slit, measured ventrally); clasper length (CL, from posterior tip of cloaca to distal-most tip of clasper).

Counts were taken from radiographs, and are summarized in Table 2. Usage of meristic characters also follows Carvalho (1999a). Counts include: propterygium radials (PRO); mesopterygium radials (MES); metapterygium radials (MET); total pectoral radials (TPR = PRO + MES + MET); pelvic radials (PVR); first dorsal fin radials (FDR); second dorsal fin radials (SDR); dorsal lobe of caudal fin radials (DCR); ventral lobe of caudal fin radials (VCR, includes radial situated in between dorsal and ventral aspects of caudal fin); total caudal radials (TCR = DCR + VCR); exposed vertical tooth rows on upper tooth band (UTR, corresponds to tooth rows visible externally on upper jaw when mouth is closed); exposed vertical tooth rows on lower tooth band (LTR, corresponds to tooth rows visible externally on lower jaw when mouth is closed); trunk vertebral centra (TC, from first whole distinguishable centrum in synarcual to anterior margin of pelvic girdle, further explained below); pre-caudal vertebral centra (PC, centra from anterior margin of pelvic girdle to origin of upper lobe of caudal fin); caudal vertebral centra (CC, from first centrum in caudal fin to last distinguishable centrum); total vertebral centra (TV = TC + PC + CC); ribs (R, elongated pleural ribs articulating with paired hemal spines, located posteriorly on disc dorsal to pelvic girdle area). The division of the vertebral column into trunk and pre-caudal centra uses the pelvic girdle

as a landmark because it was not always possible to discern monospondylous to diplospondylous transitions from radiographs. Radial elements of the pectoral and dorsal fins that are joined at base were counted as two separate elements. Tooth counts were taken under stereomicroscope and follow the method outlined in Stehmann (1978), where rows are counted following a cranial-caudal orientation. Only exposed tooth rows were counted, i.e., rows visible on tooth bands when mouth is closed (dissection is necessary to count internal tooth rows because of the strong labial cartilages immediately lateral to the tooth bands, and dissection was not always possible). Tooth counts are expressed as fractions (numerator designates the number of exposed rows on the upper jaws, and the denominator indicates the same on the lower jaws).

Comparative material of all species of *Narcine* was used for the present study, and is listed in Carvalho (1999a). Institutional abbreviations follow Leviton et al. (1985). The term "preadult" is used to indicate specimens that are not sexually mature (or "adult"). Clasper rigidity was used as an indicator of sexual maturity for males, because gonadal maturity usually closely follows clasper calcification.

Order Torpediniformes Berg, 1940  
 Family Narcinidae Gill, 1862  
 Genus *Narcine* Henle, 1834  
*Narcine leoparda*, new species  
 Figs. 1–4; Tables 1–2

*Holotype*.—USNM 222200, 277 mm TL adult female, south of Buenaventura, Colombia, 02°56'N, 078°07'W, 0–16.6 m (0–5 fathoms), R/V *Cacique* (LK 69–29, L. Knapp), 20. ix. 1969. (Fig. 1).

*Paratypes*.—USNM 222198 (7 specimens, adult and preadult), 200 mm TL female (with two pups), 174 mm TL male, 174 mm TL female, 110 mm TL female (cleared and stained), one dissected specimen (no size data available, but probably close to 150 mm TL), south of Buenaven-

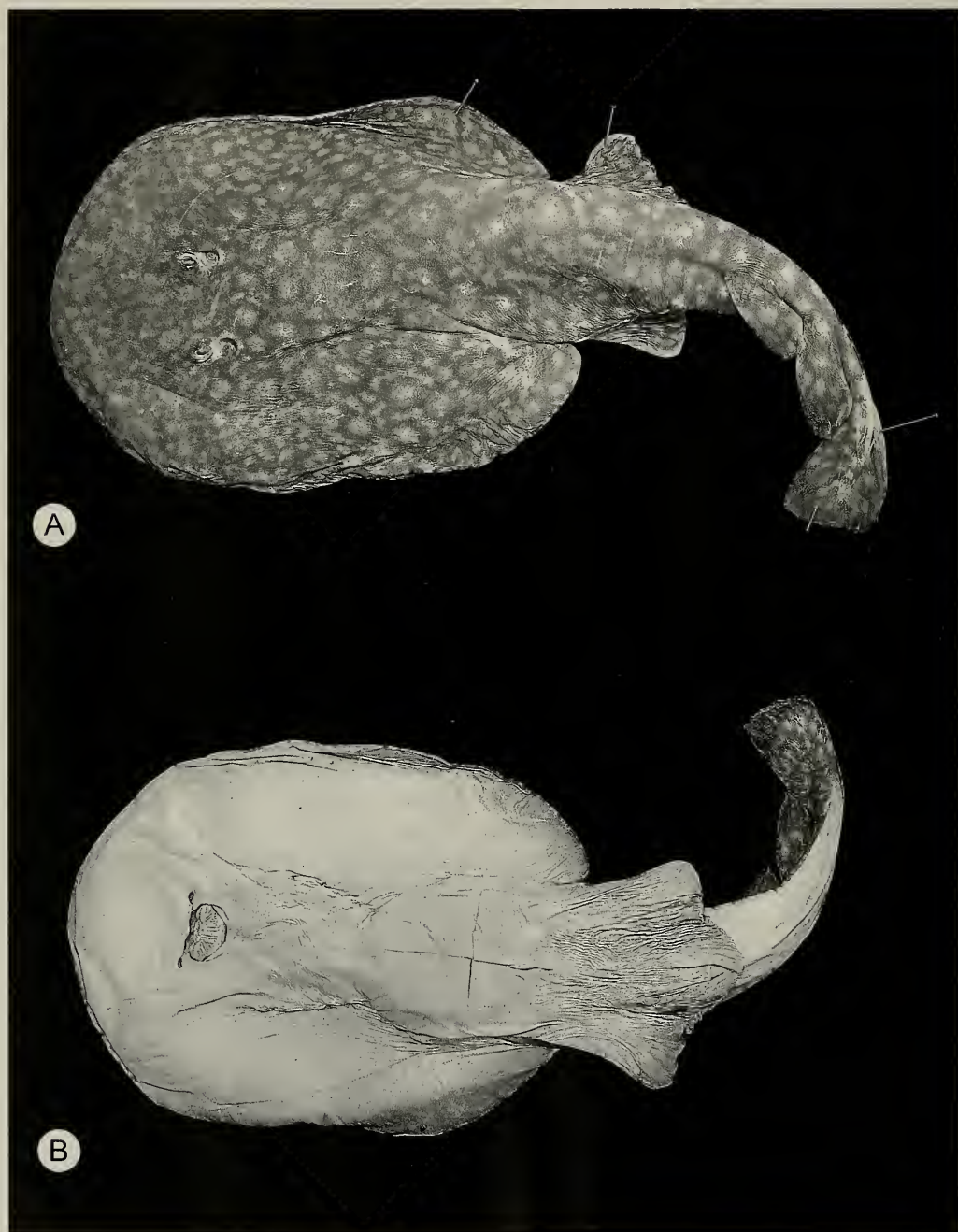


Fig. 1. Dorsal (A) and ventral (B) view of holotype of *Narcine leoparda*, n. sp. (USNM 222200, 277 mm TL adult female, from south of Buenaventura, Colombia, 02°56'N, 078°07'W, 0–16.6 m).

tura, Colombia, 03°14'N, 077°33'W, 5–7 m, sta. 357, FAO, 25. I. 1969; USNM 222199 (6, all preadult), 168 mm TL female, 163 mm TL female, 146 mm TL female, 130

mm TL female, 127 mm TL female, 86 mm TL male, south of Tumaco (Punta Manglares), Colombia, 01°39'N, 079°02'30"W–01°37'30"N, 079°02'00"W, 33.3 m (10 fath-

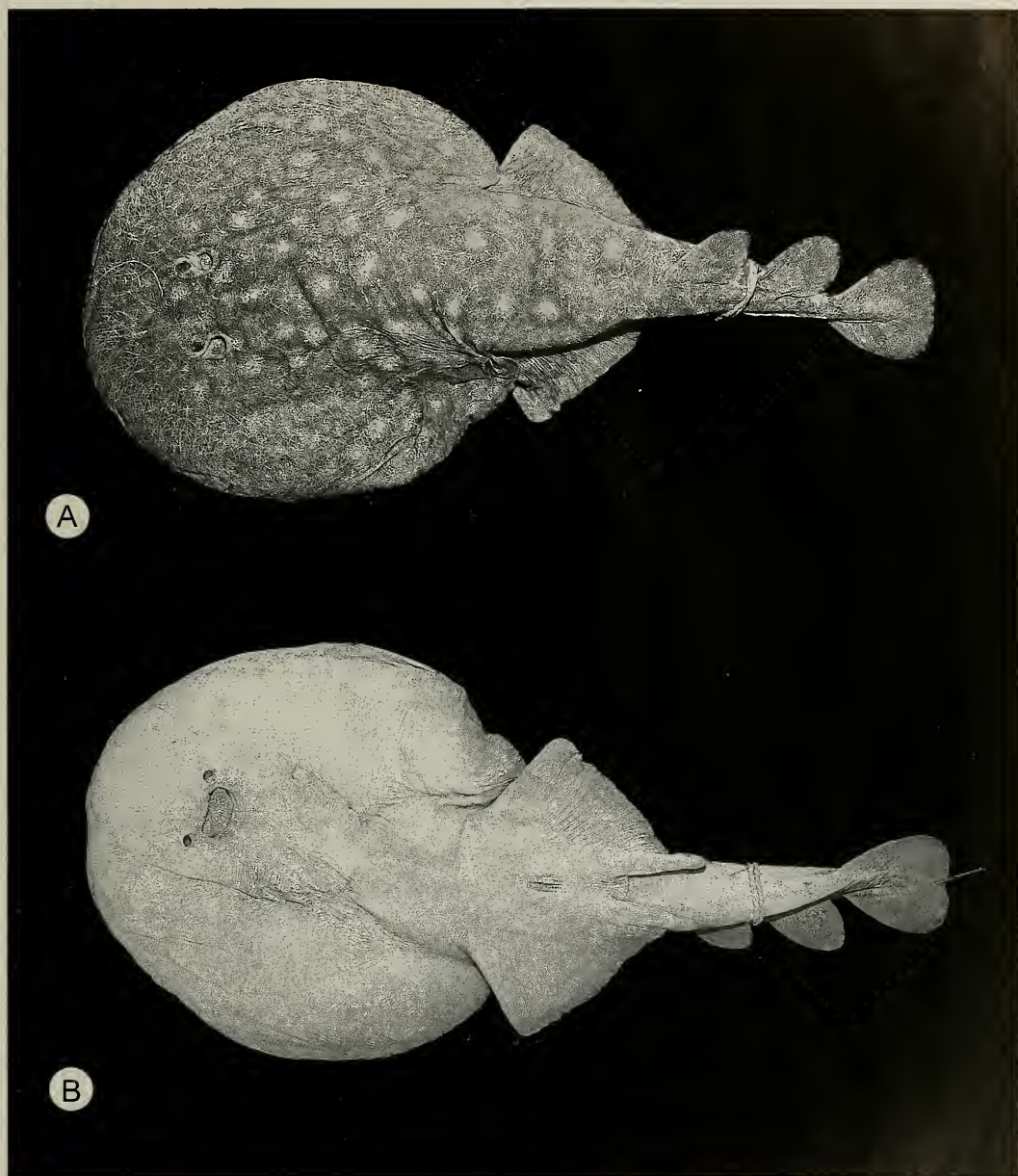


Fig. 2. Dorsal (A) and ventral (B) view of paratype of *Narcine leoparda*, n. sp. (USNM 235919, 206 mm TL adult male, south of Tumaco, Colombia,  $01^{\circ}39'N$ ,  $079^{\circ}02'30''W$ – $01^{\circ}37'30''N$ ,  $079^{\circ}02'00''W$ , 33.3 m). Caudal fin is downturned in (B).

oms), sta. 343 (1:55 p.m.–2:55 p.m.), R/V *Inderena* (LK 70-12, L. Knapp), 27. x. 1970; USNM 222498, 272 mm TL adult female (same data as holotype); USNM 222500, 230 mm TL adult male,  $01^{\circ}35'05''N$ ,  $079^{\circ}03'00''W$ – $01^{\circ}37'00''N$ ,  $079^{\circ}04'00''W$ ,

south of Tumaco (Punta Manglares), Colombia, 9.15 m, sta. 342, R/V *Inderena*, (LK 70-11, L. Knapp), 27. x. 1970; USNM 235519, 206 mm TL adult male, data as for USNM 222199.

*Diagnosis*.—A species of *Narcine* distin-

guished from all others by its unique dorsal coloration composed of numerous small white to creamy-white spots and/or ocelli on disc and dorsal and caudal fins, over a reddish-brown or brown background. Additional characters that in combination diagnose this new species include: tail length shorter than disc width or length, upper and lower external tooth bands subequal in width, spiracles with smooth rims devoid of external papillae, second dorsal fin usually slightly larger than first in both height and length of base, and lateral tail folds originating under level of first dorsal fin base.

*Description.*—Measurements and counts are summarized in Tables 1 and 2, respectively.

External morphology: Disc rounded to somewhat oval, generally about as wide as long. Disc width is somewhat more variable than disc length (see standard deviations in Table 1). Disc overlaps origin of pelvic fins only slightly, and with a very small free lobe posteriorly where it contacts sides of trunk. Greatest width of disc is just posterior to its mid-length, but somewhat variable in specimens. Snout broadly rounded anteriorly. Preorbital snout corresponds to about one-third in disc length. Electric organ originating just anterior to level of eyes dorsally and at level of nostrils ventrally. On ventral side, electric organs extend to beyond level of last gill-slit; electric organs difficult to discern in dorsal view. Gill-slits small, only slightly curved and in more or less straight line from first to last gill slit. Distance between last gill-slits generally less than branchial basket length. Spiracles and eyes adjacent, without a distinctive separation. Spiracles with somewhat developed rims devoid of papillae, circular to oval, and usually slightly longer than wide. Eyes relatively small, about as long as spiracles.

Nasal curtain wider than long (Fig. 3C), with more or less straight posterior margin, but faintly developed central lobe present in some specimens. Nostrils small and circular; distance between nostrils slightly greater than nasal curtain width at posterior mar-

gin. Prenasal snout length generally less than preorbital snout length. Mouth about as wide as distance between nostrils. Upper and lower tooth bands more or less equal in width and both circular in outline. Teeth in 12/8–16/12 exposed rows in specimens about 175 mm total length or larger, but a 146 mm total length female has 11/13 exposed teeth rows. Teeth relatively small, set in quincunx arrangement and with single, sharp cusp, even on small specimens (e.g., 146 mm TL specimen); inner rows with very sharp teeth. Crowns wider-than-long at bases; tooth bases roughly sub-circular.

Posterior lobes of pelvics more or less straight, with only a small free lobe where they contact claspers or lateral aspect of trunk (in females). Lateral corners of pelvics blunt, not acute. Pelvics generally extend from underneath posterior disc region to underneath beginning of first dorsal fin base. Claspers of larger males extend posteriorly to close to posterior aspect of first dorsal fin base, but do not project greatly beyond pelvic fins. Tail relatively short as measured from cloaca, shorter than snout to cloaca length, and much shorter than disc width and length. Tail sub-circular in cross section; its width at base moderately broad and somewhat variable. Lateral tail fold extending as a thin keel in a straight line laterally on tail, from level of mid- to posterior first dorsal fin base to lateral aspect of caudal peduncle. Second dorsal fin only slightly taller than first dorsal fin, and with a slightly longer base. Dorsal fins similar in shape, and with a small free lobe posteriorly (Fig. 3B). Caudal fin with angular apex, relatively tall and not elongated, and with more or less straight posterior margin. Length of dorsal and ventral lobes of caudal about equal, but dorsal lobe slightly taller than ventral lobe. Distance between second dorsal and caudal fins generally slightly greater than distance between dorsal fins.

Sensory pores indistinct, few in number, and scattered on ventral snout area and along margins of electric organs both dorsally (hyomandibular canal) and ventrally

Table 1.—Morphometric comparisons for *Narcine leoparda*, n. sp. *n* is number of specimens from which means and standard deviations (SD) were calculated and include specimens greater than 110 mm TL. See Methods section for abbreviations. Holotype: USNM 222200; Paratypes: USNM 222198, USNM 222199, USNM 222498, USNM 222500, USNM 235519.

	Holotype	Paratypes	<i>n</i>	<i>x</i>	<i>SD</i>
TL (mm)	277.0	110.0–272.0	13	—	—
DW (%)	48.7	46.6–57.3	13	52.0	3.5
DL (%)	53.1	50.0–58.2	13	53.4	2.3
PBS (%)	13.3	12.7–15.7	13	14.6	1.0
POS (%)	14.7	14.5–17.5	13	15.5	1.1
PNS (%)	12.3	12.0–14.4	13	13.0	0.9
SDW (%)	31.8	21.1–41.0	13	32.3	3.0
IOD (%)	6.4	6.0–8.5	13	7.4	0.8
EL (%)	2.3	1.8–3.0	13	2.4	0.4
ISD (%)	6.0	5.8–8.5	13	7.1	0.8
SPL (%)	2.2	2.1–3.0	13	2.4	0.3
SPW (%)	1.6	1.8–2.7	13	2.1	0.3
MW (%)	5.3	5.3–6.7	13	5.9	0.4
UTB (%)	2.3	2.3–3.2	13	2.6	0.3
LTB (%)	2.1	1.9–2.8	13	2.3	0.3
NCW (%)	5.0	5.1–6.6	8	5.7	0.7
NCL (%)	1.5	1.0–2.4	11	1.8	0.4
DBN (%)	5.6	5.5–7.3	13	6.1	0.5
FGO (%)	12.3	11.5–14.5	13	13.3	0.8
LGO (%)	6.9	5.9–9.5	13	7.1	0.9
BBL (%)	9.1	7.2–11.0	13	9.8	1.0
PFL (%)	19.9	17.8–23.5	13	20.7	1.9
PFW (%)	26.7	28.7–36.8	13	33.5	3.0
AMP (%)	12.7	11.3–14.2	13	12.4	0.8
PMP (%)	19.0	15.5–23.2	13	19.5	2.6
TW (%)	15.4	16.6–21.6	13	18.9	1.8
HFD (%)	7.8	6.8–9.3	13	8.2	0.8
LFD (%)	6.3	4.5–7.6	13	5.9	0.7
HSD (%)	8.8	7.5–9.9	13	8.8	0.6
LSD (%)	6.1	5.5–7.3	13	6.2	0.5
LDC (%)	11.8	11.8–13.1	13	12.3	0.4
LVC (%)	11.0	11.6–14.1	13	12.7	1.0
HDC (%)	4.7	3.2–5.0	13	4.4	0.5
HVC (%)	3.1	2.2–4.7	13	3.7	0.8
HC (%)	9.2	7.5–12.5	13	10.3	1.3
DBD (%)	2.5	2.2–3.4	13	2.6	0.4
SDC (%)	3.2	2.5–3.9	13	3.3	0.5
SCL (%)	53.1	50.0–54.8	13	52.6	1.3
CLC (%)	43.3	39.7–47.0	13	42.6	2.0
SFD (%)	65.0	65.4–70.1	13	68.0	1.6
EOL (%)	24.2	22.8–29.2	13	25.0	1.9
EOW (%)	10.1	9.8–12.1	13	10.7	0.7
CL (%)	—	15.7–17.0	3	16.2	0.7

(ampullary pores only). Few sensory pores dorsally in more or less straight rows on snout region. Pores of lateral canal on lateral aspect of tail running dorsal to lateral tail fold, apparently in a straight line and terminating on lateral aspect of caudal base.

Lateral tail fold pores are very scattered and not numerous. Pores on ventral snout area in more or less parallel antero-posterior rows, not extending posteriorly beyond level of nostrils.

Coloration: In preservative, dorsal back-

Table 2.—Meristic features of *Narcine leoparda*, n. sp. A) USNM 222200 (holotype); B) USNM 222500; C) USNM 222498; D) USNM 235519; E) USNM 222199; F) USNM 222199. B–F represent paratypes. Dashes represent counts not available in radiographs. See Methods section for abbreviations.

	A	B	C	D	E	F	Range
TL (mm)	277	230	272	206	163	168	163–277
PRO	18	17	17	17	—	18	17–18
MES	6	6	6	5	—	6	5–6
MET	11	10	12	9	—	—	9–12
TPR	35	33	35	31	—	—	31–35
PVR	19	17	19	19	20	19	17–20
FDR	8	8	6	8	—	8	6–8
SDR	10	9	7	10	10	10	7–10
DCR	26	17	23	21	—	—	17–26
VCR	27	22	24	25	—	—	22–27
TCR	53	39	47	46	—	—	39–53
UTR	16	15	16	12	13	11	11–16
LTR	9	12	13	9	10	8	8–13
TC	28	24	24	26	28	24	24–28
PC	59	59	59	59	60	59	59–60
CC	24	20	23	22	24	23	20–24
TV	111	103	106	107	112	106	103–112
R	8	8	7	8	7	8	7–8

ground coloration composed of a light, dark, reddish- or purplish-brown background, with white to creamy-white spots or ocelli covering most of disc region posterior to eyes, and extending posteriorly over tail. Dorsal and caudal fins also with small white spots on all specimens. Spots and ocelli generally not fused into irregularly shaped blotches, especially in smaller specimens where spots are clearly separated from each other (Fig. 4). Spots are round to slightly oval, varying in definition from sharply defined to somewhat fuzzy. Spots may be present between eyes, especially in smaller specimens, or anterior to eyes over dorsal snout region. Smaller specimens with spots ranging in size from small (about equivalent to diameter of eyes and spiracles) to slightly larger (about twice eye-diameter). Larger specimens have more variable coloration, with ocelli closely (holotype; Fig. 1) or loosely packed together (paratype USNM 235919; Fig. 2). Ocelli composed of central white to creamy-white spot, surrounded by ring of darker brown. Dorsal coloration mostly restricted to background coloration in two large paratypes

(USNM 222498 [Fig. 3A] and USNM 222500), but remnants of ocelli are visible, and small white spots remain present on dorsal and caudal fins. Ventral coloration uniform creamy-white, but some larger adults may have the posterior disc and pelvic fins outlined in light brown.

Skeletal features: Examination of skeletonized and cleared and stained specimens (both from USNM 222198) reveal that *Narcine leoparda* shares with other species of *Narcine*, including the type-species *N. brasiliensis* (von Olfers, 1831), the following features indicative of generic monophyly (Carvalho 1999a): fused hypobranchial plates with sinuous external margins articulating with ceratobranchials 2–4, slender posterior projection of the heart-shaped basibranchial copula, separation of ceratohyal and “hypobranchial 1” by a small gap, and presence of a separate facio-palatine foramen in the orbit. In general aspects, the skeletal anatomy of *Narcine leoparda* is similar to that of *N. brasiliensis*, with relatively wide and proximally branched antorbital cartilages that bear numerous digitiform projections distally. Lateral rostral

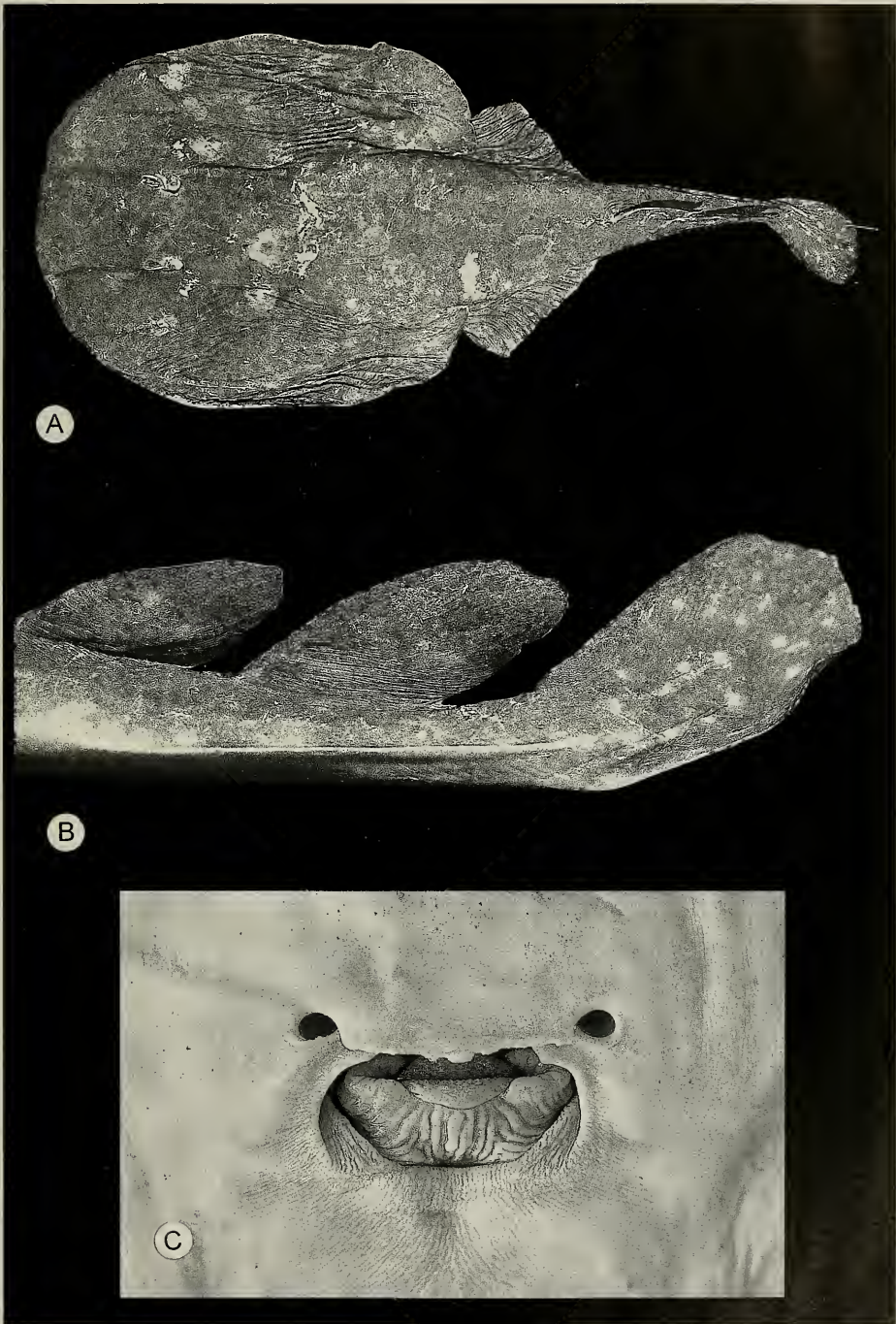


Fig. 3. A) Dorsal view of paratype of *Narcine leoparda*, n. sp. (USNM 222498, 272 mm TL adult female, from south of Buenaventura, Colombia, 02°56'N, 078°07'W, 0–16.6 m); B) lateral tail region of USNM 222498; C) nasoral region of USNM 222498. Note that caudal fin is downturned in (A).

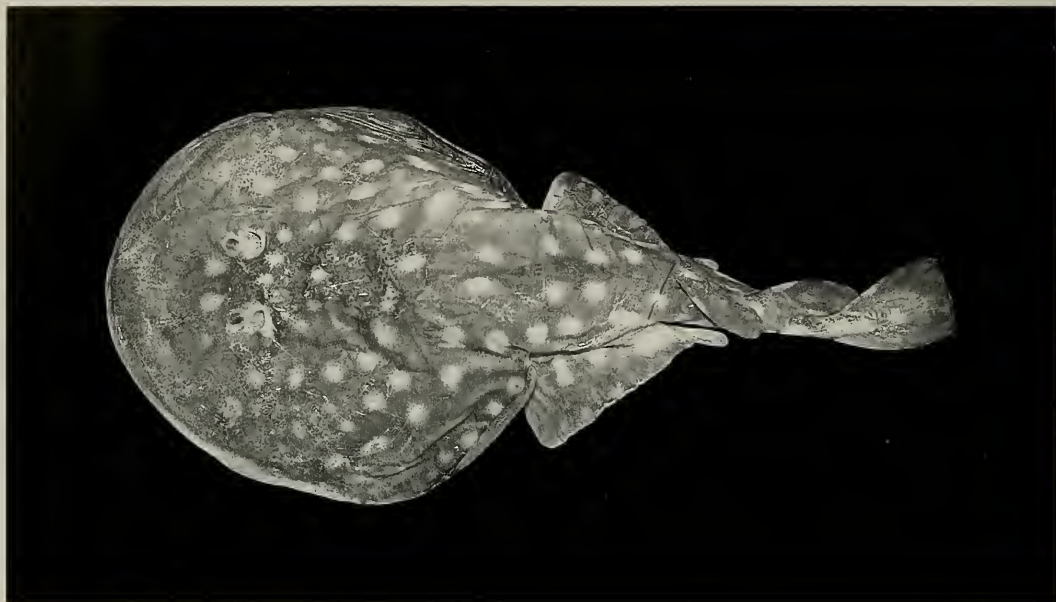


Fig. 4. Paratype of *Narcine leoparda*, n. sp. (USNM 222198, 174 mm TL male, south of Buenaventura, Colombia, 03°14'N, 077°33'W, 5–7 m).

processes are also present anteriorly adjacent to the rostral fenestra of neurocranium, providing further endoskeletal support to anterior margin of snout. Dorso-lateral projections of the nasal capsules (“nasal capsule horns” of Carvalho 1999a) are also present. One pair of triangular labial cartilages on each side of jaw symphysis give support to “lips” surrounding external tooth bands. Propterygium is subdivided into four segments; mesopterygium is small, slender and antero-laterally directed, and the metapterygium is subdivided and inconspicuous. Pelvic girdle with two pre-pelvic processes with expanded, flattened tips, and posteriorly curved iliac processes.

*Etymology.*—*leoparda*, modified from leopardus (Latin for leopard), in reference to its distinctive dorsal color pattern; interpreted as a feminine noun.

*Geographical distribution.*—*Narcine leoparda* is known from four localities on the continental shelf of Colombia, south of Buenaventura and Tumaco (off Punta Manglares), in near-shore waters ranging from 5 to 33 m in depth.

## Discussion

*Comparisons with congeners.*—Only two other valid species of *Narcine* occur in the eastern Pacific Ocean: *N. entemedor* and *N. vermiculatus*. Among these, *N. leoparda* is most similar to *N. vermiculatus* Breder, 1928, which occurs farther north along the continental shelf of Central America (reaching as far south as Costa Rica; McEachran 1995, Carvalho 1999a). Both species are clearly distinct in dorsal color pattern. *Narcine leoparda* possesses white to creamy-white spots that may be substituted by ocelli in larger specimens, with spots not fused into larger blotches or vermiculations, as in *N. vermiculatus*, and generally smaller than the markings present in the latter species. The spots in *Narcine leoparda* are present even on newly born individuals or pups extracted from uteri (USNM 222198). Newly born specimens of *N. vermiculatus*, however, clearly display laterally elongated blotches or stripes and vermiculations that are characteristic of this species (e.g., Beebe & Tee-Van 1941, fig. 1, pl. 1; Carvalho



1999a). In *N. leoparda*, the spots may be lost in larger specimens, as USNM 222500 and USNM 222498 have more uniform dorsal coloration without clearly defined spots over disc. However, small white or creamy-white spots are still present over dorsal and caudal fins, and closer inspection reveals that both specimens previously had dorsal spots over the disc as well. *Narcine leoparda* also differs from *N. vermiculatus* in having lateral tail folds that begin underneath first dorsal fin base (either at its mid-length or slightly farther posteriorly), and not in between the dorsal fins. Other differences that further separate both species are disc proportions. Disc is generally more rounded in *Narcine leoparda*, with a greater mean disc length (53.4% of TL), compared to *N. vermiculatus* (48.4% of TL), which is also reflected in relative origin of first dorsal fin (originating farther posteriorly in *Narcine leoparda* [mean distance between snout and first dorsal origin is 68.0% of TL; compared to 64.1% of TL for *N. vermiculatus*]). Both species also have disjunct, allopatric distributions, as *N. vermiculatus* has not been collected south of Costa Rica.

*Narcine leoparda* is easily distinguished from *N. entemedor*, with which it co-occurs, in presenting spiracles devoid of papillae, in morphometric proportions, size of adults and coloration (data for *N. entemedor* from Carvalho 1999a). *Narcine entemedor* generally has an olivaceous brown background color, usually with dark blotches on disc of larger specimens, and symmetrically arranged ocelli in smaller specimens. These ocelli, however, are very different from those present in the holotype of *N. leoparda* in both color and arrangement (ocelli in *N. entemedor* have dark center and are fewer in number, as only four or five are usually present on disc). *N. entemedor* is a much larger species (up to 750 mm TL) compared to *N. leoparda* (largest specimen is 356 mm TL). Males of *N. entemedor* become sexually mature only between 340 and 370 mm TL (cf. to 180 mm TL for *N. leoparda*, see below). Numerous specimens of *N. ente-*

*medor*, and of *N. vermiculatus*, have been thoroughly examined from throughout their respective ranges, and are further described in Carvalho (1999a).

*Narcine leoparda* is easily distinguished from most other species of *Narcine* in morphometric proportions (20 species of *Narcine* are recognized as valid in Carvalho 1999a). In *N. leoparda*, tail length (as measured from cloaca) is subequal to, and generally less than, disc width or length, but tail length is much greater than the disc in the five Australian species of *Narcine* (*N. tasmaniensis*, *N. westraliensis* and three undescribed species) and in *N. rierai* from the western Indian Ocean. Both upper and lower tooth bands are broadly rounded and of subequal width in *N. leoparda*, contrasting to two southeast Asian species (*N. breviliata* and an undescribed species) in which the tooth bands are roughly triangular in shape, and in which the upper tooth band is much wider than the lower. In *N. leoparda*, the second dorsal fin is subequal to, or slightly greater than, the first dorsal fin in height and length of base, separating it from two undescribed western and northern Indian Oceans forms, in which the first dorsal fin is greater than the second. Both western Atlantic species (*N. bancroftii* and *N. brasiliensis*) also have spiracles with numerous papillae, as in *N. entemedor*, and are therefore easily distinguished from *N. leoparda*. The remaining five species of *Narcine* (*N. timlei*, *N. maculata*, *N. lingula* and two undescribed species from the northern Indian Ocean and Indonesia) are distinct from *N. leoparda* in coloration, as they have either elaborate dorsal patterns composed of brown spots and/or blotches over a lighter background, or a uniform coloration (*N. timlei*).

*Biological notes.*—One partially dissected female of 277 mm TL (holotype, USNM 222200) had a large egg mass in the right uterus, while a female of 200 mm TL (USNM 222198) contained two small late-term pups in the left uterus. Both pups are female, just slightly over 50 mm TL, and

the smallest one still has remnants of a yolk-stalk. No external gill-filaments or external teeth are present, but few internal teeth with small cusps can be observed. Both specimens were probably very close to birth. One small male of 127 mm TL still has a fading yolk-scar and claspers that do not project beyond the distal tips of pelvic fins. Males probably mature at around 180 mm TL, as a 174 mm TL male has claspers almost completely firm. There are 10 spiral valve turns in the intestine of at least one specimen examined (USNM 222198, cleared and stained). Small, unidentified ctenoid scales were present in the mouths of two specimens (USNM 222500 and USNM 222199, 168 mm TL), and therefore *N. leoparda* feeds also on fishes as do other species of the genus.

Key to the Eastern Pacific species of *Narcine*

- 1a. Spiracles with papillae present on outer rim . . . . . *N. entemedor*
- 1b. Spiracles devoid of any papillae . . . . . 2
- 2a. Dorsal coloration composed of horizontally elongated, white or creamy-white stripes and blotches . . . . . *N. vermiculatus*
- 2b. Dorsal coloration with small white or creamy-white spots and/or ocelli, or relatively uniform in larger specimens with perhaps few spots over dorsal and caudal fins, but never with horizontally elongated stripes and blotches . . . . . *N. leoparda*

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## A new species of “Whale Catfish” (Siluriformes: Cetopsidae) from the western portions of the Amazon basin

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*Abstract.*—*Cetopsis parma*, a new species of the subfamily Cetopsinae of the catfish family Cetopsidae is described from locations in the Peruvian and Ecuadorian Amazon. The species differs from the other species in the subfamily by the combination of the presence of a single row of conical teeth on the dentary, the presence of a distinct blotch of dark pigmentation on the lateral surface of the body dorsal to the pectoral fin, and the possession of 44 or 45 vertebrae, 14 or 15 ribs, and 8 or 9 gill rakers.

*Resumo.*—*Cetopsis parma*, uma nova espécie da subfamília Cetopsinae da família de bagres Cetopsidae, é descrita com base em coletas realizadas na Amazônia Peruana e Equatoriana. Esta espécie difere das outras espécies na subfamília pela combinação da presença de uma única série de dentes cônicos no dentário, da presença de uma distinta mancha de pigmentação na superfície lateral do corpo dorsalmente à nadadeira peitoral, e da presença de 44 ou 45 vértebras, 14 ou 15 costelas, e 8 ou 9 rastros branquiais.

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The members of the Neotropical siluriform subfamily Cetopsinae are commonly called “Whale Catfishes” in English given the perceived similarity in overall form of cetaceans and some of the first described species of the subfamily. The reduced, or in one species absent, eyes typical of cetopsins are, in turn, the basis for their common name of “Ciego” (=Blind) or “Bagre Ciego” (=Blind Catfish) in various portions of their range. Cetopsins have long been a puzzle within catfish systematics. Recently de Pinna & Vari (1995), however, documented a number of unusual derived modifications which demonstrated that the Cetopsinae (the Cetopsidae of earlier authors) was monophyletic. The evidence indicated furthermore that the Cetopsinae was the sis-

ter group of what had previously been recognized as a separate family, the Helogenidae. de Pinna & Vari consequently united the Cetopsidae and Helogenidae of previous classifications in an expanded Cetopsidae. In commenting on this broader Cetopsidae, de Pinna (1998:292) subsequently noted that “there is some evidence that they occupy a markedly basal position within the siluriform cladogram,” thus making an understanding of the species diversity and intrarelationships within the family of particular import.

The recognized species diversity in the Cetopsinae has steadily increased within the last decade, with the 12 species of cetopsins considered valid by Burgess (1989) supplemented by four additional species subsequently described by Ferraris & Brown (1991), Lundberg & Rapp Py-Daniel

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(1994), and Ferraris (1996). Ongoing studies indicate that these 16 species are a substantial underestimate of the actual diversity in the subfamily. The species described in this paper is based on two specimens, one discovered by the first author during his examination of the Cetopsinae (Oliveira, 1988) and the second found by the second and third authors in the course of their revisionary study of that subfamily. The new species is described herein to make the name available for an ongoing phylogenetic analysis of the Cetopsidae and a revisionary study of the subfamily Cetopsinae.

#### Materials and Methods

The concepts of the Cetopsidae and Cetopsinae used in this paper are those proposed by de Pinna & Vari (1995). Standard length (SL) was measured with dial calipers to 1.0 mm. All measurements were taken as straight line distances between points. Head length (HL) was measured from the snout tip to the end of the fleshy gill cover. Interorbital width was taken as the shortest distance between the orbits, but is difficult to measure unambiguously. Vertebrae and unpaired fin rays were counted from radiographs. Vertebral counts included the four elements of the Weberian complex and one element for the ural complex and were separated into preanal, precaudal, and caudal elements. Total vertebrae is the sum of the precaudal and caudal vertebrae. In fin-ray counts, unbranched rays are indicated by lower case roman numerals and branched rays by Arabic numbers. The range of values for meristic and morphometric features in the species is presented first, followed by the values for the holotype in brackets. Institutional abbreviations are: Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM) and Museo, Escuela Politécnica Nacional, Quito, Ecuador (MEPN).

#### *Cetopsis parma*, new species

Fig. 1

*Holotype*.—MUSM 2266, 73 mm SL. Peru. Departamento de Ucayali, Provincia

Coronel Portillo, Río Tambo, Río Ucayali basin, Pucallpa, Atalaya (8°23'S, 74°32'W), collected by Hernán Ortega, 15 May 1986.

*Paratype*.—MEPN 1034, 170 mm SL. Ecuador. Provincia de Pastaza, Río Marañón basin, Río Pastaza system, near Río Chicherota, in vicinity of Montalvo (2°04'S, 76°58'W), collected by Roman Olalla and Gonzalo Herrera, February 1958.

*Diagnosis*.—The presence of a single row of teeth on the dentary in *Cetopsis parma* differentiates this species from all other cetopsins other than for *Cetopsis coecutiens* and *Hemicetopsis candiru*. The possession of conical rather than incisiform teeth distinguishes *Cetopsis parma* from *Hemicetopsis candiru* and the two species also differ in the overall form of the head and body. *Cetopsis parma* has a relatively stout body with the depth at the dorsal-fin origin approximately 3.7 times in SL and the pelvic-fin insertion at, or slightly posterior of, the vertical through the posterior of the dorsal-fin base whereas *Hemicetopsis candiru* has an elongate body with the body depth at the dorsal-fin origin approximately 5 to 5.5 times in SL and the pelvic-fin insertion distinctly posterior of the vertical through the posterior of the dorsal-fin base. *Cetopsis parma* differs from *C. coecutiens* in its possession of the diffuse dark patch on the lateral surface of the body dorsal to the pectoral fin (Fig. 1) which is lacking in the latter species. *Cetopsis parma* can be further differentiated from *C. coecutiens* in the total number of vertebrae (44 or 45 versus 47 to 50, respectively), number of gill rakers (8 or 9 versus 38 to 52, respectively), and number of ribs (14 or 15 versus 15 to 18, typically 16 or 17, respectively).

*Description*.—Body stout, slightly laterally compressed anteriorly, increasingly more so posteriorly. Body depth at dorsal-fin origin approximately 3.7–4.2 [3.7] times in SL, and slightly less than HL. Lateral line on body complete, unbranched, mid-lateral, and extending from vertical through pectoral-fin base to hypural plate. Dorsal profile of body straight and obliquely slant-

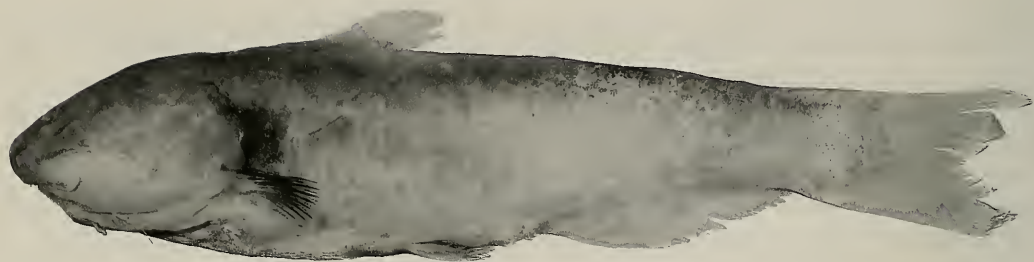


Fig. 1. Holotype of *Cetopsis parma*, new species; MUSM 2266, 73 mm SL; Peru, Departamento de Ucayali, Río Tambo, Pucallpa, Atalaya (8°23'S, 74°32'W).

ed from nape to dorsal-fin origin, straight from dorsal-fin origin to caudal-fin base. Ventral profile of body convex along abdomen, approximately straight, but posterodorsally slanted, along anal-fin base. Caudal-peduncle depth slightly greater than caudal-peduncle length in holotype, slightly greater than caudal-peduncle length in much larger paratype. Caudal peduncle distinctly compressed transversely.

Head in lateral view triangular with bluntly rounded snout. Dorsal profile of head gently convex from tip of snout to vertical through anterior margin of eye, more rounded from that line to nape. Ventral profile of head convex. Profile of snout in dorsal view broadly rounded. Profiles of postorbital portion of each side of head running in parallel. Dorsal surface of postorbital part of head with enlarged jaw musculature obvious. Laterosensory canals and pores on head not obvious.

Branchial membranes attached to isthmus posteriorly as far as vertical through pectoral-fin origin. Opercular opening moderate, extending ventral of horizontal through pectoral-fin origin for distance equal to snout length and dorsal of pectoral-fin origin for distance slightly less than snout length.

Eye situated on lateral surface of head; located one orbital diameter dorsal of horizontal through pectoral-fin origin; eye visible in lateral and dorsal views. Middle of orbit located slightly anterior to anterior one-quarter of HL. Eye diameter approximately one-third length of snout in holo-

type, apparently proportionally smaller but impossible to measure accurately in much larger paratype as consequence of thicker skin overlying eye. Interorbital width distinctly larger than distance from tip of snout to rear of orbit and approximately 2.0–2.5 [2.5] in HL. Anterior narial opening circular, surrounded by short, anteriorly-directed, tubular rim of skin and located along horizontal through both tip of snout and maxillary-barbel origin. Distance between anterior nares approximately equal to length of snout plus orbit. Posterior narial opening nearly round and without obvious long axis; located on dorsal surface of snout at vertical through anterior margin of orbit. Anterior two-thirds of narial opening bordered by flap of skin only slightly higher anteriorly. Distance between posterior nares slightly less than distance between anterior nares.

Mouth inferior, wide, its width approximately one-half of HL. Margin of lower jaw nearly transverse, its posterior limit reaching vertical through posterior margin of orbit. Premaxillary tooth patch elongate and crescentic, continuous across midline; anterior margin convex, posterior margin transversely aligned and nearly straight. Premaxillary teeth relatively small, conical, and sharply pointed, with teeth arranged in four or five irregular rows (five rows in larger paratype). Palatal teeth arranged in one gently curved row continuous across midline. Palatal teeth large and bluntly conical. Dentary with one row of teeth similar in size and shape to those on palate.

Maxillary barbel slender, its length ap-

proximately equal to length of snout; barbel origin located along vertical through anterior margin of orbit. Mental barbels about equal in size and length to maxillary barbel and to each other. Origin of medial-mental barbel located at vertical through posterior margin of orbit. Origin of lateral-mental barbel located slightly posterior to vertical through posterior margin of orbit. Tip of adpressed mental barbels not reaching margin of branchial membranes.

Dorsal-fin rays i,6 [i,6]. Dorsal fin relatively small, with length of base approximately one-third of HL. Distal margin of dorsal fin straight, with first ray longest and equal in length to one-half of HL. Dorsal-fin spinelet absent, first dorsal-fin ray not spinous and with short filamentous extension. Dorsal-fin origin located slightly posterior of one-third of SL and at vertical extending through distal one-quarter of adpressed pectoral fin. Tip of adpressed dorsal fin reaching to vertical through pelvic-fin base. Last dorsal-fin ray without posterior membranous attachment to body.

Principal caudal-fin rays 8+9 [8+9]. Caudal fin moderately forked and symmetrical; tips of lobes bluntly pointed. Length of longest caudal-fin rays about one and one-half times length of middle rays.

Anal-fin rays v–vi,18–25 [v,25]. Anal-fin base relatively short, approximately 3.7–4.2 [3.7] times in SL. Anal-fin origin located well posterior to middle of SL and slightly posterior to middle of TL. Anal-fin margin straight. First branched anal-fin ray longest, with subsequent rays becoming gradually shorter. Last anal-fin ray without posterior membranous attachment to body.

Pelvic-fin rays i,5 [i,5]. Pelvic fin short, with distal margin slightly convex and first branched ray longest. Pelvic-fin origin located anterior to middle of SL and just posterior to vertical through posterior terminus of dorsal-fin base. Tip of adpressed pelvic fin extending beyond middle of SL, but not reaching vent. Last pelvic-fin ray with membranous attachment to body along its basal one-half.

Pectoral-fin rays i,8–9 [i,8]. Pectoral fin very short, its length about one-half of HL. Pectoral-fin margin slightly sigmoid with first and middle rays longest. First pectoral-fin ray not spinous and with very short filamentous extension in both specimens.

Preanal vertebrae 19–20 [19]. Precaudal vertebrae 15–16 [15]. Caudal vertebrae 29 [29]. Total vertebrae 44–45 [44]. Ribs 14–15 [14]. Gill rakers 8–9 [9].

*Coloration*.—Head and body slightly darker dorsally. Sides of body dark as far ventrally as level of horizontal through pectoral-fin base. Irregular, vertically-elongate dark blotch on lateral surface of body dorsal to pectoral fin. Height of blotch approximately equal to length of pectoral fin, proportionally slightly higher in paratype. Ventral surface of head and abdomen pale. Sides of head dark as far ventrally as horizontal through base of maxillary barbel. Snout margin dark. Dorsal fin pale in holotype, irregularly covered with dark pigmentation in paratype. Caudal fin pale in holotype, covered with scattered eye-sized dark spots in much larger paratype. Anal fin dusky basally and pale distally in both specimens. Pectoral fin with interradiial membranes darkly pigmented on dorsal surface except along fin margin. Pelvic fin with scattered dark pigmentation on dorsal surface of interradiial membranes, except along fin margin.

*Sexual dimorphism*.—Both the holotype and paratype are presumed to be females, given their possession of the straight anal-fin margin which is typical of females in the sexually dimorphic species in the Cetopsinae (RPV & CJF pers. obs).

*Distribution*.—*Cetopsis parma* is only known from two localities in the western portions of the Amazon basin in the Río Pastaza of the Río Marañon basin in Ecuador and the Río Tambo in the Río Ucayali basin of Peru.

*Etymology*.—The species name, *parma*, is from the Latin word, *parma*, a type of small shield, is in reference to the dark mark on the lateral surface of the body im-

mediately dorsal to the pectoral fin. It is used as a noun in apposition.

*Remarks.*—Various authors (Ferraris & Brown 1991, Lundberg & Rapp Py-Daniel 1994, and Ferraris 1996) have grappled with the problem of generic definitions within the subfamily Cetopsinae (the family Cetopsidae of authors prior to de Pinna & Vari 1995). Lundberg & Rapp Py-Daniel (1994:381) well summarized the situation with their comment that the “systematic understanding of the South American Cetopsidae is poorly developed”. The resolution of these problems lies far beyond the limits of this study and will be addressed in a future publication dealing with the phylogenetic relationships among cetopsins. For the purposes of this paper, we consequently place the new species into *Cetopsis* using the concept of that genus proposed by Schultz (1944) which is based on the combination of the possession of a restricted gill opening and conical teeth arranged in multiple rows on the premaxillae. We recognize, however, that the limits of the genus may be modified by a more rigorous phylogenetic analysis.

The holotype and paratype of *Cetopsis parma* demonstrate various morphometric differences which likely reflect the pronounced differences in the size of the specimens (73 versus 170 mm SL, respectively). The holotype and paratype show noteworthy variation in only one meristic feature, the number of branched anal-fin rays (18 versus 25, respectively) and the associated morphometric value, the proportional length of the base of the anal fin. Until such time as additional material which shares the distinctive pigmentation and dentition characters present in these specimens becomes available, we conservatively consider this difference to represent intraspecific variation, perhaps reflective of populational differences associated with the river distances separating the two localities.

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## A new species of the luvarid fish genus †*Avitoluvarus* (Acanthuroidei: Perciformes) from the Eocene of the Caucasus in southwest Russia

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*Abstract.*—A new species of the luvarid fish genus †*Avitoluvarus*, *A. eocaenicus*, is described from the middle Eocene of Russia (Kuma Horizon, North Caucasus) based on a single imprint of its skeleton (incomplete posteriorly). *Avitoluvarus* previously has been known only from the terminal (uppermost) Paleocene of Turkmenistan, where it is represented by two species, *A. diana*e and *A. mariannae*.

The fossil luvarid genus *Avitoluvarus* was described recently (Bannikov & Tyler 1995) from the Danata Formation in Turkmenistan, where it is represented by two species, *A. diana*e Bannikov & Tyler, 1995, and *A. mariannae* Bannikov & Tyler, 1995. The exact age of the fish-bearing layer of the Danata Formation in Turkmenistan has been questioned, with the fishes from this layer dated as both Late Paleocene (Danilchenko 1968, Bannikov 1985) and Early Eocene (Tyler & Bannikov 1992b, Patterson 1993, Bannikov & Tyler 1995). We accept here the analysis of Muzylev (1994) indicating that the fish-bearing layer of the Danata Formation is synchronous with the Upper Thanetian sapropel of more western regions, corresponding to global Late Paleocene anoxic events.

In 1999, excavations in the North Caucasus by the first listed author yielded the imprint of a skeleton (incomplete posteriorly) that represents a new species of *Avitoluvarus*. This specimen was found in the bituminous marls of the Kuma Horizon in the Gorny Luch locality (Pshekha River, Apsheronsk District, about 0.5 km from the Gorny Luch farmstead). The Kuma Horizon correlates with the Bartonian stage. The Kuma Horizon previously has been as-

signed to the Upper Eocene (Tyler & Bannikov 1992a, Bannikov 1993) but according to Cavelier & Pomerol (1986) only the Priabonian (but not the Bartonian) should be included in the Upper Eocene, and thus the Kuma Horizon fishes are of late Middle Eocene age.

A preliminary, and far from complete, list of Kuma fishes (Bannikov & Parin 1997) includes at least 27 species representing 25 families in 10 orders. Based on the recent excavations in 1999, this list can be extended by a number of taxa representing their first discoveries at the generic and familial levels at the Gorny Luch locality; e.g., a champsodontid, an *Antigonia*-like caproid, a *Seriola*-like carangid, a *Sarda*-like scombrid, a percoid fish probably belonging to a new genus of uncertain family, and the new species of luvarid described below. The great majority of the teleost species from the Gorny Luch assemblage are oceanic pelagic (epi- and meso-) and the new species of *Avitoluvarus* described below is presumably epipelagic like the only Recent representative of the family, *Luvarus imperialis* Rafinesque, 1810.

The new species represents the first record of the genus *Avitoluvarus* outside of Turkmenistan and extends the stratigraphic

distribution of this genus from the Late Paleocene to the end of the Middle Eocene.

Family Luvaridae Gill, 1885

Genus *Avitoluvarus* Bannikov & Tyler,  
1995

*Avitoluvarus eocaenicus*, new species  
Figs. 1–3

*Material*.—Holotype, Paleontological Institute (PIN), Moscow, no. 4425/32, estimated 38 mm SL, imprint of poorly preserved skeleton, incomplete posteriorly, single plate, and counterpart of the head and cleithrum.

*Type locality and horizon*.—Left bank of Pshekha River, about 0.5 km from the Gorny Luch farmstead, Apsheronk District, Krasnodar Region; Kuma Horizon, upper part of the Middle Eocene.

*Etymology*.—For the Eocene age of the new species.

*Diagnosis*.—*Avitoluvarus eocaenicus* has all the available characters (those of the caudal peduncle are unknown because of the incompleteness posteriorly of the holotype) diagnostic of the genus *Avitoluvarus* (see diagnosis in Bannikov & Tyler 1995: 6). *Avitoluvarus eocaenicus* differs from both of the other two species of the genus, *A. diana* and *A. marianna*, by the anteroventral inclination of the third to fifth haemal spines, versus these spines being oriented relatively vertically in *A. diana* and inclined posteroventrally in *A. marianna* (for comparative data on the two previously described species, here and following, see Bannikov & Tyler 1995). Additionally, *A. eocaenicus* differs from the other two species by a combination character: the haemal spines of the first two caudal vertebrae are slender and make contact with one another in their middle regions, versus these haemal spines being slender but not contacting one another in *A. marianna*, or relatively stout and contacting one another in *A. diana*. These diagnostic haemal spine characters do not change appreciably ontogenetically within the size ranges known for the other

two species of *Avitoluvarus*, and the single specimen of *A. eocaenicus* (38 mm SL) is within the size range of the specimens of *A. marianna* (34–190 mm SL) and *A. eocaenicus* (38–120 mm SL).

*Description*.—The holotype of *Avitoluvarus eocaenicus* is probably a juvenile based on the presence of ridges on the skull bones and serrations on the dorsal- and pelvic-fin spines. Such ridges and serrations are present in other small juvenile (less than about 50 mm SL) luvarids (e.g., as in *A. marianna* and *Luvarus imperialis*) but these are lost at larger sizes. Also, the skeleton of *A. eocaenicus* seems to be about as weakly ossified as in *A. marianna* and somewhat less well ossified than in *A. diana*.

The body is fusiform, and its greatest depth is about 41% SL. The head is relatively long, about 35% SL. The upper head profile is gently curved and the mouth is small (gap equal to about orbit diameter or less). The round orbit is situated in the lower part of the upper half of the head and has a horizontal diameter of about 23% of the head length.

*Skull*: The limits of the individual bones of the weakly ossified occipital and otic regions are not clear, but the frontals seem to be relatively wide and the supraoccipital lacks a prominent crest. The bones of the cranial roof (probably of the frontals) have remnants of larval ridges, and we presume that these ridges were serrate as in other acanthuroids even though we cannot be absolutely sure of this because of poor preservation of the single specimen; one ridge is along the dorsal midline and another, shorter one, is anterior to the orbit.

The ethmoid region is exceptionally weakly ossified. The parasphenoid is slender and slightly convex where it is exposed at the lower edge of the orbit. The shaft of the hyomandibular is oriented anteroventrally. The pterygoid bones and the palatine are unclear. The quadrate is broad, triangular, and has a small articular facet for the lower jaw. The symplectic is an elongate



Fig. 1. *Avitoluvarus eocaenicus*, new species, photograph of the holotype, PIN 4425/32, estimated 38 mm SL (incomplete posteriorly), wet with alcohol to improve contrast, Middle Eocene of North Caucasus (Kuma Horizon), Russia. Scale bar is 10 mm.

rod, somewhat stouter posteriorly than anteriorly. There is a faint remnant of a structure in the ethmoid region above the anterior part of the parasphenoid that can be interpreted as a long slender process or prong of the lachrymal similar to that of juvenile specimens of *Luvarus imperialis* (see Tyler et al. 1989).

The lower jaw articulation is situated well in front of the level of the anterior edge of the orbit. The lower jaw is rather short but deep, with the dentary and articular of about equal size. The dentary bears a single row of small conical teeth. The alveolar process of the premaxilla is slender, elongate, and bears a single row of small conical teeth, whereas the ascending process is short but prominent. The maxilla seems to be relatively wide.

The thin, flat bones of the opercular region are poorly preserved, with the limits of the individual bones unclear. The opercle appears to be subtriangular and has several bony ridges radiating from the condylar region. The preopercle is curved along its anterior border, with an angle of about  $100^\circ$ .

Several radiating ridges appear to be present in the upper part of the preopercle.

The hyoid and branchial arches are not clear, but there are five sabre-like branchiostegal rays.

**Pectoral fin and girdle:** The posttemporal is slender and elongate; it extends from the posterodorsal aspect of the head ventrally and slightly posteriorly. A short intercalar process extends anteriorly from the lower part of the posttemporal. The supracleithrum is elongate and tapered anterodorsally; this bone is disarticulated in the present specimen. The large cleithrum has a gently curved c-shape, with the upper and lower ends inclined, respectively, slightly anterodorsally and anteroventrally. The upper limits of the postcleithrum are poorly preserved, but the long shaft of the bone below the pectoral-fin base is sturdy and reaches ventrally below the ventral edge of the anterior extension of the first anal-fin pterygiophore (this extension is probably displaced postmortem somewhat dorsally) or almost to the ventral margin of the body. There is no evidence of a division of the

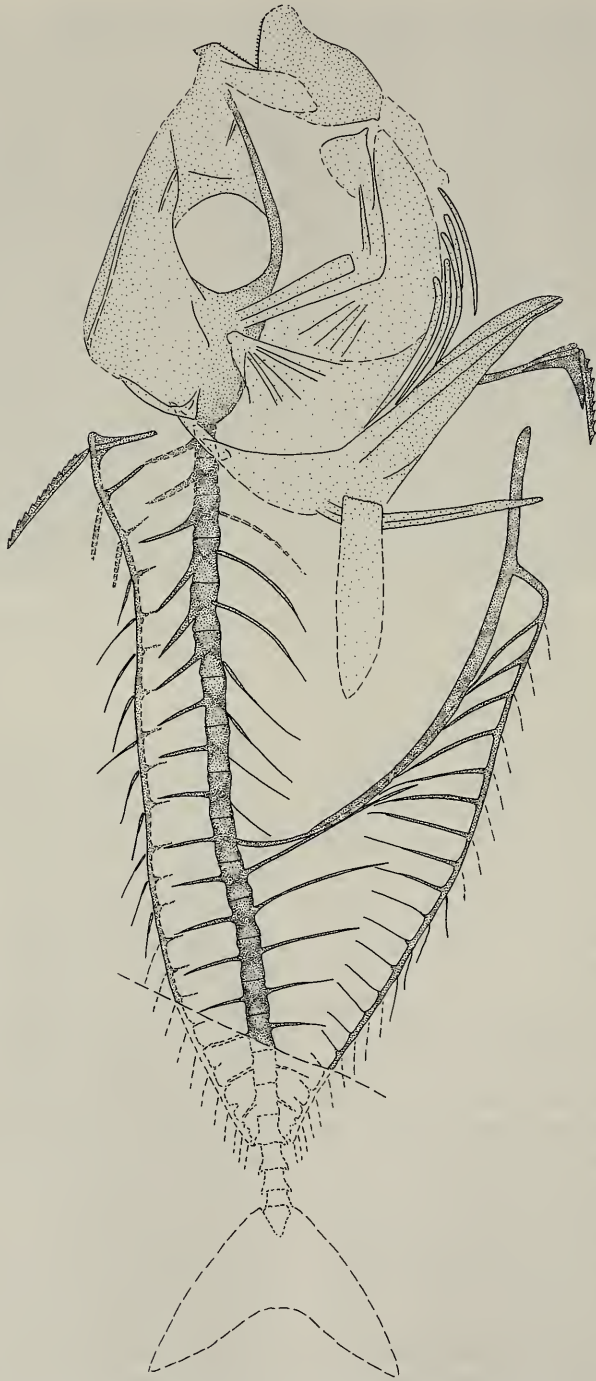


Fig. 2. *Avitoluvarus eocaenicus*, new species, reconstruction of the holotype (for data see legend for Fig. 1). The unstippled parts of the skeleton posterior to the dashed fracture line through the sixth caudal vertebra are missing and hypothesized here as having the conditions of all other species of the family Luvaridae (e.g., a total of 13 caudal vertebrae, the pterygial truss extending posteriorly to the ninth caudal vertebra, four vertebrae in the caudal peduncle, and a forked caudal fin deeply overlapping the hypural plate).

long postcleithral shaft into two pieces, and we presume that the postcleithrum is a single bone (the right and left postcleithra are preserved close alongside one another, except where they overlap ventrally, and are so shown in the reconstruction). The coracoid is elongate, of decreasing width anteroventrally.

The base of the pectoral fin is situated in the middle of the body, slightly above the middle of the distance between the vertebral column and the ventral profile. The pectoral fin is poorly preserved and its length and number of rays cannot be determined.

**Pelvic fin and girdle:** The pelvis is L-shaped. The long ascending (pubic) process is oriented slightly posterodorsally toward the cleithrum. The posterior (ishial) process is well developed, reaching almost to the level of the anterior end of the anterior extension of the first anal-fin pterygiophore. The posterior process is tapered and shorter than the ascending process. There is essentially no anterior (iliac) process.

The pelvic spine is relatively long (longer than the posterior process of the pelvis), about 8% SL, robust, and bears serrations along its anterior edge, being similar to the first dorsal-fin spine except somewhat shorter. No soft rays are evident in the pelvic fin. The pelvic fin of luvareids becomes rudimentary with increasing specimen size, or it is absent (Bannikov & Tyler 1995:33), so it can be anticipated that when larger specimens of *A. eocaenicus* become available the pelvic-fin spines will be much shorter (or absent) than in the present specimen of ca. 38 mm SL.

**Vertebral column:** There are probably 9 + 13 = 22 vertebrae, as in all other species of both fossil and Recent luvareids; if so, the posterior seven vertebrae are missing in the only specimen of *A. eocaenicus* (the missing vertebrae are indicated hypothetically by dashed lines in the reconstruction, Fig. 2). The first two abdominal vertebrae are obscured, but can be reasonably estimated on the basis of the space available for them

between the rear of the skull and the front of the centrum that is the first to be clearly exposed (presumably the third abdominal vertebra). The vertebral column is elevated anteriorly and articulates relatively high on the rear of the cranium. All of the preserved centra are somewhat elongate anteroposteriorly. All of the preserved neural spines are short, slender, and only slightly curved. Most of the neural spines are inclined posteriorly, but the orientation of those of the last abdominal and first two caudal vertebrae is close to vertical. The neural spines of the first five caudal vertebrae are shorter than the corresponding haemal spines. The abdominal vertebrae lack parapophyses. Short and slender ribs (pleurals) are present on the third to ninth abdominal vertebrae, becoming slightly shorter posteriorly. The ribs are inclined posteroventrally and reach to a level less than one-half the distance between the vertebral column and the ventral profile of the body. Epineurals are not evident.

The haemal spine of the first caudal vertebra is only slightly thicker than that of the second caudal vertebra; it is only moderately curved anteroventrally in its lower region. The first haemal spine is so closely articulated along its anterior edge to the first anal-fin pterygiophore that its full length cannot be determined. The haemal spine of the second caudal vertebra is very slender and almost straight. The second haemal spine is angled anteriorly from its base at the centrum and closely approaches or contacts the posterior edge of the middle of the first haemal spine, distal to which point of contact these two haemal spines diverge. The haemal spines of the third to sixth caudal vertebrae are exceptionally slender, straight or only slightly curved, and of decreasing length posteriorly in the series. The third to fifth haemal spines are inclined anteroventrally, whereas the sixth haemal spine is oriented slightly posteroventrally, and close to vertical.

The caudal peduncle, caudal skeleton, and caudal fin are missing.

Dorsal and anal fins: The posterior parts of these fins are missing and the total number of dorsal- and anal-fin elements cannot be determined exactly. However, based on the assumption that the missing parts of the dorsal fin are similar to those of other luvarids, we estimate that there are about 24 dorsal-fin elements. The first dorsal-fin element is definitely a spine. It is relatively long, about 11% SL, borne in supernumerary association on the first dorsal-fin pterygiophore, and bears serrations along its anterior edge. The second and third elements are represented by faint remnants; these are evidently thicker than the subsequent elements, and therefore are probably spines. The remaining elements are clearly soft rays that are unsegmented, unbranched, and bilaterally paired (as seen in some elements that are separated into slightly displaced left and right halves). The rays are much shorter than the first dorsal-fin spine. The dorsal-fin pterygiophores are very poorly preserved and the majority of their ventral shafts are unclear. The distal expansions of the dorsal-fin pterygiophores apparently form a continuous truss, but we cannot determine its thickness. The upper region of the ventral shaft of the first dorsal-fin pterygiophore is expanded into lamellar plates both anteriorly and posteriorly. Based on its position, the lower region of the ventral shaft of the first dorsal-fin pterygiophore is situated in what we estimate to be the pre-neural space in front of the distal end of the neural spine of the first vertebra.

Only a few of the anal-fin rays are preserved, in about the middle of the fin, but based on the number of pterygiophores preserved and of missing parts being similar to those of other luvarids, we estimate that there are about 22 anal-fin rays. The anal-fin rays are unsegmented, unbranched, and bilaterally paired, similar to those of the dorsal fin and of about the same length. The anal-fin pterygiophores are mostly T-shaped in lateral view, with a dorsally oriented shaft and an anteroposteriorly expanded distal end. The first anal-fin pterygiophore

has a long, thick anterior extension beneath most of the abdominal cavity, and a long, equally stout posterodorsal process whose upper end firmly articulates along the anterior edge of the lower end of the haemal spine of the first caudal vertebra. The second and more posterior anal-fin pterygiophores have the distal ends expanded into shallow anterior and posterior processes that form a continuous truss that we presume must have been extensively interdigitated even though we cannot determine the details of this because of poor preservation.

As preserved, the ventral edge of the truss in the abdominal region just behind the anterior extension of the first anal-fin pterygiophore is strongly convex (Figs. 1, 2), uniquely so among luvarids. However, we do not believe that this is an autapomorphy of the new species, but, rather, a postmortem artifact associated with the upward displacement of the anterior extension of the first anal-fin pterygiophore above the level of the lower end of the postcleithrum; the weak ossification in this juvenile specimen would lend itself to this distortion. In Figure 3 we show this region of the truss as preserved (A) and as we believe it would appear if undistorted (B).

With the exception of the first anal-fin pterygiophore, the other pterygiophores are very slender. The shafts of the second to sixth pterygiophores are situated between the haemal spines of the first and second caudal vertebrae (first interhaemal space), and those of the seventh to ninth pterygiophores are in the second interhaemal space. The succeeding three interhaemal spaces accommodate two or three pterygiophore shafts each. The shafts of the anal-fin pterygiophores are not especially convergent toward the haemal spines.

Scales: Tiny scales cover the entire body, but poor preservation precludes detailed description.

#### Discussion

Bannikov & Tyler (1995) proposed nine unequivocal synapomorphies for the super-

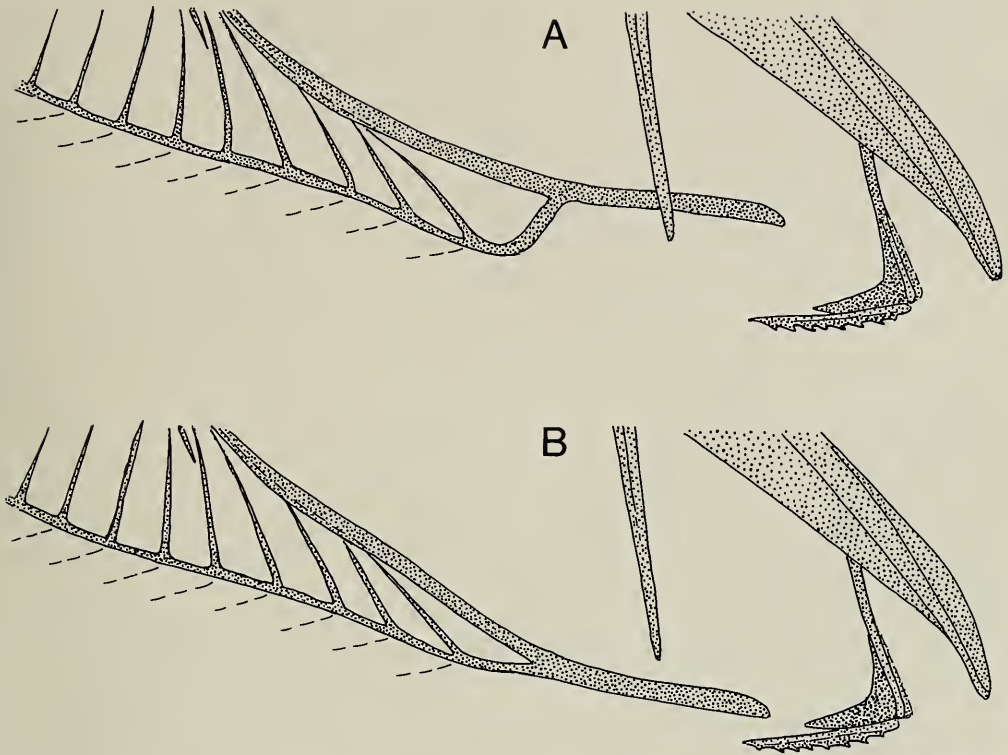


Fig. 3. *Avitoluvarus eocaenicus*, new species: A, structure of the anterior pterygiophores of the anal fin as preserved with postulated convex distortion of the lower edge of the first pterygiophore in the region behind the anterior process, and with upward displacement of the anterior process above the level of the ventral end of the postcleithrum; B, our interpretation of how the anterior pterygiophores of the anal-fin would appear if undistorted.

family Luvaroidea (Luvaridae + †Kushlu-kiidae) and six unequivocal synapomorphies for the family Luvaridae (with two species of Paleocene *Avitoluvarus*, and two species of *Luvarus*, one Paleocene and one Recent; Tyler et al. 1989, previously documented a far larger number of synapomorphies for the Luvaridae based only on the single Recent species, but many of these features cannot be determined in fossils or are unique to the Recent species). Within the Luvaridae, the preponderance of derived features were found in *Luvarus*, whereas *Avitoluvarus* was shown to possess only two unequivocal synapomorphies: (1) the truss formed by the interdigitation of the distal regions of the dorsal- and anal-fin pterygiophores is relatively shallow and not extensively interdigitated; and (2) the prox-

imal shafts of a total of seven to 11 (rarely six) anal-fin pterygiophores are situated in the first two interhaemal spaces (here and following, character numbers are in parentheses and correspond to those in the cladogram, Fig. 4).

Within *Avitoluvarus*, Bannikov & Tyler (1995) identified one autapomorphy of *A. diana* as (3) the posterodorsally oriented proximal shaft of the first anal-fin pterygiophore is especially thick and stout, and three autapomorphies of *a. mariannae* as: (4) the proximal shafts of a total of 10 to 11 anal-fin pterygiophores are situated in the first two interhaemal spaces (the greater increase in number of pterygiophores in these two spaces in *A. mariannae* being a more derived condition than the lesser increase in *A. diana*); (5) the ribs are rela-

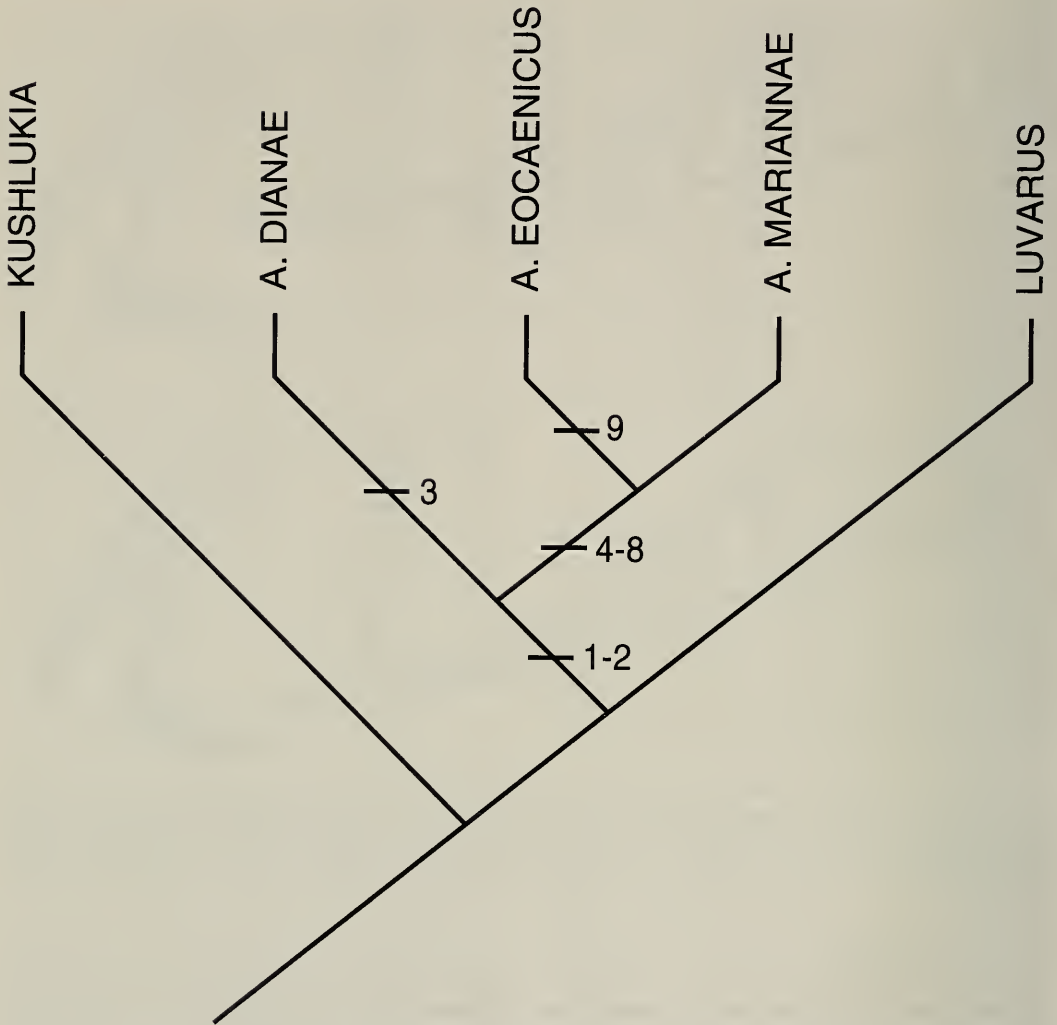


Fig. 4. Cladogram of the proposed relationships within *Avitoluvarus*. Derived character states, discussed in the text, are: (1) pterygial truss shallow and not extensively interdigitated; (2) proximal shafts of a total of 7–11 (rarely 6) anal-fin pterygiophores situated in the first two interhaemal spaces; (3) posterodorsally oriented proximal shaft of the first anal-fin pterygiophore especially thick and stout; (4) proximal shafts of a total of 10–11 anal-fin pterygiophores situated in the first two interhaemal spaces (5) ribs relatively short and thin, ending at the level of the upper third of the abdominal cavity; (6) ventral half of pterygial truss especially shallow; (7) first two haemal spines only slightly thickened; (8) proximal shafts of the second and many of the more posterior anal-fin pterygiophores exceptionally slender; (9) third to fifth haemal spines inclined anteroventrally. Character states 1–6 and 9 are unequivocal apomorphies, but states 7–8 are equivocal and apomorphic only under the assumption of delayed transformation, favoring independent acquisition over reversal. For data supporting this and the sister group relationships of *Kushlukia* with *Avitoluvarus*+*Luvarus*, see Bannikov & Tyler (1995).

tively short and thin, ending at the level of about the upper third of the abdominal cavity; and (6) the ventral half of the pterygial truss formed from the distal ends of the anal-fin pterygiophores is very shallow.

Moreover, *A. mariannae* was shown to possess two equivocal autapomorphies (which assume delayed transformation, favoring independent acquisition over reversal, with the ancestor possessing the plesiomorphic



condition of the outgroups): (7) the first two haemal spines are only slightly thickened; and (8) the proximal shafts of the second and more posterior anal-fin pterygiophores, except for the last few, are exceptionally slender.

The new species, *A. eoceanicus*, shares four derived character states (5–6 unequivocal, 7–8 equivocal) with *A. mariannae* and lacks the single autapomorphy (3) of *A. diana*, all of which indicates a sister group relationship between *A. eoceanicus* and *A. mariannae*.

For one character (4), *A. eoceanicus* is intermediate between *A. diana* and *A. mariannae*. Two to five anal-fin pterygiophore shafts in the first two interhaemal spaces is ancestral for acanthuroids (Bannikov & Tyler 1995), and the increase in number of such pterygiophores in *Avitoluvarus* can be considered an ordered transformation series of increasing specialization from the six to seven in *A. diana* to the eight in *A. eoceanicus*, to the 10–11 in *A. mariannae*. For this character within *Avitoluvarus*, we consider the eight or more pterygiophores in these two spaces as a derived condition synapomorphic for *A. diana* and *A. mariannae*.

We identify an autapomorphy of *A. eoceanicus* as (9) the third to fifth haemal spines are inclined anteroventrally. We consider posteroventral to vertical inclination of the third to fifth haemal spines as ancestral for acanthuroids because this is the condition found in fossil and Recent scatophagids (the first outgroup for acanthuroids), siganids, zancids, and most acanthurids (including those considered to be the most basal): see illustrations in Tyler et al. 1989, Blot & Tyler 1991, Tyler & Bannikov 1997, Tyler & Sorbini 1999). Among the luvarid + †kushlukiid clade (Bannikov & Tyler 1995), anteroventral orientation of the third to fifth haemal spines is found only in one of the two species of *Kushlukia* (in *K. permira*, versus posteroventral orientation in *K. sp.*), in one of the two species of *Luvarus* (in *L. imperialis*, versus vertical to posteroventral in *L. necopinatus*), and in

one of the three species of *Avitoluvarus* (in *A. eoceanicus*, versus posteroventral in *A. mariannae* and vertical in *A. diana*). It is most parsimonious to propose that the anteroventral orientation has arisen independently in the single species of *Kushlukia*, *Luvarus*, and *Avitoluvarus*; therefore, the anteroventral orientation of the third to fifth haemal spines is an autapomorphy of *A. eoceanicus*.

### Conclusion

The addition of another new species to the record of fossil luvarids reinforces the notion (Bannikov & Tyler 1995:40) that the luvaroid fishes were far more diversified in the early Tertiary (six species in two families, with four species from the uppermost Paleocene of the Danata Formation, Turkmenistan, alone) than they are today, when only a single species survives.

### Acknowledgments

We thank the National Geographic Society, Washington DC, for grant no. 6555-99 that allowed the first listed author to make excavations in the North Caucasus in 1999, where the holotype of *Avitoluvarus eoceanicus* was obtained. The manuscript was improved by the suggestions of G.D. Johnson, Smithsonian Institution, and an anonymous reviewer. The photograph of the holotype was made by A.V. Mazin (PIN, Moscow).

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***Pseudothyone levini*, a new species of sea cucumber (Echinodermata:  
Holothuroidea) from the northeastern Pacific**

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*Abstract.*—*Pseudothyone levini*, new species (Sclerodactylidae), based on 12 specimens collected between Graham Island, Queen Charlotte Islands, British Columbia and Tacoma, Puget Sound, Washington, U.S.A. in the northeastern Pacific Ocean, is described. It ranges in depth from the intertidal zone to 70 meters on rock and in mud or gravel. Body is beige or white. Podia are scattered but more numerous in the five ambulacra. Usually ten brown dendritic tentacles. *P. levini* has mostly round or oval skin ossicles with a smooth surface, a wavy margin and small holes. Another less numerous plate is larger and thicker with scalloped margins and numerous large holes. Tails of the radials on the calcareous ring are short and curved. Tentacle ossicles range from large robust, curved rods perforated at the ends, to small curved, perforated plates. *Pseudothyone levini* is compared to seven other species currently recognized in the genus.

The family Sclerodactylidae is well represented in the Northern hemisphere, primarily in the Atlantic, from shallow water to bathyal depths (Pawson 1982). Three species in two genera of Sclerodactylidae inhabit the northwestern coast of North America. *Eupentacta pseudoquinquesemita* Deichmann ranges from Alaska to Washington, and *E. quinquesemita* (Selenka) ranges from southern Alaska to southern California (Lambert 1997). *Pachythyone rubra* (H. L. Clark) is known from Monterey Bay to Los Angeles Harbor, California (Bergen 1996).

Since 1986, five new species of holothuroids have been added to the known fauna of the northeastern Pacific (Lambert 1997, 1998). Here we describe a sixth new species of sea cucumber based on material from British Columbia and Washington. The genus *Pseudothyone* is represented by three species in the Atlantic, one in the Mediterranean, one in the Persian Gulf, one

in the western Pacific, and now this one in the northeastern Pacific.

#### Materials and Methods

Ossicle slides were prepared as in Lambert (1985) and measurements of ossicles followed the procedures described in Lambert (1998). Ossicles were sampled from the dorsal tentacles of all specimens, mid-dorsal regions of intact specimens, and from anterior and posterior regions of partial specimens.

#### Results

Order Dendrochirotida Grube  
Family Sclerodactylidae Pawson & Fell,  
1965

*Diagnosis.*—Body lacks a test of imbricating plates; body wall soft; ossicles small and inconspicuous. Calcareous ring complex, with paired or unpaired processes; elements of ring not composed of a mosaic

of minute pieces. Tentacles 10–20. Body may be U-shaped. Calcareous ring not as massive as in the Phyllophoridae. Tube feet usually scattered in the radii and interradia, but tendency for them to be restricted to the radii (Pawson 1982).

Subfamily Sclerodactylinae Panning, 1949; restricted by Thandar (1989).

*Diagnosis*.—Tentacles 10. Calcareous ring compact, short, tubular, with the radial and interradial plates fused for most of their length; posterior paired processes of the radial plates of medium length, usually broken into a few large pieces of calcite; rarely, processes unbroken.

Type genus: *Sclerodactyla* Ayres.

*Pseudothyone* Panning, 1949

*Diagnosis*.—Tentacles 10. Calcareous ring undivided; radialia with medium length forked-tails, which are solid or in a few large pieces. Skin ossicles consist entirely of plates.

Type species: *Pseudothyone raphanus* Düben & Koren, 1846

*Pseudothyone levini* new species

Figs. 1–3

*Diagnosis*.—Ten equal tentacles. Body cylindrical; length to 140 mm. Podia scattered but more numerous and regular in the ambulacra. Majority of skin ossicles thin, round smooth plates, with smooth wavy edges and a few small holes. Less common are round to oval plates with scalloped margins and many large perforations. Tentacle ossicles range from small curved, lacy perforated plates with scalloped margins to large, heavy curved rods. Radials of calcareous ring with short curved posterior processes; posterior edge of interradials concave; radials and interradials about three times longer than wide.

*Material examined*.—Twelve specimens from nine localities. Material borrowed from: California Academy of Sciences

(CASIZ), Canadian Museum of Nature (CMNI), Friday Harbor Laboratories (FHL), and the Royal British Columbia Museum (RBCM). Depths in meters.

*Holotype*.—RBCM 999-475-1, collected by Andy Lamb with aid of SCUBA, 13 Nov 1999, length 14 cm, female.

*Type locality*.—Point Defiance, Tacoma, Washington, USA, 47°18.4'N, 122°30.8'W, 12 m, muddy sand.

*Paratypes*.—RBCM 990-393-22, collected by F.W. Schueler, 4 Feb 1989, British Columbia, Queen Charlotte Islands, Graham Island, Jungle Beach, 3 km south of Lawnhill, intertidal, 1 specimen, 3 cm long. RBCM 984-223-1, collected by D.B. Quayle, 8 May 1961, British Columbia, Queen Charlotte Islands, Hecate Strait, Burnaby Narrows, 52°20.4'N, 131°20.4'W, intertidal, 1 specimen, length 8.0 cm, male. RBCM 980-343-20, collected by P. Lambert, 6 Jul 1980, British Columbia, Kyuquot Sound, Rugged Point Light, 49°58.3'N, 127°15'W, <20 m on rock, 1 specimen, 11 cm long, male. RBCM 978-315-19, collected by P. Lambert, 26 Oct 1978, British Columbia, Gulf Islands, Prevost Passage, 48°43'N, 123°20'W, 55–64 m in gravel, 1 specimen, 12 cm long, male. FHL 819, collected by S. Van Neil, 13 Aug 1964, Washington, Orcas Island, Potato Patch [local name], 48°34.9'N, 122°50.8'W, 40–55 m, 1 specimen, length 9 cm, female. CASIZ 057397, collected by Mr. and Mrs. Oldroyd, Jul 1917, Washington, San Juan Island, Friday Harbor, 48°32.7'N, 123°0.2'W, est. 46–110 m, 1 specimen, length 4.5 cm, male. RBCM 996-193-1, collected by A. Lamb, 4 Jul 1996, Washington, San Juan Island, Friday Harbor, 48°32.6'N, 123°0.7'W, 12–18 m in soft mud, 1 specimen, length 9 cm, male.

*Other material*.—RBCM 975-34-3, collected by John Fleury, 15 Aug 1962, British Columbia, Queen Charlotte Islands, Houston Stewart Channel, 52°6.7'N, 131°8.2'W, 30 m in gravel, 1 partial specimen, 1 cm posterior end. CMNI 1980-2097, collected by N.A. Powell, 17 Jul 1967, British Columbia, Vancouver Island, Strait of Geor-



Fig. 1. Holotype of *Pseudothyone levini* collected by Andy Lamb from a mud bottom near Point Defiance, Tacoma, Washington, USA.

gia, Nanoose Bay, 49°15.3'N, 124°8.0'W, 19–24 m, in gravel, 2 partial specimens, anterior end 3.5 cm and posterior end 2 cm long. CMNI 1980-2192, collected by N.A. Powell, 18 Aug 1967, Nanoose Bay, dredged parallel to the north end of the harbor, 49°15.6'N, 124°10.0'W, 9–15 m in gravel, 3 partial specimens, 4 cm anterior end, two posterior ends 2.4 cm and 3.4 cm long. CMNI 1980-2107, collected by D. Popham, Aug 1967, British Columbia, Haro Strait, Moresby Island, 48°45.0'N, 123°20.4'W, assumed to be a D.V. Ellis Sta-

tion, 70 m, 1 specimen, anterior piece 3 cm long.

*Description.*—Body cylindrical, tapering gradually to posterior. Length of eight preserved specimens, 3–14 cm (Holotype 9 cm) with soft fleshy skin. In alcohol, skin yellowish white, flesh slightly darker. No obvious difference in color of ventral and dorsal surfaces. Tentacles white to dark brown. Living holotype beige with dark brown tentacles and purplish introvert (Fig. 1). Ambulacral podia in five regular quadruple rows and also thinly scattered be-

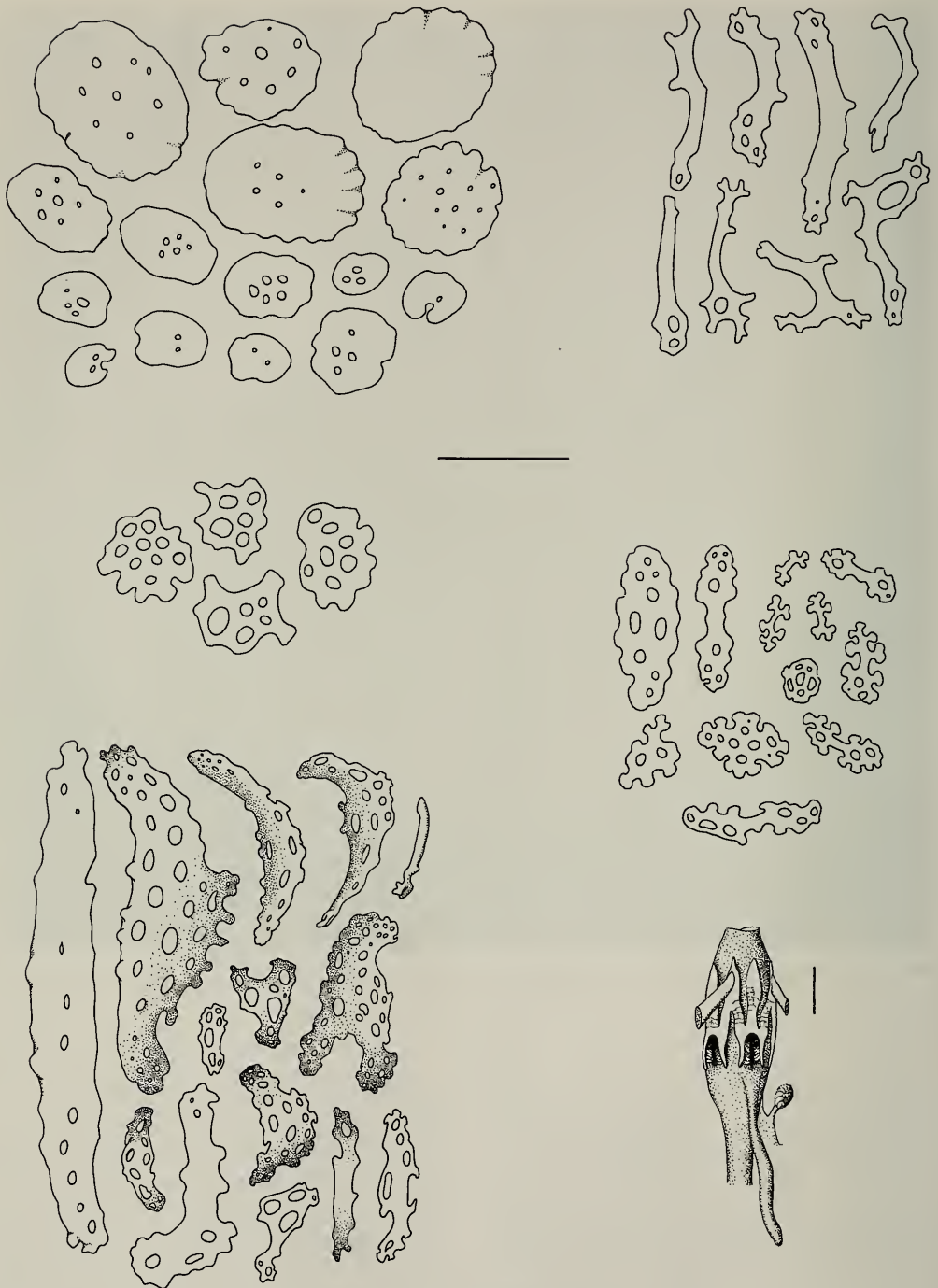


Fig. 2. Top left: typical small-holed skin ossicles. Top right: supporting rods from podia. Mid left: large-holed skin ossicles. Mid right: plates and branched rods of the introvert. Bottom left: rods and plates from tentacles. Bottom right: calcareous ring, madreporite and polian vesicle. Upper scale = 100  $\mu$ m. Lower right scale = 5 mm.



Fig. 3. Known distribution of *Pseudothyone levini* based on museum records.

tween the ambulacra. Podia usually flush with the skin surface in preserved specimens.

Ten dendritic tentacles; usually equal; encircling the mouth. Eight specimens have ten equal tentacles; two have eight equal and two small ventral tentacles; and one has nine equal tentacles. Two small tentacles of one specimen white, eight larger tentacles brown.

One polian vesicle in holotype, from zero to four in others. Usually one madreporite, but one specimen had a stone canal attached near calcareous ring and a second one posterior to that. Madreporite suspended in the dorsal mesentery (Fig. 2) but varying in position between the midpoint of the calcareous ring and 15 mm posterior to the tips of the ring. Madreporic body ranging from globular and furrowed, as in holotype, to oblong and smooth. Mean length of madreporic body  $1.9 \pm 0.6$  mm, width  $1.2 \pm 0.4$  mm.

Radialia with short posterior processes; some are solid but others in small pieces. Other parts of calcareous ring variably solid or in pieces. Posterior edges of the interradials concave. Radials and interradials about three times longer than wide (Fig. 2).

Immediately posterior to each interradial, all specimens have a characteristic depression or pit in the membrane (Fig. 2).

Five retractor muscles attach to body wall at one third of body length from anterior end. Holotype has wide, entire retractors; in two specimens, all the retractors split longitudinally; in one specimen, one of the five retractors is split. Gonad two tufts of simple unbranched tubules, one on each side of dorsal mesentery. Each respiratory tree Y-shaped; dorsal branch often extending as far as the tentacle bulb; ventral branch shorter. Base of trees join cloaca on each side of intestinal attachment.

Generally two types of plates in skin. Commonly thin, round plates with smooth wavy margins and a few small holes; mean length  $57 \pm 22$   $\mu\text{m}$  ( $n = 367$ ); Holotype  $65 \pm 11$  ( $n = 40$ ); width  $42 \pm 15$   $\mu\text{m}$ , Holotype  $50 \pm 8$ ; mean number of holes  $4 \pm 2$ , Holotype  $4 \pm 1$  with a maximum diameter of  $6 \pm 4$   $\mu\text{m}$ , Holotype  $10 \pm 3$  (Fig. 2). Holes appear to get smaller with age, and some plates have none. Another type of plate, more common in smaller animals, round to oval and thick, with large holes and scalloped margins; mean length  $80 \pm 27$   $\mu\text{m}$  ( $n = 147$ ); width  $56 \pm 17$   $\mu\text{m}$ ; mean number of holes  $6 \pm 3$ , with a maximum diameter of  $13 \pm 5$   $\mu\text{m}$  (Fig. 2) Holotype has none of this type. Tentacular ossicles range from small, lacy perforated plates to large rods. Small perforated plates curved, with scalloped margins; vary from oval to triangular with mean length of  $90 \pm 60$   $\mu\text{m}$  ( $n = 240$ ), Holotype  $84 \pm 20$  ( $n = 40$ ); width  $39 \pm 22$   $\mu\text{m}$ , Holotype  $35 \pm 13$ , mean number of holes  $9 \pm 7$ , Holotype  $13 \pm 5$ , with a maximum diameter of  $16 \pm 7$   $\mu\text{m}$ , Holotype  $15 \pm 5$  (Fig. 2). Tentacular rods follow the circumference of the tentacle, thus vary in size, depending on location. Also, depending on orientation when viewed, they may appear narrow and curved with a few holes, or wide and heavy with many perforations (Fig. 2). Mean length of tentacular rods  $212 \pm 123$   $\mu\text{m}$  ( $n = 280$ ), Holotype  $241 \pm 108$  ( $n = 40$ ).

Table 1.—Distribution and morphology of all known species of *Pseudothyone*.

	<i>P. levini</i> This paper	<i>P. belli</i> Ludwig, 1886	<i>P. buccalis</i> Stimpson, 1855	<i>P. buccalis pallida</i> Clark, 1938	<i>P. farnesini</i> Cherbonnier, 1969	<i>P. mosatica</i> (Koehler & Vaney, 1910)	<i>P. raphanus</i> Düben & Koren, 1846	<i>P. sculptoneca</i> Cherbonnier, 1958
Distribution	In mud or gravel from the Queen Charlotte Islands south to Puget Sound, Washington. Shore to 110 m.	Albrolhos Reef, Brazil to Harbour of Colon, Panama, and Torgutas, Florida. Shore to 22 m (Deichmann 1930).	In soft mud around rocks from Japan to Aden in the North, Port Jackson to Delagoa Bay in the south, Northern coast of Australia. Shore to 15 m (Clark 1938).	On mud flat, collected with <i>P. buccalis</i> near Broome, W. Australia. Near low water mark (Clark 1938).	In sandy mud, fine sand, gravel and pebbles from Bay of Biscaia, 489–1045 m (Cherbonnier 1969).	Arabian Sea (Daniel & Halder 1974); Persian Gulf (Koehler and Vaney); 53 fms.	In sand or mud from Trondhjem Fjord to Mediterranean sea. 10–1050 m (Mortensen 1977).	In sand, cobble or gravel from off Blanes, NE Spain in Mediterranean, edge of shelf (200 m) and 83 m in Adriatic Sea (Froggia 1975).
Dimensions	Up to 90 mm long.	8 to 50 mm.	Up to 110 mm long, 18–20 mm thick.	65 mm long; 15 mm thick.	About 15 mm long; 4.3 mm thick.	12 mm long; 4.5 mm thick.	Up to 60 mm (Mortensen 1977).	Up to 22 mm long by 8 mm thick.
Tentacles	10 equal.	8 equal, 2 small ventral.	10; 3–4 small ventral.	Same as <i>P. buccalis</i> .	8 equal, 2 small ventral.	Probably 10.	10 equal.	8 equal, 2 small ventral.
Skin ossicles	Round plates with smooth wavy margins, few small holes. Fewer large round to irregular, plates with scalloped margins and many large perforations.	1) 4 holed knobbed buttons with 4–8 marginal knobs; 2 central knobs united by a handle. 2) plates with more holes and knobs. 3) smooth plates with several holes.	Medium thick layer of small plates with 4 central holes. Plate edged with small bumps. Strap like handle on top and bottom of plate. Occasionally 2 round mushroom shaped bumps in place of strap (Panning 1949).	Similar to <i>P. buccalis</i> .	Thick round to oval plates some larger and more irregular.	Large round calcareous plates that form a mosaic with podia emerging.	Large, irregular, smooth plates with variable number of small (0.11–0.22 mm) holes (Panning 1949).	Small smooth plates with handles, several handles form a tube around a podia. Large smooth plates with 30–50 holes and scalloped edges at caudal end.



Table 1.—Continued.

	<i>P. levini</i> This paper	<i>P. belli</i> Ludwig, 1886	<i>P. buccalis</i> Stimpson, 1855	<i>P. buccalis pallida</i> Clark, 1938	<i>P. firmestini</i> Cherbonnier, 1969	<i>P. mosatica</i> (Koehler & Vanev, 1910)	<i>P. raphanus</i> Dibben & Koren, 1846	<i>P. sculponia</i> Cherbonnier, 1958
Other ossicles	Tentacles: small, curved, perforated plates with scalloped margins. Rods range from small, thin, sharp with a few holes to thick, heavy, long, with more holes.	Tentacles: rosettes and delicate perforated rods. Well developed end plates. Ob-long supporting tables with rudimentary spire. (Deichmann 1930) and (Sluiter 1910).	Radials with long forked tails. Broad radials and interradials merge with one another. Anterior radials to a point, with parallel edges. Anterior interradials lance shaped (Panning 1949).	Tentacles and introvert: without rosettes but many slender rods, with few holes, or holes at ends. (Clark 1938).	Tentacles: rods with wide perforated ends. No supporting rods in podia; rudimentary end-plate; Introvert: rods with scalloped edges, and small plates.	Supporting tables in podia.		Tentacles: rods up to 700 $\mu$ m long, and rosettes. No ossicles in podia except end-plate with radiating spokes.
Calcareous Ring	Radials with short curved tails. Interradials with concave posterior edge. Radials and interradials about 3 X as long as they are wide.	Radials with long slender processes, cleft almost to the middle of the interradials. Radials and interradials high and narrow. Inter-radials slightly incised behind (Deichmann 1930).	Same as <i>P. buccalis</i> .		Radials with medium length tails made of 5 pieces; anterior or of radials narrow with gutterlike groove; interradials with flattened or pointed tips.	Radials with long tails in about 5 pieces; radials with notch at anterior end.	Radials with rounded slender tip, and medium length undivided forked tails. Delicate. Radials and interradials broad in the middle (Panning 1949).	Radials with forked tails of moderate length; trough-like groove at anterior end; interradials with pointed anterior and curved posterior edge.
Other comments	Body cylindrical and curved.	Body slightly curved (Deichmann 1930).	Body fusiform, indistinctly 4 or 5 angled (Theel 1886).	Pure white body, otherwise, same as <i>P. buccalis</i> .	Body short and thick; u-shaped; narrow caudal end; podia scattered but also in rows.	Body curved and stiff with covering of plates.	Body with a long, thin "tail" (Mortensen 1977).	Caudal end without podia.

Introvert has small branched rods or rosettes; mean length  $65 \pm 23 \mu\text{m}$  (Fig. 2). No end plates found in podia; podia with branched rods similar to tentacles. Larger specimens have fewer ossicles in podia and skin; many have eroded edges. Deterioration is likely natural rather than due to preservatives because tentacle ossicles in the same specimen not eroded.

*Etymology.*—The species is named after Dr. Valery S. Levin, of the Kamchatka Institute of Fisheries and Oceanography, Petropavlovsk, Russia in recognition of his numerous contributions to holothuroid systematics and ecology.

*Distribution and bathymetric range.*—Collections range from Graham Island, Queen Charlotte Islands, British Columbia ( $53^{\circ}23'N$ ,  $131^{\circ}55'W$ ) to Point Defiance, Tacoma, Puget Sound, Washington ( $47^{\circ}18.4'N$ ,  $122^{\circ}30.8'W$ ) (Fig. 3). Depths range from intertidal to 70 meters, on rock or in mud or gravel. One record was between 46 and 110 meters but the precise depth could not be confirmed. Most specimens occurred in less than 60 meters. Andy Lamb collected two specimens from mud with the aid of SCUBA. One specimen was collected in a subtidal exposed rocky habitat from a pocket of gravel and two specimens were collected from the intertidal zone.

### Discussion

The family Sclerodactylidae is morphologically intermediate between the Phyllophoridae with complex calcareous rings and the Cucumariidae with simple rings (Pawson 1966). Thandar (1989, 1990) states that several seemingly unrelated forms are included in the family, with some genera fitting equally well in the Phyllophoridae, which are characterized by long tubular calcareous rings composed of a mosaic of minute pieces. The family Sclerodactylidae currently contains three subfamilies: the 10-tentacled Sclerodactylinae and Sclerothyoninae, largely Atlantic in distribution, and

the Cladolabinae found typically in the Indo-West Pacific (Thandar 1989). Pawson & Fell (1965) state that having undivided processes is the key character of Sclerodactylidae that separates it from the Phyllophoridae; however, Thandar (1989) feels that this is a poor character because even within a single species of Sclerodactylidae the processes may be divided or undivided. He prefers to emphasize the short compact nature of the calcareous ring in this family (Thandar 1989, Fig. 1b). The calcareous ring of *Pseudothyone levini* is compact with short curved processes. While the processes in most specimens appear to be in small pieces, some are undivided. This variability in the posterior processes and the general character of the calcareous ring agree with the subfamily Sclerodactylinae as Thandar defined it.

Table 1 compares the distribution and morphology of the new species with the seven known species of *Pseudothyone*, all of which have only plate ossicles in the body wall and generally inhabit mud in shallow water. *Pseudothyone levini* can be distinguished from other species of *Pseudothyone* by skin ossicles and the form of the calcareous ring. *Pseudothyone levini* of different sizes, and presumably different ages, show differences in the form of their skin ossicles as do specimens from rocky habitats versus mud. Specimens greater than 10 cm long had few of the large-holed plates found in small animals. This variability in ossicles may represent growth stages, but a more complete size series of specimens is required before the relationship of size and ossicle form can be determined. One specimen from a rocky substrate had larger small-holed skin ossicles than those from mud. Apart from the one rock-dwelling specimen the skin ossicles seemed to deteriorate in larger animals. This deterioration was unlikely a function of poor preservation as the tentacle ossicles in these specimens appeared normal.

*Pseudothyone levini* appears to be most closely related to *P. raphanus* (Düben &

Koren, 1846) from the North Atlantic. The skin ossicles of *P. raphanus* are a single type of perforated plate with large holes. *Pseudothyone levini* has a few large-holed perforated plates like the former but the dominant ossicles of mature specimens are smooth, rounded plates with small holes. The curved body of *P. raphanus* has an expanded anterior part and long slender caudal portion while *P. levini* is curved but only slightly tapered. *Pseudothyone raphanus* lives in soft substrates with its tail protruding and ingests the bottom material directly according to Mortensen (1977). On a night dive, Andy Lamb observed the tentacles of *Pseudothyone levini* extended above the mud surface presumably feeding on suspended particles. He collected one specimen and saw several other individuals in the same posture. On a second dive at the same location during daylight, none were seen. Several dredged specimens consist of only anterior and posterior portions, suggesting that the animal assumes a U-shaped position with anterior and posterior ends at the surface or protruding from the sediment.

Four *Pseudothyone* species have calcareous rings with long posterior processes, three have medium length tails, and *P. levini* has short curved tails.

Unlike most specimens examined, two possessed small ventral tentacles. We speculate that these may have been regenerating after an injury or in the case of the 3-cm specimen, may be a juvenile characteristic, but more specimens would be required to determine this. Tentacle sizes among the species of this genus vary (see Table 1). Either this character is variable in the genus or the genus is not well characterized and needs to be revised. We assume that variations in the shape of the retractor muscles are artifacts that may have been caused by sudden contractions during preservation.

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usual species and for collecting two specimens that helped us to complete the description started a few years ago. The paper was improved by the constructive criticisms of Dr. Alex Kerr and one anonymous reviewer. The authors thank the Director of the Royal B.C. Museum for research funding and for supporting one of us (KO) during a University of Victoria Co-op work term in the fall of 1997 when the initial work on this new species was done.

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**A new leucosiid crab of the genus *Nursia* Leach, 1817 from Vietnam  
(Crustacea: Decapoda: Brachyura), with redescription of  
*N. mimetica* Nobili, 1906**

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*Abstract.*—A new species of leucosiid crab, *Nursia guinotae*, is described from Vietnam. It is similar to *N. mimetica* Nobili, 1906 from the Tuamotu Archipelago and *N. alata* Komatsu & Takeda, 1999 from the Ryukyu Islands, in the projecting epistome, the expanded epibranchial region, and the dorsal ridges, but is distinguished from them by the dentate epibranchial ridge and well-developed posterior lobes. *Nursia mimetica*, a species not reported since its original description, is redescribed based on the syntype specimen.

Recently, we had the opportunity to examine specimens of the genus *Nursia* Leach, 1817 deposited in the Muséum national d'Histoire naturelle, Paris, through the courtesy of Prof. D. Guinot. Among this material, a small specimen which was collected in Vietnam and preliminarily identified as *N. plicata* (Herbst, 1804) was found. Unfortunately, detailed locality of this specimen is unknown. This very small specimen has an expanded branchial region and a dentate epibranchial ridge, and actually represents an undescribed species. Herein, we describe it as a new species, and redescribe an allied species, *N. mimetica* Nobili, 1906, from Rikitea, Tuamotu Archipelago, French Polynesia, to clarify the identity of both species, because the original and subsequent descriptions of *N. mimetica* by Nobili (1906, 1907) are very poor and insufficient.

Measurements, given in millimeters (mm), are of the greatest carapace length (including the posterior lobe) and breadth, respectively. The descriptive terminology follows Ihle (1918), including the abbreviations R and T in abdominal formulae

which indicate Rest and Telson in German, respectively. The specimens remain deposited in the Muséum national d'Histoire naturelle, Paris (MNHN).

Family Leucosiidae Samouelle, 1819

*Nursia guinotae*, new species

Figs. 1, 2

*Material examined.*—Holotype, female, 2.7 × 3.2 mm, Vietnam, coll. Gallardo, MNHN-B 9947.

*Description of holotype.*—Carapace (Figs. 1, 2a, b) rhomboidal in general outline, 1.3 times broader than long, uniformly covered with minute, flat granules, provided with postfrontal, median, and epibranchial ridges. Front well developed, 0.3 times as broad as carapace; margin slightly ridged, divided into 2 truncate lobes by shallow median notch; postfrontal ridges rising from near frontal-orbital angles, converging, meeting at midline. Orbit with 2 vestigial, longitudinal fissures on dorsal roof and V-shaped notch on infraorbital lobe. Pterygostomian margin forming general outline.

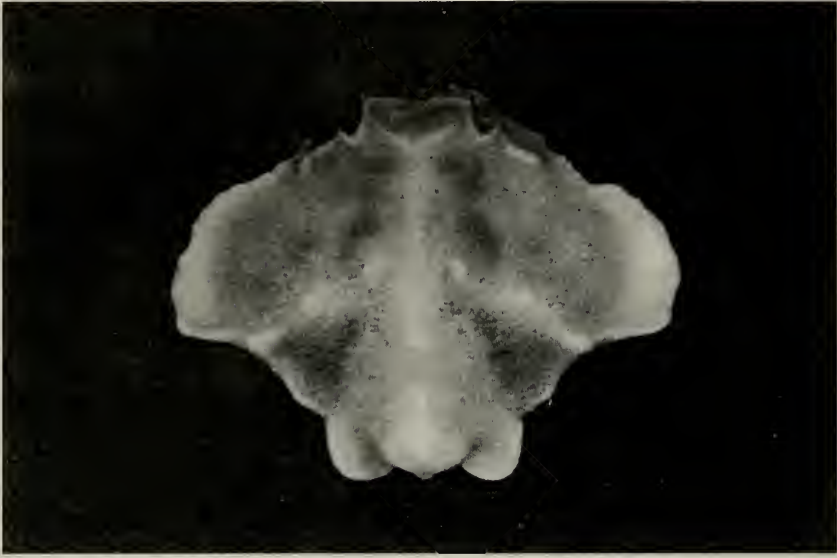


Fig. 1. *Nursia guinotae*, new species, holotype, ovigerous female, Vietnam,  $2.7 \times 3.2$  mm (MNHN-B 9947). Scale equal 1 mm.

with small angle near posterior end. Hepatic region faintly defined; margin inside general outline of carapace, angled near posterior end. Mesogastric median ridge gentle, narrow, rising from junction of postfrontal ridges. Gastric region with pair of tubercles and 1 median pearl-like granule slightly anterior to tubercles. Cardiac region medially prominent, faintly separated from intestinal region by shallow transverse groove. Intestinal region strongly prominent, with median ridge, culminating slightly anterior to posterior end. Epibranchial region strongly expanded, sloping anteriorly from ridge; margin thin, upturned, rounded, somewhat incurved near posterior end, forming right angle with metabranchial margin; epibranchial ridge dentate, obliquely extending from near gastric tubercle to posterolateral margin, prominent at middle and distal end; prominences on epibranchial ridge, gastric tubercle, and gastric median granule almost coming into line. Metabranchial region deeply concave between epibranchial and intestinal ridges; margin weakly upturned, incurved at anterior 0.7, obtusely angled at posterior 0.3. Posterior margin trilobate; lateral lobes triangular with rounded tip, well

developed far beyond median lobe; median lobe small, triangular, with rounded tip, situated slightly lower than lateral lobes.

Third maxilliped (Fig. 2c, d) covered with minute granules; ischium 1.2 times as broad as exopod in maximum breadth; merus 1.2 times as long as ischium along mesial margin; exopod arcuate and rimmed with short setae along lateral margin, with larger granules on distal part; internal mesial ridge vestigial, with mesially directed, long setae.

Cheliped (Fig. 2e) stout, entirely covered with granules of various sizes, sparsely frilled with short setae; merus subcylindrical, granules large and acute near inner and outer margins; carpus short, arcuate on outer margin; palm medially swollen, somewhat arcuate on inner margin, outer margin divided into 3 lobes, as long as movable finger along outer margin; both cutting edges of fingers with several minute, obtuse teeth, gaping and blunt at proximal 0.3.

Ambulatory legs (Fig. 2f) slender, similar in shape, gradually decreasing in length from first to fourth, covered with minute granules except dactyli; meri subcylindrical, slightly longer than combined length of

carpi and propodi, with sparse soft setae; carpi slightly shorter than propodi; dactyli 1.2 times as long as propodi, with vestigial, inconspicuous dactylo-propodal locks near proximal borders on dorsal surfaces (Fig. 2g).

Abdomen (Fig. 2h) entirely covered with minute granules on ventral surface; formula  $2+R+T$ ; first segment completely concealed beneath carapace; second segment short, transversely zonal, bent proximally at median part; main fused section composed of third to sixth segments, ovoid, convex ventrally, divided into subregions by 2 longitudinal and 3 transverse grooves, with obtuse triangular prominence near distal border; telson tongue-shaped, directed dorsally in natural position.

*Etymology.*—This species is dedicated to Prof. D. Guinot, who kindly gave the authors the opportunity to examine many valuable specimens deposited in the Muséum national d'Histoire naturelle, Paris.

*Color.*—In preserved condition, body and appendages generally light brown; ridges, margins and posterior lobes of carapace off white.

*Remarks.*—This species is similar to *N. alata* Komatsu & Takeda, 1999 from the Ryukyu Islands, Japan, in the strongly expanded epibranchial region, the development of the frontal region, and the deeply concave metabranchial region. It is, however, distinguished from *N. alata* as follows: the epibranchial ridges are dentate, whereas in *N. alata* the ridges are continuous; the mesogastric ridge is narrow and gentle, whereas in *N. alata* the ridge is broad, with a median shallow groove; the posterior lobes are more strongly expanded, whereas in *N. alata* the lobes are moderately expanded. The new species also resembles *N. mimetica* Nobili, 1906, but is distinguished from the latter by the dentate epibranchial ridge, the small projection of the pterygostomian margin, and the well-developed posterior lobes.

*Nursia guinotae*, *N. alata*, and *N. mimetica* can be distinguished from *N. plicata*

(Herbst, 1804) as follows: the hepatic and transverse ridges of the carapace are absent, whereas in *N. plicata* the ridges are present; the posterior margin of carapace is trilobate, whereas in *N. plicata* the posterior margin is bilobed; the abdominal formula of female is  $2+R+T$ , whereas in *N. plicata* the formula is  $1+2+3+R+T$ .

*Nursia mimetica* Nobili, 1906

Fig. 3

*Nursia mimetica* Nobili, 1906:261 (type locality: Rikitea, Tuamotu Archipelago); 1907: 380, pl. 1(13); Komatsu & Takeda, 1999: fig. 1D.

*Material examined.*—Syntype, 1 ovig. female,  $2.7 \times 3.7$  mm, off Rikitea, Mangaréva I., Gambier Is., Tuamotu Archipelago, French Polynesia, 4–5 m, 1905, coll. G. Seurat, MNHN-B 17102.

*Redescription.*—Carapace (Fig. 3a) transversely rhomboidal in general outline, 1.4 times broader than long, closely covered with minute granules, provided with postfrontal, median, and epibranchial ridges. Front moderately developed, 0.2 times as broad as carapace; margin slightly ridged, divided into 2 truncate lobes by small median notch; postfrontal ridges obliquely converging from frontal-orbital angles but not meeting together. Orbit with 2 grooved, longitudinal fissures on dorsal roof; infraorbital lobe bearing V-shaped notch, with terminal sharrow pit. Pterygostomian margin forming general outline, almost straight, roundly angled at posterior end. Hepatic region faintly defined; margin inside general outline of carapace, obtusely angled near posterior end. Mesogastric ridge broad, with longitudinal, shallow groove along midline, with some pairs of small pits on both sides of posterior end of ridge. Gastric region gently convex bilaterally. Cardiac region weakly separated from intestinal region by faint transverse groove. Intestinal region gently swollen, with faint median ridge extending from cardiac region. Epibranchial region strongly

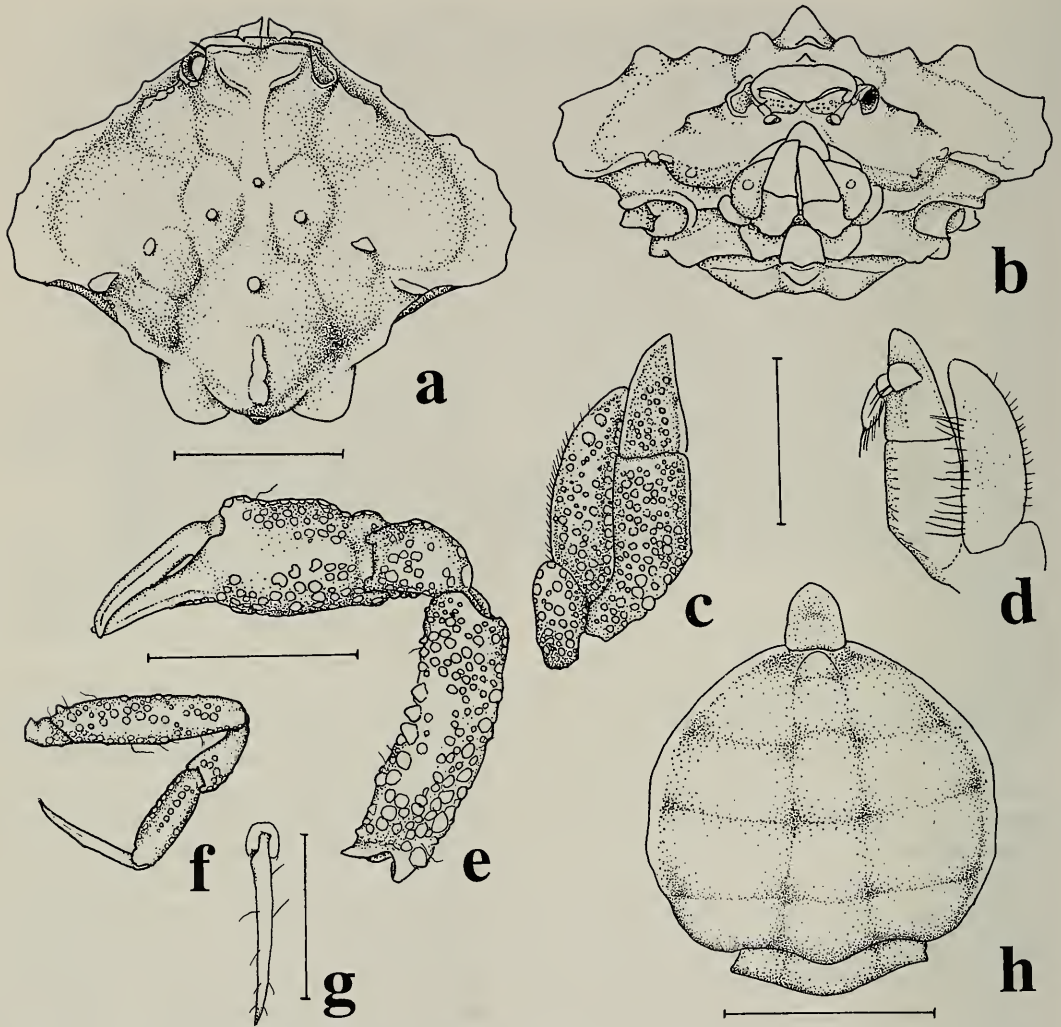


Fig. 2. *Nursia guinotae*, new species, holotype, ovigerous female, Vietnam, 2.7 × 3.2 mm (MNHN-B 9947): a, carapace, dorsal view; b, same, frontal view; c, right third maxilliped, external view; d, same, internal view; e, right cheliped, dorsal view; f, right first ambulatory leg, dorsal view; g, dactylus of same, lateral view; h, abdomen, ventral view. Scales equal 1 mm (a–b, e–f, h), and 0.5 mm (c–d, g).

expanded, sloping anteriorly from epibranchial ridge; margin thin, weakly upturned, separated from pterygostomial margin by small notch, obtusely angled at posterior 0.4, forming rounded, obtuse angle with metabranchial margin; epibranchial ridge weak, extending from near gastric convexity to metabranchial margin, interrupted medially. Metabranchial region shallowly concave between intestinal and epibranchial ridges, with 2 pairs of shallow pits on both

sides of cardiac and intestinal regions; margin gently converging on anterior 0.3, inwardly arcuate on posterior 0.7. Posterior margin trilobate, not well developed; laterel lobes situated lower than metabranchial region; median lobe small, situated lower than lateral lobes.

Third maxilliped (Fig. 3b, c) entirely covered with minute granules of various sizes; ischium longitudinally convex in lateral 0.7; merus 1.2 times longer than ischi-



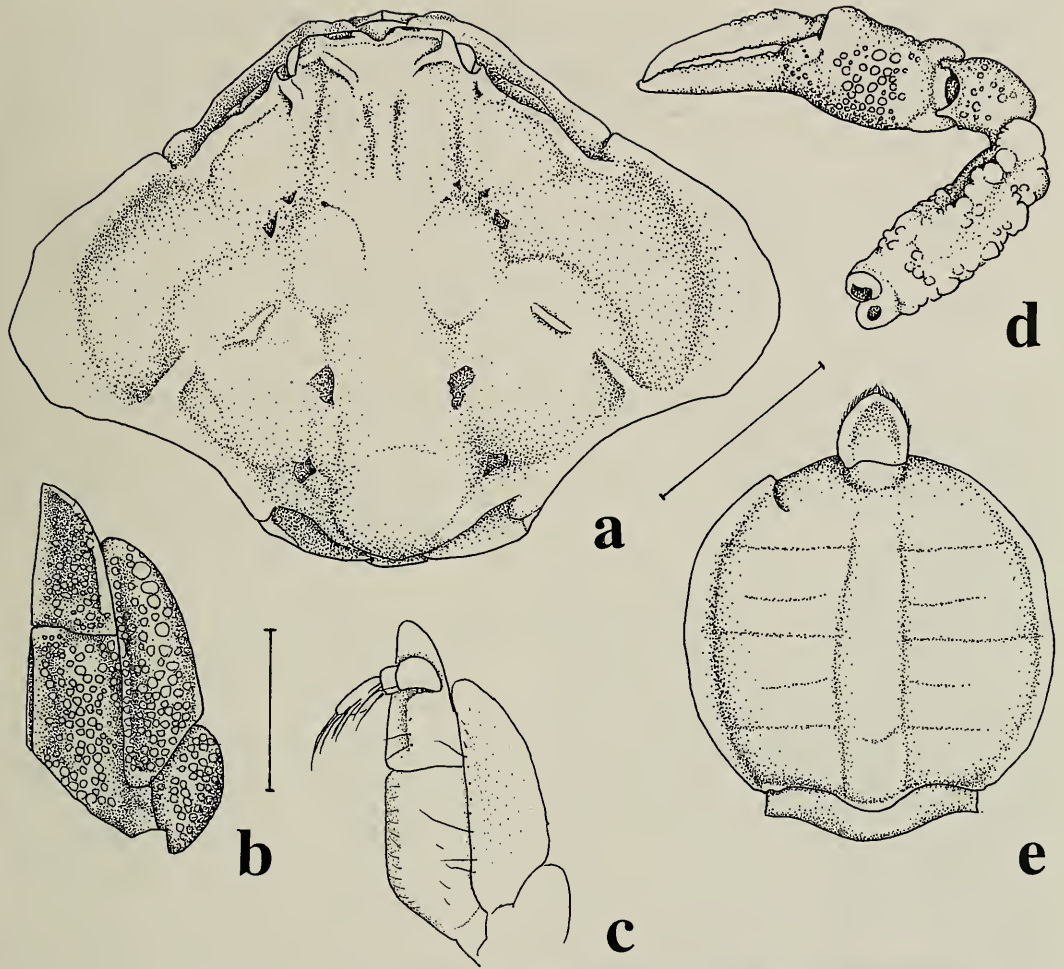


Fig. 3. *Nursia mimetica* Nobili, 1906, syntype, ovigerous female, Rikitea, Tuamotu Archipelago,  $2.7 \times 3.7$  mm (MNHN-B 17102): a, carapace, dorsal view; b, left third maxilliped, external view; c, right maxilliped, internal view; d, right cheliped, dorsal view; e, abdomen, ventral view. Scale equal 1 mm (a, d-e), and 0.5 mm (b-c).

um along mesial margin, arcuate on lateral margin; exopod slightly convex along midline, with row of large granules, arcuate on lateral margin; internal mesial ridge vestigial, with several mesially directed, long setae.

Right cheliped (Fig. 3d) moderate, 1.1 times longer than carapace, covered with granules of various size; merus subcylindrical, slightly arcuate on outer margin; carpus short, convex dorsally; palm swollen; movable finger 1.4 times as long as palm along outer margin; both cutting edges of

fingers furnished with several triangular teeth on distal 0.4, blunt on proximal 0.6. Left cheliped missing.

Ambulatory legs missing.

Abdomen (Fig. 3e) entirely covered with minute granules; formula 2+R+T; first segment completely concealed beneath carapace; second segment short, transversely zonal, proximal border gently convex medially; main fused section composed of third to sixth segments, ovate, slightly convex ventrally, with 3 medially interrupted transverse grooves and 2 short translucent

Table 1.—Differences between *Nursia mimetica* Nobili, 1906, *N. alata* Komatsu & Takeda, 1999, and *N. guinotae*, new species.

	<i>N. mimetica</i>	<i>N. alata</i>	<i>N. guinotae</i>
Mesogastric ridge	broad with median groove	broad with median groove	narrow
Epibranchial ridge	oblique	oblique	oblique and dentate
Posterior margin	indistinctly trilobate, lower than metabranchial margin	trilobate	distinctly trilobate
Distribution	Tuamotu Archipelago	Ryukyu Islands	Vietnam

bands between grooves, with subtriangular prominence just near distal border, proximal border convex medially; telson short, tongue-shaped, with short setae around apex.

*Remarks.*—This species is known only from the specimens used by Nobili (1906, 1907), two females, from off Rikitea, Tuamotu Archipelago. Nobili noted that they mimic fragments of the calcareous alga, *Halimeda opuntia*. Tan & Richer de Forges (1993) also reported some mimetic crabs belonging to the family Leucosiidae. Although Nobili recorded two females in his descriptions, only one ovigerous female (syntype, MNHN-B 17102) is now deposited in MNHN. We inquired with the Museo Regionale de Scienze Naturali, Torino, for the remainder of the syntype specimens, but they were not found there (L. Levi, in litt.). The present specimen agrees well with Nobili's descriptions, but is missing all its legs except the right cheliped.

The comparison of *N. mimetica*, *N. alata*, and *N. guinotae* is summarized in Table 1.

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**First record of the portunid crab *Arenaeus cribrarius* (Lamarck, 1818) (Crustacea: Brachyura: Portunidae) in marine waters of Argentina**

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*Abstract.*—The first record of the portunid crab *Arenaeus cribrarius* (Lamarck, 1818) in marine waters of Mar del Plata, Buenos Aires province, Argentina (38°S, 57°W) is documented. Juveniles and preadult specimens of the species were captured in waters at depths between 6 and 10 m on sand and mud-sand bottom, 10°C of temperature and 34‰ of salinity. This report extends the southern limit of distribution of *A. cribrarius* by more than 500 km. This species was previously known in the southwestern Atlantic from Massachusetts to Uruguay.

*Resumen.*—El trabajo documenta el primer hallazgo del cangrejo portúnido *Arenaeus cribrarius* (Lamarck, 1818) en aguas marinas frente a Mar del Plata, provincia de Buenos Aires, Argentina (38°S, 57°W). Los ejemplares juveniles y preadultos de la especie fueron capturados a profundidades entre 6 y 10 m sobre fondo arenoso y areno-fangoso, en aguas con temperaturas de 10°C y 34‰ de salinidad. Con esta mención se extiende la distribución de *A. cribrarius* mas de 500 km. La especie es conocida previamente en el Atlántico Sudoccidental desde Massachusetts hasta Uruguay.

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In June 2000, Mr. José L. Ungarelli, a local fisherman captured three specimens of what appeared to him as a strange crab for the marine waters near Mar del Plata (38°S, 57°W), Buenos Aires province, Argentina. The specimens were identified as *Arenaeus cribrarius* (Lamarck, 1818) (Fig. 1) a portunid crab known to range broadly from shallow waters of Vineyard Sound, Massachusetts, U.S.A., throughout the Caribbean Sea, to Brazil and Uruguay (Williams 1965, 1984; Juanicó 1978; Melo 1996, 1998, 1999). The type locality is Brazil.

This coastal species found in the Virginian to Argentinean zoogeographical provinces in the southwestern Atlantic (Boschi 2000a, 2000b) had not been previously captured south of Uruguay. The present report

in the Mar del Plata region (38°S), extends the distribution of *A. cribrarius* by more than 500 km from the previous southern limit in the southwestern Atlantic Ocean (Juanicó 1978).

The specimens were captured using a beam trawl at depths of 6 to 10 m over sand and mud-sand bottom. Water was 10°C in temperature, and 34‰ in salinity.

Specimens were measured for carapace width (CW) excluding lateral spines, and in carapace length (CL), from basal region between the frontal teeth to the postero-medial border of carapace (Pinheiro & Fransozo 1993, 1998). Measurements are in millimeters, and were obtained with a caliper to the nearest 0.1 mm accuracy. Specimens were weighed (W) in a digital scale (0.001 grams sensibility).

Family Portunidae Rafinesque, 1815  
*Arenaeus cribrarius* (Lamarck, 1818)  
 Fig. 1

*Portunus cribrarius*.—Lamarck 1818:259.  
*Arenaeus cribrarius*.—Williams 1965:173,  
 fig. 153.—1984:362–363, fig. 292.—  
 Melo 1998:476.—1999:450, fig. 37.

*Material examined*.—3 juveniles females  
 CW 35.5, 36.5 and 40.2 mm, CL 20.2, 21.5  
 and 24.0 mm, W 5.8, 6.59 and 8.82 g. Two  
 small specimens were deposited in the col-  
 lections of the Departamento de Ciencias  
 Marinas, Universidad Nacional de Mar del  
 Plata, and the larger specimen in the Museo  
 Argentino de Ciencias Naturales “Bernar-  
 dino Rivadavia”, Buenos Aires, Argentina  
 (Collection number: MACN 34616).

*Remarks*.—The specimens showed white  
 spots characteristic of the species, and mor-  
 phologically agree with the characters pro-  
 vided by Williams (1984). The small crabs  
 still showed a white stripe on the carapace,  
 indicative of a juvenile stage. All three  
 specimens are juvenile females, with the  
 pleon plate still adhered to the sternum and  
 they have a triangular shaped abdomen  
 characteristic of juvenile stages as indicated  
 by Pinheiro & Fransozo (1998).

### Discussion

In recent years several new records of  
 crustaceans from Argentinean marine wa-  
 ters have been reported in papers and/or  
 meetings. Lini et al. (1995) documented the  
 first record of the isopod *Joeropsis dubia* in  
 Mar del Plata; Spivak & Bas (1999) found  
 the grapsid crab *Planes marinus* Rathbun,  
 1914 in Mar Chiquita, 80 km north of Mar  
 del Plata, together with other crustaceans  
 such as the cirriped *Lepas anatifera* L.,  
 1758 and the amphipod *Caprella andreae*  
 Mayer, 1890, all representing first records  
 for the southwestern Atlantic Ocean.

Several hypotheses have been proposed  
 for the presence of these species, including  
 ships fouling and ballast water, drifting  
 plankton larvae, and surface current trans-

port associated with floating objects. Ac-  
 cording to specialists of fishes (López  
 1964), phytoplankton (Balech 1964), crus-  
 taceans (Boschi et al. 1992, 2000a, 2000b)  
 the Argentinean biogeographic province is  
 the area between 23°S (Rio de Janeiro, Bra-  
 zil) to 43°S (Rawson, Chubut). According  
 to López (1964) it is possible to distinguish  
 two districts: southbrazilian and bonaerense,  
 with a limit around 34°S, but that limit can  
 be modified according movements of water  
 masses, specially near the coasts, reaching  
 near San Jorge Gulf, Argentinean Patagonia  
 during summer months. Low salinity waters  
 of Río de la Plata are considered as a natural  
 barrier for the dispersion of marine fauna.  
 As it was stated by Lucas et al. (1999:105).  
 . . . “the presence of winds that force onshore  
 flow to the south seem to be favorable for the  
 southward extension of low salinity water  
 from Río de la Plata and are most likely to  
 occur in spring-summer. Anomalously high  
 discharge from the Río de la Plata associ-  
 ated with ENSO (El Niño south oscillation)  
 conditions in spring of 1997 and summer of  
 1998 showed a correlation with a coastal low  
 salinity intrusion as far south as Miramar”.  
 . . . more than 40 km south of Mar del Plata.  
 Eventually, warm waters south to the bonaerense  
 littoral would be associated to a intrusions  
 of the Brazil Current (Balech 1965, 1986),  
 water circular movements or eddies (Piola &  
 Rivas 1997), or the so called Argentinean  
 flux (waters of subtropical origin) according  
 to Severov (1990). Other hypotheses postu-  
 late that the presence of marine biota of  
 southbrazilian origin in bonaerense coastal  
 region will be caused by the diminishing  
 caudal of fresh-water from Río de la Plata,  
 at it happened during summer and fall of  
 the year 2000 (Mianzan et al. 2000).

The number of brachyuran crabs living  
 in littoral waters of Argentina reach 39  
 species (Boschi 1964; Boschi et al. 1992;  
 Spivak & Bas 1999), of which three are  
 portunids: *Ovalipes trimaculatus* (de  
 Haan, 1833), *Coenophthalmus tridentatus*



Fig. 1. *Arenaeus cribrarius* juvenile: A) dorsal view, B) ventral view. Scale in millimeters.

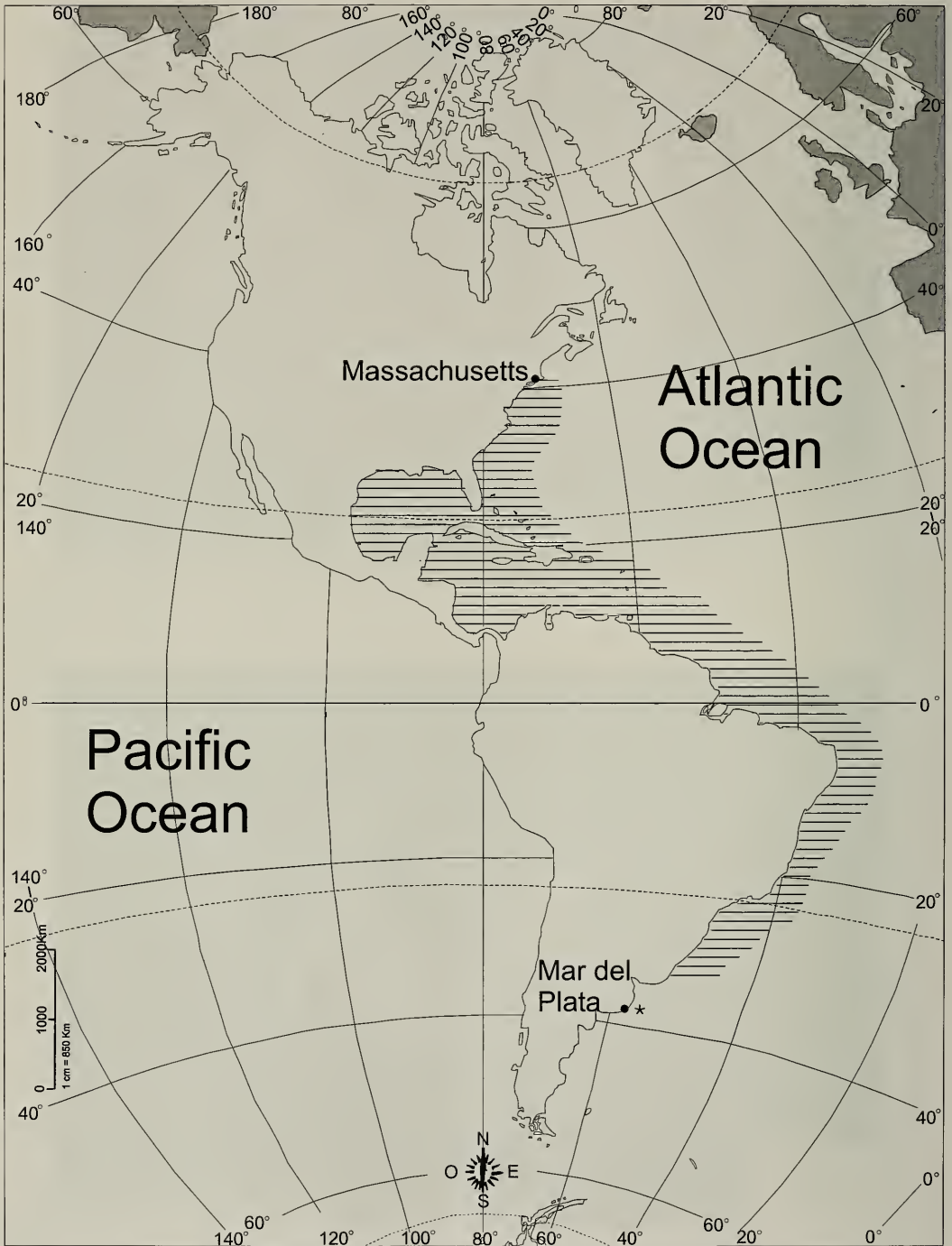


Fig. 2. Geographical distribution of *Arenaeus cribrarius* in the western Atlantic Ocean. \* Indicates new record.

A. Milne Edwards, 1879 and *Callinectes sapidus* Rathbun, 1896. The presence of *A. cribrarius* adds another species to this region. *Arenaeus cribrarius* lives in shallow waters along ocean beaches from the water line to 68 m (Williams 1984; Melo 1996, 1998, 1999). Ovigerous females of this species are present during September in Venezuela and Brazil (Williams 1984) and during all months in Ubatuba region (Pinheiro & Fransozo 1998). The presence of this species near Mar del Plata can be explained based on larval transport by plankton drifting from coastal subtropical waters during spring-summer, crossing Río de la Plata after metamorphoses, and then growing to CW of 35.5 to 40.2 mm; or larvae introduced by ballast water of ships, as mentioned for other portunidae species in other localities of the western Atlantic and the Caribbean Sea (Lemaitre 1995; Tavares & Mendonça 1996; Mantelatto & Dias 1999). The specimens reported herein represent juvenile stages, and thus it appears that the adult population is not yet established. The occasional finding of juveniles in marine waters of Mar del Plata, Argentina as well as in Uruguay by Juanico (1978) will be considered as expatriation areas in the distribution of the species in the southern Atlantic ocean (Fig. 2).

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## First record of larvae of the rare mud shrimp *Naushonia* Kingsley (Crustacea: Decapoda: Laomeidiidae) from Asian waters

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*Abstract.*—Larvae of an undetermined species of the laomeidiid genus *Naushonia* Kingsley are reported from plankton samples collected in Gokasho Bay, Pacific coast of Japan. The presence of stage 1 zoeas suggests that adult shrimps of *Naushonia* are distributed in the neighboring district. This is the first record of *Naushonia* from Asian waters.

The rare laomeidiid genus *Naushonia* Kingsley, 1897 consists of seven species, none of which are known from Asian waters (Martin & Abele 1982, Berggren 1992, Alvarez et al. 2000). There is scant larval information on these rare mud shrimps to date, although all known species of *Naushonia* occur in very shallow benthic waters. Since Thompson's (1903) work, planktonic larval stages of *Naushonia* species have been described for *N. crangonoides* Kingsley, 1897, *N. portoricensis* (Rathbun, 1901) and two undetermined species (Gurney & Lebour 1939, Dakin & Colefax 1940, Kurian 1956, Goy & Provenzano 1978).

During plankton collections made at Gokasho Bay, Japan, in the summer of 2000, zoea 1 larvae belonging to an undetermined species of *Naushonia* were found. These zoeas are described in this study, representing the first record of the genus in Asian waters.

### Materials and Methods

The zoea 1 larvae were taken in a 300  $\mu\text{m}$  mesh and 46 cm diameter tow-net, at depths of 5–10 m, at Gokasho Bay, Mie Prefecture, Japan, 34°20'N, 136°42'E, on 27 Jul, 2 and 10 Aug 2000. Water temperature and salinity of the collection sites ranged from 25 to 27°C and 33.5 to 33.7‰ respectively.

Living specimens were observed and sorted under a Nikon SMZ-10 stereomicroscope. After fixation in 3% buffered formalin, the appendages were dissected with fine insect pins or sharpened tungsten needles under the stereomicroscope, and mounted on a silicon-coated glass slide. Drawings and measurements were made with a drawing tube attached to an Olympus BH-2 microscope. A color image of a living specimen was captured with an Olympus HC-300/OL digital camera connected to the microscope. All illustrations were made with Illustrator™ 5.5J (Adobe Systems Inc.) on a Macintosh™ OS (Apple Co. Ltd.). Carapace length (CL) was measured from the tip of the rostral spine to the medial posterior border of the carapace.

Voucher specimens have been deposited in the Natural History Museum and Institute, Chiba, Japan, under accession numbers CBM-ZC 5573-5575.

### Description of zoea 1

Size: CL =  $0.73 \pm 0.036$  mm (range 0.70–0.77 mm, 3 specimens).

Color (Fig. 1): Small red and large yellowish chromatophores dispersed on antennule, and mainly ventral side of carapace and abdomen.

Carapace (Fig. 2A, B): Rostral spine short, slender, upturned distally. Posterolateral border rounded. Eyes sessile.



Fig. 1. Photograph of a living specimen of zoea 1 of *Naushonia* sp. Note chromatophores on ventral side. Scale = 0.1 mm.

Antennule (Fig. 3A): Uniramous, about half-length of CL, unsegmented with 5 aesthetascs terminally, and long plumose seta subterminally.

Antenna (Fig. 3B): Biramous. Protopod with simple spine at base of exopod. Endopod with 3 long plumose setae distally. Exopod (=antennal scale) flat, elongated, oval, with 10 plumose setae on inner margin.

Mandibles (Fig. 3C): Asymmetrical. Left with incisor process large, sickle-shaped, with 2 subterminal inner spines; right small, conical, with subterminal inner spine. Right and left molar processes almost equal in size, but different in dentation. Paragnath of left side (Fig. 3C') slender sickle-shape as in left mandible.

Maxillule (Fig. 3D): Coxal endite with 4 simple setae and subterminal small seta. Basal endite with 2 large teeth and 2 simple setae. Endopod unsegmented with 3 terminal setae.

Maxilla (Fig. 3E): Coxal endite bilobed, proximal lobe small, with 1 long and 1 short plumose setae, and distal lobe with simple 3 setae. Basal endite bilobed with 5+4 simple setae, respectively. Scaphognathite without proximal lobe, and with 5 plumose setae on margin.

Maxilliped 1 (Fig. 3F): Biramous. Coxa without setae. Basis with 1+2+3 inner setae. Endopod 4-segmented with 2,1,2,5+I (I = dorsal seta) seta. Exopod with 4 natatory plumose setae terminally, symmetrically arrangement in 2 tiers (Fig. 3F').

Maxilliped 2 (Fig. 3G): Biramous. Coxa and basis with no setae. Endopod 4-segmented with 0,0,2,4+I setae. Exopod as in maxilliped 1.

Maxilliped 3 (Fig. 3H): Uniramous, 3-segmented, without setae.

Pereiopods: Rudimentary.

Abdomen (Fig. 2A): Smooth, 5 somites plus forked triangular telson. Abdominal somite 1 with short rod-like pleural projection (Fig. 2A') and somite 2-5 with anteriorly procurved pleural hooks.

Telson (Fig. 2C, C'): Triangular, with deep notch and 7 pairs of posterior processes; outermost process stout, unarticulated spine; second process thin plumose seta (=anomuran hair) on ventral side of telsonal fork (Fig. 2C'); third through seventh processes large articulated plumose setae.

#### Discussion

The infraorder Thalassinidea consists of 11 families (Poore 1994) and larval stages

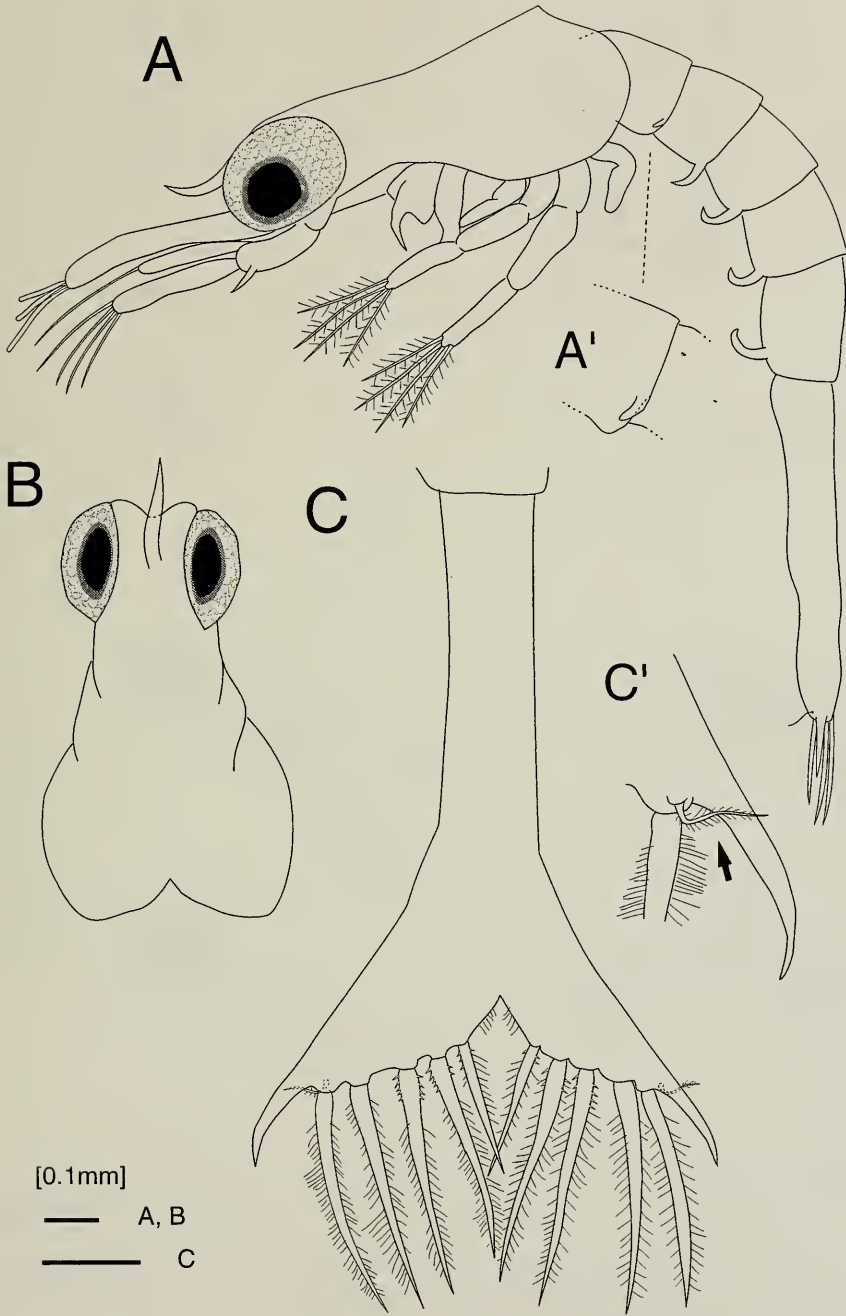


Fig. 2. *Naushonia* sp., zoea 1. A, whole animal, lateral view; A', enlarged posterior part of abdominal somite 1; B, carapace, dorsal view; C, telson, dorsal view; C', enlarged right telsonal fork, ventral view, showing 'anomuran hair' (arrow).

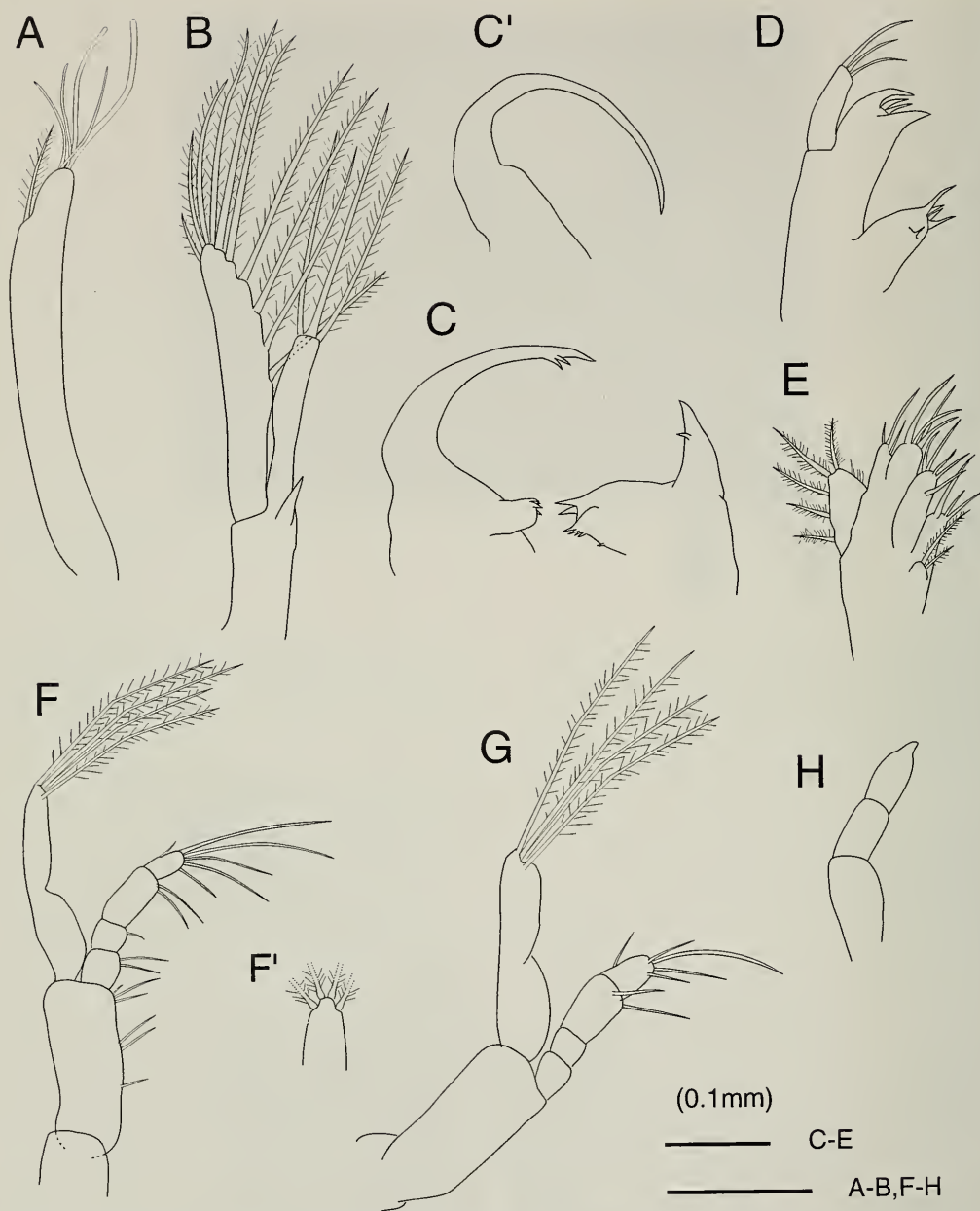


Fig. 3. *Naushonia* sp., zoea 1. A, antennule; B, antenna; C, mandibles; C', left paragnath lobe; D, maxillule; E, maxilla; F, maxilliped 1; F', tip of exopod of maxilliped 1; G, maxilliped 2; H, maxilliped 3.

have been described for species in six families. Laomediid zoeal larvae differ from those of other decapod shrimps by the considerably asymmetrical mandibles and procurved pleural hooks on the abdominal somites (see Konishi 1989). A recent study of

*Thalassina anomala* (Herbst, 1804) of the Thalassinidae Latreille, 1831, has revealed that its zoea also has a sickle-shaped asymmetrical pair of mandibles as in the Laomediidae Borradaile, 1903 (Uchino 1993). Zoeas of *T. anomala*, however, have a

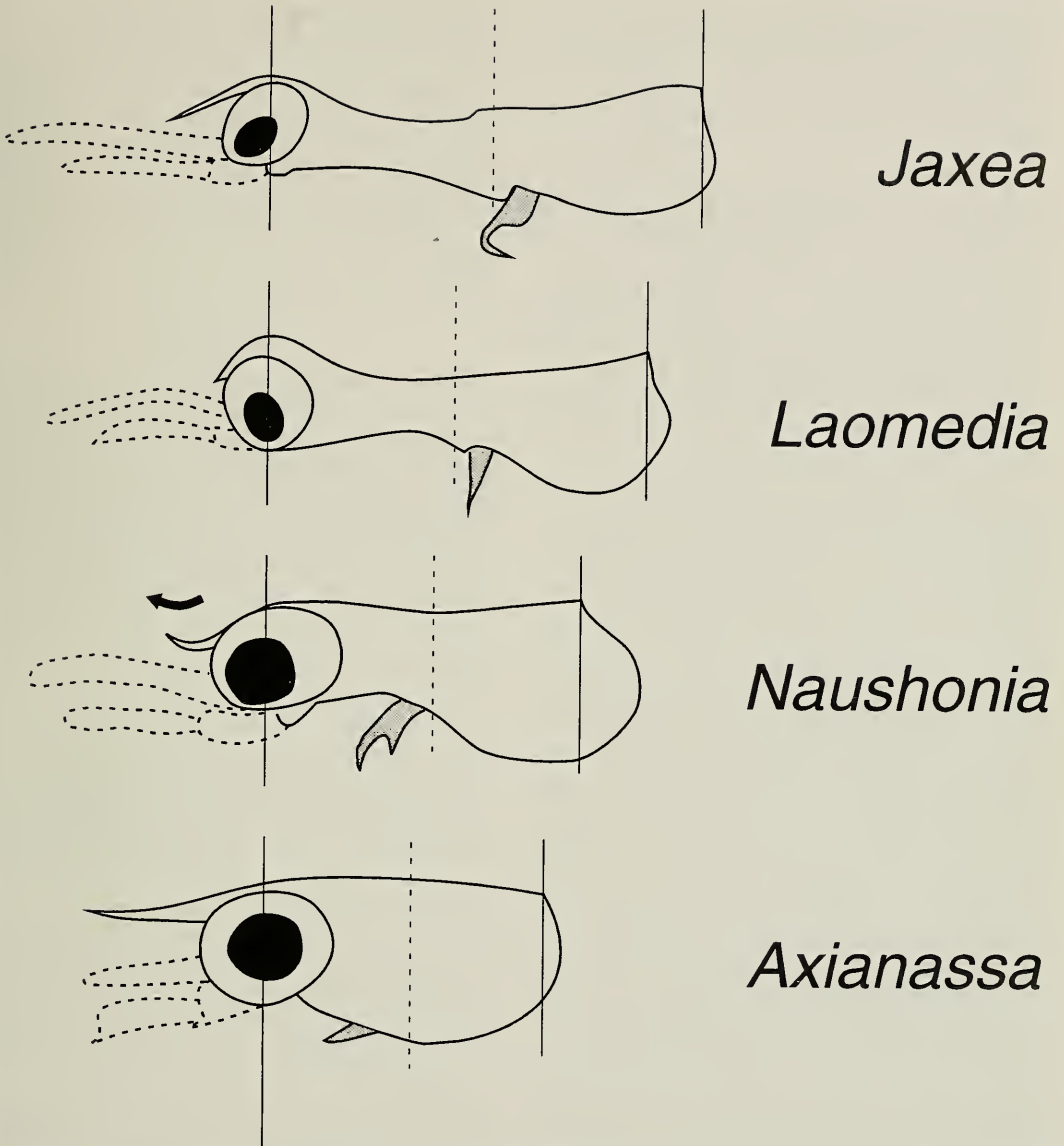


Fig. 4. Diagrammatic representation of zoeal cephalothoraxes in four laomediid genera showing relative position of mandible (shaded). Vertical dotted line indicates midpoint of carapace length. (Based on Gurney 1924; Ngoc-Ho 1981; Fukuda 1982).

unique larval character: i.e., the extremely elongated endopod of maxilliped 2. Thus, the laomediid zoeas can be easily separated from the Thalassinidae despite similarities in the mandibles.

The Laomediididae includes 5 genera as follows (Ngoc-Ho 1981): *Laomedea* De Haan, 1841, *Naushonia*, *Jaxea* Nardo,

1847, *Axianassa* Schmitt, 1924, and *Lauretiella* Le Loeuff & Intes, 1974. Larval stages are known for representative species in all of them except *Lauretiella* (Thompson 1903, Caroli 1924, Gurney 1924, Gurney & Lebour 1939, Dakin & Colefax 1940, Kurian 1956, Sakai & Miyake 1964, Goy & Provenzano 1978, Ngoc-Ho 1981,

Fukuda 1982, Rodrigues & Shimizu 1992). Their zoeas are clearly distinguishable between genera. The mandibles of *Naushonia* and *Axianassa* are located anterior to the mid point of the carapace as in typical decapod zoeas, while those of *Jaxea* and *Laomedea* are posterior (Fig. 4). The rostrum of *Naushonia* is short and upturned whereas it is long and straight in *Axianassa*. In addition, the abdomen of *Axianassa* zoea bear a pair of posterolateral spines on somite 5 instead of procurved pleural hooks on somite 2-5 as found in *Jaxea*, *Naushonia* and *Laomedea*. Therefore, zoeas of *Naushonia* species are easily identified.

The morphology of the herein reported Japanese zoeas is different from those of *N. crangonoides* and *N. portoricensis* described by Goy & Provenzano 1978 and Gurney & Lebour 1939, in antennule, maxillule and pleural projection on abdominal somite 1. The antennule, has two subterminal plumose seta in *N. crangonoides*, whereas only one in the present zoea. The coxal endite of maxillule bears a small proximal lobe in the present zoea, whereas there is no lobe in the zoea of others. The present zoeal specimens, therefore, seems to belong to a species different from those for which larvae are known, or perhaps to an unknown species of the genus.

Until now, the Laomedidae was represented in Japan by only one genus *Laomedea* (Miyake, 1998). The present zoeas, however, are clearly assignable to *Naushonia* species. According to findings for rearing of plankton-caught zoeas of *N. crangonoides* by Goy & Provenzano (1978), zoea 1 molt to the next instar within 5.24 days in average when they were incubated at 25°C. This strongly suggests that adult shrimps of *Naushonia* must be distributed in the neighboring district of Gokasho Bay in Japan or very nearby waters.

There may be two reasons why *Naushonia* larvae have not been reported previously from Japan and adjacent waters. First, they may be of very rare species (Berggren 1992) in Japan and adjacent

Asian waters. Second, *Naushonia* does not have native representative, and the present zoeas are from recent introduction of an exotic species, as has occurred with the Mediterranean portunid crab in Tokyo Bay, Japan (Sakai 1986). A careful faunal survey, and further larval studies of the coast of Japan, may be needed to answer this question.

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**A new cavernicolous species of freshwater crab (Crustacea:  
Brachyura: Potamidae) from Pulau Tioman, peninsular Malaysia**

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*Abstract.*—A new freshwater potamid crab species, *Johora gua*, is described from Pulau Tioman, an island off the east coast of Peninsular Malaysia. It differs from most of its congeners by the relatively longer and slenderer ambulatory legs as well as various other characters in the carapace and male first pleopod. This is the fifth species of *Johora* Bott to be described from Pulau Tioman, and the first cavernicolous crab to be reported from Peninsular Malaysia.

Specimens of an unusual freshwater crab recently collected from a cave on Pulau Tioman, an island off the east coast of Peninsular Malaysia, proved to be a new potamid species of the genus *Johora* Bott, 1966. This new species differs from most of its congeners by the relatively longer and slenderer ambulatory legs as well as various other characters of the carapace and male first pleopod. The genus *Johora* Bott, 1966 [type species: *Potamon (Potamon) johorensis* Roux, 1936], is endemic to the Malay Peninsula, occurring northwards from Singapore into the southern half of Peninsular Malaysia along the central highlands. Species of this genus are replaced by those of *Stoliczia* Bott, 1966, in the northern half through to southern Thailand (Ng 1988). A total of 13 species have been placed in *Johora*, with Pulau Tioman alone accounting for four species, all island endemics, viz., *J. counsilmani* (Ng, 1985), *J. grillator* Ng, 1988, *J. punicea* (Ng, 1985), and *J. tiomanensis* (Ng & Tan, 1984) (see Ng 1988, 1990; Ng & Takeda 1992; Yeo et al. 1999). In the present study, the fifth *Johora* species known from Pulau Tioman is described, bringing the total number in the genus to 14.

Ng (1988: 142) earlier referred to the "...existence of an unknown species of white crab in Malayan caves..." but this

has yet to be discovered. The new species of *Johora* herein described is the first true cavernicolous freshwater crab to be reported from Peninsular Malaysia. The cave-dwelling habits of this species are, to some extent, reflected in slight troglomorphic features although these are less significant when compared with other known cavernicolous crabs.

The following abbreviations are used: G1, male first pleopod; G2, male second pleopod; cw, carapace width; and asl, above sea level. Measurements are given in millimeters (mm) as carapace width  $\times$  length. Terminology used essentially follows Ng (1988). Malay words used in the text are 'Pulau', island; 'Gua', cave; and 'Gunung', mountain. Specimens remain deposited in the Zoological Reference Collection, Raffles Museum of Biodiversity Research, Department of Biological Sciences, National University of Singapore (ZRC). As comparative material, the types and supplementary specimens of the other four *Johora* species from Pulau Tioman in the ZRC were examined. A detailed listing of this material can be found in Yeo et al. (1999).

*Johora gua*, new species  
Figs. 1A–C, E–H, 2A–G

*Material examined.*—Holotype: male 11.4  $\times$  8.5 mm (ZRC 2000.2236), Gua



Tengkuk Ayer, route to Gunung Kajang from Juara, Pulau Tioman, ca. 900 m asl., Peninsular Malaysia, coll. H. H. Tan & T. M. Leong, 1 Sep 2000. Paratype: male  $9.5 \times 7.2$  mm (ZRC 2000.2237), same data as holotype.

*Diagnosis.*—Carapace distinctly broader than long, not elevated; dorsal surface flat, glabrous. Epigastric cristae distinctly rugose; postorbital cristae not sharp, rugose. Frontal region smooth; antennular fossae broadly subrectangular; corneas slightly reduced, about 0.4 times length of eyestalks. External orbital angle low, broadly triangular, outer or lateral margin about 4 times longer than inner or medial margin; epibranchial tooth weak, triangular; anterolateral margin gently convex, very weakly cristate; branchial region indistinctly rugose; metabranchial region with distinct oblique striae. Epistome with weak, broadly triangular median tooth on posterior margin. Third maxilliped exopod with well-developed flagellum, longer than merus width. Cheliped with carpus armed with robust subdistal spine on inner margin. Ambulatory legs sparsely setose, long, slender; dactyli elongated, slender, merus unarmed. Suture between anterior thoracic sternites 2 and 3 faint; thoracic sternite 8 completely separated by longitudinal median line, lacking transverse ridge on midline; abdominal cavity reaching imaginary line joining anterior edge of cheliped bases. Male abdomen triangular. G1 terminal segment about 0.4 times length of subterminal segment, very slender, subcylindrical, curved outwards, lacking dorsal flap; subterminal segment distinctly broader in proximal half, not neck-like distally, without shelf or cleft on upper part of outer margin. G2 distal segment distinctly longer than half of basal segment.

*Color.*—Live specimens are light orange in overall coloration.

*Etymology.*—The specific name, “gua”, is Malay for cave, alluding to its cavernicolous habitat. Used as a noun in apposition.

*Ecological notes.*—The specimens of *Jo-*

*hora gua*, new species, were obtained several meters inside a small granite cave, not higher than 1 m in height, with a shallow underground stream, about 2–15 cm deep, flowing slowly over sandy and rocky substratum. The water pH was 7.8. No surface (epigeal) streams were found in the vicinity (T. M. Leong & H. H. Tan, pers. comm.; Ng et al. 1999: 171). Organic input into this system include swiftlet and porcupine droppings. Tadpoles of a species of megophryid frog, *Leptolalax gracilis* (Günther), and a species of fish, the blind cave loach, *Sundoreonectes tiomanensis* Kottelat, were found syntopically, along with the fully aquatic freshwater crab species *J. tiomanensis* (T. M. Leong & H. H. Tan, pers. comm.). Despite its presence in the cave, and the absence of surface streams nearby, *J. tiomanensis* is still regarded as an epigeal species, as it is commonly found in surface streams at lower altitudes throughout the southern half of the island (see Yeo et al. 1999).

*Remarks.*—*Johora gua*, new species, is immediately separated from all its congeners except *J. grallator* Ng, 1988, by its much longer and slenderer ambulatory legs. *Johora gua* could be mistaken for a juvenile of *J. grallator*, as they are superficially similar in the long, slender legs as well as light orange live coloration (see Yeo et al. 1999). However, specimens of *J. gua* are much smaller, similar in size to the holotype ( $11.4 \times 8.5$  mm, ZRC 2000.2236), which clearly possesses well-developed adult G1s. In contrast, two similar sized male specimens of *J. grallator* (largest  $11.7 \times 8.9$  mm, ZRC 1996.1730) have undeveloped G1s and are clearly juvenile. The ambulatory legs of *J. gua* are relatively stouter than those of *J. grallator*, as reflected in the proportions of the merus of the second leg (4.3–4.4 vs. 5.3–5.7 times longer than broad); and merus of the fourth leg (3.4–3.6 vs. 4.4–4.7 times longer than broad) (Fig. 2A, B; Ng 1988: fig. 23A). Furthermore, *J. gua* differs from *J. grallator* in the following characters: postorbital cristae relatively more ru-

gose and less sharp (vs. postorbital cristae distinctly smoother and sharper); corneas reduced, shorter than half the length of the eyestalks (vs. normal-sized corneas, about half the length of the eyestalks); antennular fossae distinctly broader than the epistome (vs. antennular fossae as broad as epistome); and epistome posterior margin with poorly developed median tooth (vs. epistome posterior margin with well-developed median tooth) (Fig. 1A, C; Ng 1988: fig. 23A, B; Yeo et al. 1999: fig. 5A, B). The shape of the G1 of *J. grallator* is unknown, as no mature males have been collected (see Ng 1988; Yeo et al. 1999). However, the external morphological differences discussed are sufficient to show that the two species are clearly not conspecific. Most of these external differences are also applicable in distinguishing *J. gua* from *J. tiomanensis* (Ng & Tan, 1984), and *J. counsilmani* (Ng, 1985), two other large, fully aquatic *Johora* species that are endemic to Pulau Tioman (see Ng 1988: figs. 20A, B, 21A, B). In addition, *J. gua* can be further separated from these species by its almost smooth sub-branchial, sub-hepatic and pterygostomial regions (vs. sub-branchial, sub-hepatic and pterygostomial regions distinctly rugose); and by its G1 terminal segment always lacking a dorsal flap (vs. G1 terminal segment with dorsal flap); and G1 subterminal segment lacking a distal cleft on the outer margin (vs. G1 subterminal segment with a distinct subrectangular distal cleft on the outer margin) (Figs. 1C, 2C–F; Ng 1988: figs. 20B, 21B; Yeo et al. 1999: figs. 4A–C, F–H, 7B–E, G–H).

*Johora gua* is most similar to *J. punicea* (Ng, 1985), also from Pulau Tioman. Both species share a relatively smooth carapace dorsal surface, with weakly cristate anterolateral margins, and relatively blunt postorbital cristae, and very low, poorly developed epistome posterior margin median tooth (Fig. 1A, C; Ng 1988: fig. 22A, B). The G1 structure in both species is also very similar in having a long, slender outwardly curved or sickle-shaped terminal

segment that lacks a dorsal flap, and a relatively broad subterminal segment that lacks a distinct distal cleft on the outer margin (see Fig. 2C–F, H; Yeo et al. 1999: fig. 6B–D). However, *J. gua* can be distinguished from *J. punicea* by the distinctly slenderer ambulatory legs (e.g., dactylus of second leg 11.4–15.0 vs. 5.9–7.5 times longer than broad; second ambulatory leg merus 4.3–4.4 vs. 3.5–4.0 times longer than broad) (Fig. 2A, B; Ng & Chong 1986; Ng 1988: pl. 1 fig. D, fig. 22A); G1 terminal segment being less strongly hooked or outwardly curved (vs. G1 terminal segment more strongly hooked or curved outwards in appearance); and G1 subterminal segment being relatively slenderer (vs. G1 subterminal segment relatively broader) (Fig. 2C–F, H; Yeo et al. 1999: fig. 6B–D). Furthermore, specimens of *J. punicea* are larger than those of *J. gua*, with specimens of *J. punicea* (e.g., male, 11.3 × 8.8 mm, ZRC 1996.1733) similar in size to the holotype of *J. gua* (11.4 × 8.5 mm, ZRC 2000.2236), possessing undeveloped juvenile G1s (Fig. 2I, J).

In addition to the above primary differences, *J. gua* can also be immediately separated from juvenile as well as adult specimens of *J. punicea* by its light orange live coloration (vs. deep purple in large adults; pink to light purple in juveniles) and proportionately smaller corneas, about 0.4 times length of the eyestalks (vs. normal-sized corneas, subequal to half length of eyestalks) (Fig. 1A, C, D; Ng & Chong 1986; Ng 1988: pl. 1 fig. D, fig. 22A, B). These secondary characters, together with the long and slender ambulatory legs seem to reflect the cave-dwelling habit of *J. gua*. It is interesting to note here that *J. gua* is more similar to juvenile specimens of *J. punicea*, which have relatively slenderer albeit undeveloped G1s, lighter pigmentation and slenderer ambulatory leg segments compared to adult specimens, suggesting a possible progenetic origin for *J. gua* from *J. punicea*.

*Johora gua* appears to be a true caver-

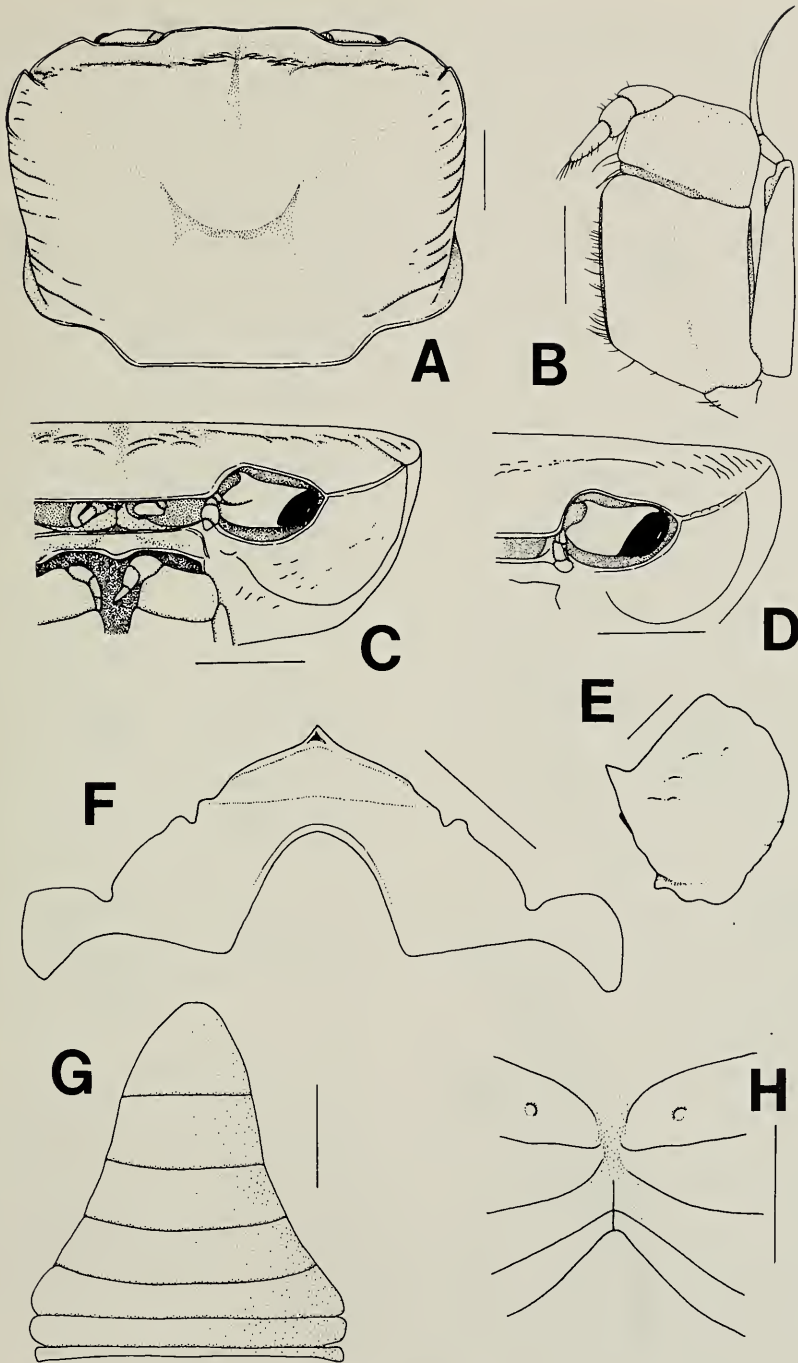


Fig. 1. A–C, E–H, *Johora gua*, new species, holotype male (11.4 × 8.5 mm) (ZRC 2000.2236); D, *Johora punicea* (Ng, 1985), male (11.3 × 8.8 mm) (ZRC 1996.1733). A, dorsal view of carapace; B, left third maxilliped; C, D, frontal view of carapace, left side; E, dorsal view of carpus of right cheliped; F, anterior thoracic sternum (sternites 1–4); G, male abdomen; H, posterior thoracic sternum (sternites 5–8). Scales = 2.0 mm (A, C, D, F–H); 1.0 mm (B, E).

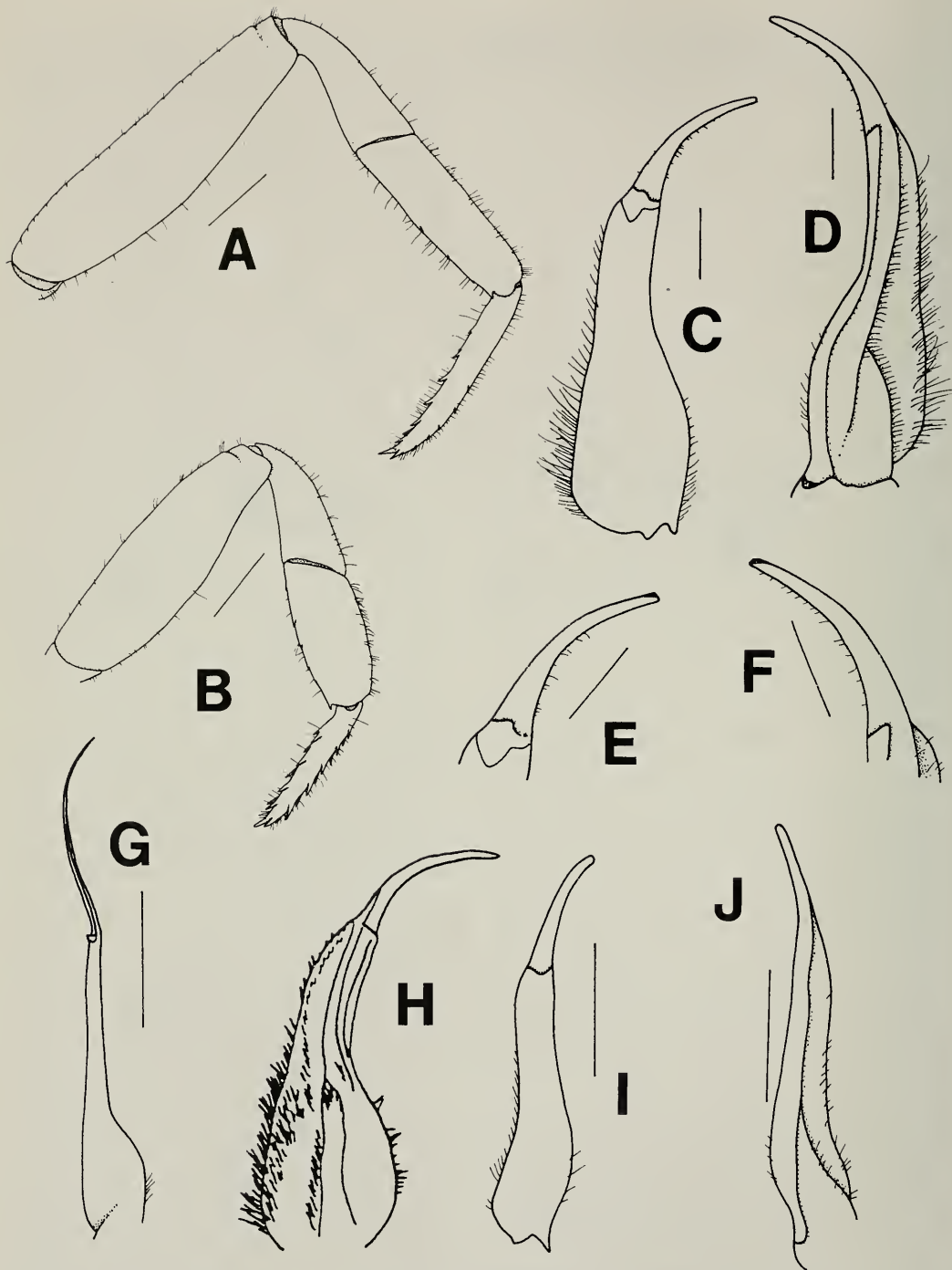


Fig. 2. A-G, *Johora gua*, new species, holotype male (11.4 × 8.5 mm) (ZRC 2000.2236); H-J, *Johora punicea* (Ng, 1985), H, holotype male (19.7 × 15.5 mm) (ZRC 1984.6803) (after Ng, 1988), I, J, male (11.3 × 8.8 mm) (ZRC 1996.1733). A, right second ambulatory leg; B, right fourth ambulatory leg; C, I, dorsal view of right G1; D, J, ventral view of right G1; E, dorsal view of right G1 terminal segment; F, ventral view of right G1 terminal segment; G, right G2; H, ventral view of left G1. Scales = 2.0 mm (A, B); 1.0 mm (G, I, J); 0.5 mm (C-F).

niculous species, as it has not been found in any surface streams on Pulau Tioman despite extensive and intensive sampling on the island over several years (see Yeo et al. 1999). In addition, *J. gua* possesses a combination of troglomorphic features in its proportionately long, slender ambulatory legs, slightly reduced corneas and reduced pigmentation (relative to *J. punicea* adults). Such features are commonly seen in various combinations and degrees in troglobitic crabs in response to life in a cave habitat, where light is either severely reduced or entirely absent, and the sense of touch becomes more important than sight (see Guinot 1988; Ng & Sket 1996; Yeo & Ng 1999). *Johora gua*, however, may be an incipient troglobite as its troglomorphic features are not as highly specialized as that of other known troglobitic crabs, such as the potamid *Erebusa calobates* Yeo & Ng, 1999, from Laos, which has much longer and slenderer legs together with reduced eye-stalks and corneas; the parathelphusid *Sundathelphusa sottoae* Ng & Sket, 1986, from Philippines, which has very reduced pigmentation as well as corneas; and the hymenosomatid *Cancrocaeca xenomorpha* Ng, 1991, from Sulawesi, which has very long, slender legs, and no pigmentation, eyes or orbits (see Ng 1991; Ng & Sket 1996; Yeo & Ng 1999).

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**Symbionts of the hermit crab *Pagurus longicarpus* Say, 1817  
(Decapoda: Anomura): New observations from New Jersey waters  
and a review of all known relationships**

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*Abstract.*—The gastropod shell-*Pagurus longicarpus* complex harbors a variety of associates representing different kinds of symbiosis. There are 31 known relationships, 24 of which have been found with hermit crabs from New Jersey, U.S.A. These involve species from eight phyla, living on, embedded in, or in the lumen of the gastropod shells, as well as on or in the crab host. Crabs primarily inhabited the shells of *Nassarius obsoletus* (75.7%;  $n = 6757$ ). The hydroid *Hydractinia symbiolongicarpus* and the bryozoan *Alcyonidium albescens* dominated the outside surfaces of shells (51.5% and 26.5%, respectively), and a predatory relationship between the bryozoan and the nudibranch *Corambe obscura* was observed. *Dipolydora commensalis* and *Lepidonotus sublevis* were the most common polychaetes living in shell burrows (38.9%) and in the shell lumen (25.8%), respectively. Acrothoracican barnacles, *Trypetesa lampas*, were embedded in 4.7% of shells. In New Jersey *P. longicarpus* is parasitized by the isopods *Stegophryxus hyptius* and *Paguritherium alatum*. Among known parasites of the crab not yet recorded from New Jersey are the isopod *Asymmetrione desultor*, plerocercoid larvae of the cestode *Calliobothrium verticillatum*, and cystacanth larvae of the acanthocephalan *Polymorphus* sp.

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The longwrist hermit crab *Pagurus longicarpus* Say, 1817, resides in Atlantic coastal waters of the United States from Maine to the Gulf of Mexico (Williams 1984). In the mid-Atlantic region crabs are abundant intertidally in depressions on exposed muddy sand flats during the warmer months, but retreat to the subtidal for the winter (Rebach 1974, 1978; McDermott, pers. obs.). Many aspects of the crab's biology have been studied, including feeding, shell acquisition, environmental tolerances, reproduction, and symbiotic relationships (see McDermott 1999). The term *symbiosis* is used in the original and general way referring to "the living together of unlike organisms" (Committee on Terminology 1937).

*Pagurus longicarpus* harbors a variety of symbionts, which are attached to the outside or inside of occupied gastropod shells,

burrowed into the shell, or free in the shell's lumen, and the crab itself is host to several species of ecto and endosymbionts. Some of the symbionts are specific for this hermit crab, while others, although showing predilections for the crab, are found often on a variety of other surfaces. Thus, *P. longicarpus* with its molluscan shell serves as host for a diversity of organisms from protozoans to crustaceans.

The present paper documents the species of gastropod shells utilized by *P. longicarpus* and symbionts associated with the shells and the crabs themselves from the waters of New Jersey. This is followed by a review of the biology of all known symbiotic relationships. As stated so colorfully by Allee (1923), "*Pagurus longicarpus* apparently roams at will . . . carrying with him, willy-nilly his commensals."

## Materials and Methods

An intertidal population of *Pagurus longicarpus* located in Hereford Inlet estuary (Grassy Sound Channel 39°01.72'N, 74°48.10'W) has been under study since the mid-1960's (Biggs & McDermott 1973, Lytwyn & McDermott 1976, McDermott 1998, 1999). Water temperatures range from 1° to >25°C, and mean salinity is ~30‰. Crabs were collected randomly by hand on exposed tidal flats from 1986 to 1990. They were isolated in the field in compartmentalized, plastic boxes containing sea water (each of 18 compartments were 51 × 43 × 39 mm), or were immediately preserved in bulk in 10% sea water-Formalin and later transferred to 70% ethyl alcohol. The gastropod shells harboring hermit crabs were identified, and their lengths were measured with Vernier calipers to 0.1 mm. External symbionts on these shells were identified, and those that could be removed (e.g., nudibranchs or calyptraeid gastropods) were preserved for later study. Shells were then cracked with a hammer, crabs were isolated in fresh sea water, and symbionts embedded in the shell fragments or found in the lumen were identified. Isolated crabs were sexed and the length of the anterior shield of the carapace (SL) was measured with Vernier calipers to 0.05 mm. Preserved crabs were treated in a similar manner; however, the prevalence of animals not cemented to the shells (e.g., nudibranchs from the outside of the gastropod shells, and polyclad turbellarians, polychaetes and calyptraeid gastropods from the lumen) could not be determined from the preserved collections. Observations on reproduction were made on some of these symbionts. The prevalence of epicaridean isopod parasites was determined from live and preserved crabs as described in McDermott (1998), although crabs were not routinely dissected to look for other internal parasites.

## Results

Of the 6757 shells inhabited by *Pagurus longicarpus*, 95.0% were *Nassarius obsoletus* (Say) and *N. trivittatus* (Say), 75.7% and 19.3%, respectively (Table 1). Crabs occupied 137 shells of *Urosalpinx cinerea* (Say) (2.0%), and the other 13 gastropod species made up only 3.0%.

A partially annotated list of all symbionts found within the host shell-*Pagurus longicarpus* complex in this study, as well as all other known symbionts, appears in Table 2.

There were 20 species of invertebrates associated with shells harboring *P. longicarpus* from the live and preserved crab collections from New Jersey waters (Table 3;  $n = 5041$ ). The hydroid *Hydractinia symbiolongicarpus* and the ctenostome bryozoan *Alcyonidium albescens* were the dominant species encrusting outside surfaces of hermit shells, while the polynoid polychaete *Lepidonotus sublevis* was the main inhabitant of the shell lumen. The two calyptraeid gastropods *Crepidula convexa* and *C. plana*, found on the outside and inside of the shell, respectively, were equally prevalent. Spat of the blue mussel *Mytilus edulis* was attached to the outside and inside of the shell and the exoskeleton of the crab predominately from January to April.

A prey-predator relationship exists between the bryozoan *Alcyonidium albescens* and the nudibranch *Corambe obscura*. The bryozoan was attached to 701 of the 2838 (24.7%) shells, while the nudibranch and/or its coiled egg strings were found on 78 (2.8%) shells. Three of these shells were without the snail itself, but since its egg strings were present, it was assumed that at least one nudibranch from each shell had been dislodged when the crabs were collected. Except for three shells which lacked *A. albescens*, *C. obscura* was otherwise found only on shells harboring the bryozoan (96.2%). Only three of the 2137 shells without *A. albescens* (0.14%) had the nudibranch, while 75 of the 701 shells with the bryozoan (10.7%) harbored the preda-

Table 1.—Gastropod shells inhabited by *Pagurus longicarpus* in the Hereford Inlet estuary of New Jersey, based on all collections from 1985 to 1990 ( $n = 6757$ ). Arranged in order of decreasing abundance.\*

Species	Number	Percent
<i>Nassarius obsoletus</i> (Say)	5112	75.65
<i>Nassarius trivittatus</i> (Say)	1306	19.33
<i>Urosalpinx cinerea</i> (Say)	137	2.03
<i>Neverita</i> (= <i>Polinices</i> ) <i>duplicata</i> (Say)	59	0.87
<i>Eupleura caudata</i> (Say)	45	0.67
<i>Busycon carica</i> (Gmelin)	23	0.34
<i>Littorina littorea</i> (Linnaeus)	21	0.31
<i>Euspira</i> (= <i>Lunatia</i> ) <i>heros</i> (Say)	19	0.28
<i>Littoraria</i> (= <i>Littorina</i> ) <i>irrorata</i> (Say)	12	0.18
<i>Busycotypus</i> (= <i>Busycon</i> ) <i>canaliculatus</i> (Linnaeus)	9	0.13
<i>Costoanachis</i> (= <i>Anachis</i> ) <i>avara</i> (Say)	7	0.10
<i>Astyris</i> (= <i>Mitrella</i> ) <i>lunata</i> (Say)	3	0.04
<i>Epitonium rupicola</i> (Kurtz)	2	0.03
<i>Littorina obtusata</i> (Linnaeus)	1	0.02
<i>Nassarius vibex</i> (Say)	1	0.02

\* Classification based on American Fisheries Society (1998).

tor. Thus, *C. obscura* was 76.4 times more abundant on shells with this bryozoan.

Ninety-nine specimens of *C. obscura* were recorded from 78 shells (1–4/shell), and egg strings were found on 17 shells (1–7/shell). The maximum number of seven strings occurred with a single nudibranch. Observations suggested that there are two periods of reproduction, April–May and September–November. Veligers hatched only from eggs collected in October and November. Mean length of living nudibranchs was  $2.41 \pm 1.49$  mm, range 0.69–4.40 mm ( $n = 14$ ), and snails approximately  $\geq 3.0$  mm were mature. One circular egg string measured 2.3 mm in diameter.

The spionid polychaete *Dipolydora commensalis* was the dominant species that bores into the shell, having a prevalence approximately eight times that of the acrothoracican barnacle *Trypetesa lampas*. The prevalence of these symbionts was compared between the two most common host shells, *Nassarius obsoletus* and *N. trivittatus*. *Dipolydora commensalis* occurred in 761 of 2110 (36.1%) of *N. obsoletus* shells and 243 of 570 (42.6%) of *N. trivittatus* shells (significant difference, contingency  $\chi^2 = 8.28$ ,  $p = <0.005$ ). The worm also occurred in shells of six of the other gas-

tropod species listed in Table 1 (31 of 157, 19.8%). Worms were reproducing most of the time that crabs were on the intertidal flats, but no data are available while crabs were subtidal during the winter (December–February). Female worms with mature ova, along with their egg cases in the burrows were seen as early as March, and 3-setiger larvae were hatching in April when the water temperatures during these months ranged from approximately 7° to 12°C. Recently settled juveniles appeared to be most common in the fall. Numbers of worms per shell were usually not counted, but a maximum of eight worms were found in a single burrow, only one of which was a mature female.

*Trypetesa lampas* was found in 66 of 2110 (3.1%) *N. obsoletus* shells and 9 of 571 (1.6%) *N. trivittatus* shells (significant difference, contingency  $\chi^2 = 4.01$ ,  $p = <0.05$ ). A maximum of four barnacles were found in *N. obsoletus* shells, while no more than one occurred in *N. trivittatus*. Unlike *D. commensalis*, *T. lampas* was not found in 157 of the other shell species. Barnacles with eggs and developing nauplii were observed in August and September of 1987, and liberated nauplii were seen in August 1988.



Epicaridean symbionts on and in the hermit crabs from the same population were studied recently (McDermott 1998) and are listed in Table 2. Their prevalence and biology, along with other crab parasites (Table 3) not yet found in New Jersey waters (Table 2) are discussed below.

### Discussion

*Crab shell utilization* (Table 1).—The species of gastropod shells used by *P. longicarpus* varies over the latter's geographical range. In waters north of New Jersey (Connecticut and Rhode Island) the shells of *Littorina littorea* are used in numbers equal to those of *Nassarius obsoletus* (~25%) (Blackstone & Joslyn 1984), or greatly outnumber the latter by ~80% to <5% (Scully 1979). The habitat of *N. obsoletus* in New England has gradually contracted due to competitive exclusion since the introduction of *L. littorea* from Europe in the mid-1880's (Brenchley & Carlton 1983). New Jersey is near the southern limit of *L. littorea*, and its populations are relatively small. Shells of the intertidal gastropods *Littorina saxatilis* (Olivier) and *Nucella lapillus* (Linnaeus), species not found in New Jersey, are inhabited infrequently by *P. longicarpus* in Rhode Island (Scully 1979). At Beaufort, North Carolina, where *L. littorea* is rare, *N. obsoletus* and the more southern *N. vibex* are utilized in equal numbers (~30%) (Kellogg 1977). In the same area *Costoanachis avara*, *Terebra dislocata* (Say) and *Urosalpinx cinerea* are each represented at ~8%. In the North Inlet estuary of South Carolina, Young (1979) found that 56.5% of 1208 *P. longicarpus* were in *Nassarius* spp. shells (he did not distinguish the species, but the majority were probably *N. vibex*). *Terebra dislocata* and *U. cinerea* were each used by ~15% of the crabs. In the northeastern Gulf of Mexico (Florida) *Littoraria irrorata* and *N. vibex* are inhabited by 80% of the *P. longicarpus* population (Kuhlmann 1992). In the Galveston area of the Texas coast, Fotheringham

(1976) recorded 47% of the crabs in shells of *Neverita duplicata* and ~15% each in *L. irrorata* and *Stramonita (=Thais) haemastoma floridana* (Conrad). *Littoraria irrorata*, the southern periwinkle, is rarely found in New Jersey and northward (Blackstone 1986, McDermott, pers. obs.). In all of the cases mentioned above, it is primarily the shell of the dominant gastropods in the region that are used by *P. longicarpus*. As Fotheringham (1976) and others have noted, shell-use patterns are influenced by a variety of factors including: abundance of shells, shell size, internal volume and shell morphology, crab ontogeny, sex, intra and interspecific competition, and attached symbionts. Besides the 15 gastropod shells in Table 1 and *Terebra dislocata* and *Stramonita haemastoma floridana*, Sumner et al. (1913) noted that *Euspira triseriata* (Say), *E. immaculata* (Totten) and *Colus pygmaeus* (Gould) were also used by *P. longicarpus*. Thus, *P. longicarpus* has been shown to utilize a total of 20 different gastropod species along its range on the east coast.

*Symbionts associated with the shell* (Tables 2, 3).—The colonial hydroids *Hydractinia symbiolongicarpus* Buss & Yund and *Podocoryne carnea* Sars are both facultative symbionts. The former has recently been recognized as one of three sibling species associated with *P. longicarpus*. It is distinguished from *H. symbiopollicaris* Buss & Yund, *H. polyclina* (Agassiz) and the European *H. echinata* (Fleming) by breeding incompatibilities, electrophoretic analyses, morphometrics, and some specificity for crab hosts (Buss & Yund 1989). *H. symbiolongicarpus* and *H. symbiopollicaris* are found mainly on the shells occupied by *P. longicarpus* and *P. pollicaris* Say, respectively, but the reverse sometimes occurs. Originally *H. polyclina* was found only on shells inhabited by *Pagurus acadianus* Benedict, and not on *P. longicarpus* or *P. pollicaris* (Buss & Yund 1989), but a more recent study has shown that *H. polyclina* may also be found on shells harboring

Table 2.—Master list of symbionts of *Pagurus longicarpus* arranged according to their location in the host shell-hermit crab complex and in phylogenetic order within the location. Most were found in crabs from New Jersey waters.

Symbionts	Remarks*
<b>On Outside of Shell</b>	
<b>Cnidaria</b>	
<i>Hydractinia symbiolongicarpus</i> Buss & Yund	One of three sibling species associated with crabs in genus <i>Pagurus</i> (see Discussion)
<i>Podocoryne carnea</i> Sars	Shows a predilection for the shells of <i>Nassarius trivittatus</i>
<b>Ectoprocta</b>	
<i>Alcyonidium albescens</i> Winston & Key	Facultative symbiont
<i>Conopium tenuissimum</i> (Canu)	Facultative symbiont
<i>Membranipora tenuis</i> Desor	Facultative symbiont
<i>Schizoporella unicornis</i> (Johnston)	Facultative symbiont
<b>Annelida</b>	
<i>Hydroides dianthus</i> (Verrill)	Facultative symbiont
<i>Sabellaria vulgaris</i> (Verrill)	Facultative symbiont
<b>Mollusca**</b>	
<i>Crepidula convexa</i> Say	Shows some predilection for hermit shells
<i>Crepidula fornicata</i> (Linnaeus)	Seldom with this crab, often on <i>P. pollicaris</i>
<i>Cuthona (nana ?)</i> (Alder & Hancock)	Predator of <i>Hydractinia</i>
<i>Corambe (=Doridella) obscura</i> (Verrill)	Predator of <i>Alcyonidium</i> and other encrusting bryozoans
<i>Mytilus edulis</i> Linnaeus	Seasonal symbiont as spat in breeding seasons (January to April and June)
<b>Arthropoda</b>	
<i>Anoplodactylus (lentus)</i> Wilson	Found among the polyps of <i>Hydractinia</i>
<i>Balanus eburneus</i> Gould	Facultative symbiont
<i>Balanus improvisus</i> Darwin	Facultative symbiont
<b>Bored into Shell</b>	
<b>Annelida</b>	
<i>Dipolydora (=Polydora) commensalis</i> (Andrews)	Bores into columella, and may make contact with shell lumen; obligate symbiont
<i>Dipolydora socialis</i> (Schmarda)***	Superficial burrow on outside of shell
<i>Polydora neocaeca</i> Williams and Radashevsky***	Lives in an unbranched U-shaped burrow in hermit shells as well as living gastropods and bivalve shell fragments
<i>Polydora websteri</i> Hartman***	Superficial burrow on outside of shell
<b>Arthropoda</b>	
<i>Trypetesa lampas</i> (Hancock)	Bores from lumen side of body whorl
<b>Lumen of Shell</b>	
<b>Platyhelminthes</b>	
<i>Stylochus zebra</i> (Verrill)	Embryo predator of <i>P. pollicaris</i>
<b>Annelida</b>	
<i>Lepidonotus sublevis</i> Verrill	Obligate symbiont
<b>Mollusca</b>	
<i>Crepidula plana</i> Say	Shows predilection for hermit shells
<b>External on Crab</b>	
<b>Protozoa</b>	
<i>Lagenophrys eupagurus</i> Kellicott***	Tests containing peritrichous ciliate attached to gills
Unidentified folluculinid ciliate	Tests containing heterotrichous individuals cemented to body

Table 2.—Continued.

Symbionts	Remarks*
Mollusca	
<i>Mytilus edulis</i> Linnaeus	Seasonal symbiont
Arthropoda	
<i>Asymmetrione desultor</i> Markham***	Bopyrid isopod in branchial chambers
<i>Stegophryxus hyptius</i> Thompson	Bopyrid isopod on abdomen
Internal in Crab	
Platyhelminthes	
<i>Calliobothrium verticillatum</i> (Rudolphi)***	Plerocercoids of tetraphyllidean cestode in <i>Pagurus pollicaris</i> , but possibly also in <i>P. acadianus</i> and <i>P. longicarpus</i>
Acanthocephala	
<i>Polymorphus</i> sp.***	Cystacanths in abdominal hemocoel
Arthropoda	
<i>Paguritherium alatum</i> Reinhard	Entoniscid isopod in hemocoel

\* Additional information in Discussion.

\*\* Mollusk classification based on American Fisheries Society (1998).

\*\*\* Not identified from New Jersey crabs.

*P. longicarpus* (Folino & Yund 1998). *Hydractinia* from New Jersey is assumed to be *H. symbiolongicarpus*. The high prevalence of *Hydractinia* on hermit shells (>50%) in New Jersey is consistent with Lytwyn's (1979) observations in the same state in the 1970's. In Texas waters its prevalence was approximately 30% (Fotheringham 1976).

The prevalence of *Podocoryne carnea* on hermit shells from New Jersey was much lower (0.5% of 2838 crabs) than for *H. symbiolongicarpus* (Table 3). McFadden (1986) found that *P. carnea* was rare among the epifauna of *P. longicarpus* shells collected in Long Island Sound. She also noted that recruits of this hydroid were found on only 0.2% of 1663 shells but did not record the species of gastropod shells that harbored *P. carnea*. All 15 colonies of this species from New Jersey crabs were on the shells of *Nassarius trivittatus*, which agrees with Crowell (1945) who showed that *P. carnea* has a predilection for the crab-occupied shells of *N. trivittatus*, almost never being found on the shells of *Littorina littorea*, at least in the Woods Hole

region of Massachusetts. He found both *P. carnea* and *Hydractinia* sp. on crab-occupied shells of *Busycon* sp., *Urosalpinx cinerea*, *Eupleura caudata*, *Nassarius obsoletus*, and others. Unlike Crowell, Edwards (1972) identified colonies of *P. carnea* on *Littorina* shells occupied by hermit crabs from the British Isles. *Podocoryne carnea* has free medusae in its life cycle (unlike *Hydractinia*), which are liberated from gonozooids whose white color makes the colony easily recognizable. Gonozooids may be seasonal. Medusae develop and are liberated from late May to early August in colonies on New Jersey crabs. The presence of *P. longicarpus* inside of a *Nassarius trivittatus* shell covered with *P. carnea* in some manner allows for the differentiation of spiral zooids around the periphery of the aperture (Braverman 1960). Although the mechanism involved in this differentiation and the functional significance of this phenomenon have not been explained, it is possible that these elongated zooids may be utilized for capturing food items stirred up from the sediments by the hermit crab or crab zoeae liberated from the shell aperture.

Table 3.—Prevalence of symbionts found on, in, or in the lumen of gastropod shells inhabited by *Pagurus longicarpus* from the Hereford Inlet estuary of New Jersey 1986–1990, based on the examination of shells with live ( $n = 2838$ ) and preserved crabs ( $n = 2203$ ). Species within each phylum are arranged alphabetically.

Species	Live crabs		Preserved crabs	
	Number	Percent	Number	Percent
<b>Cnidaria</b>				
<i>Hydractinia</i> spp.	1475	52.0	1120	50.8
<i>Podocoryne carnea</i>	15	0.5	ND*	
<b>Ectoprocta</b>				
<i>Alcyonidium albescens</i>	701	24.7	634	28.8
Other encrusting species**	35	1.2	76	3.4
<b>Platyhelminthes</b>				
<i>Stylochus zebra</i>	2	0.1	ND	
<b>Annelida</b>				
<i>Dipolydora commensalis</i>	1038	36.6	922	41.9
<i>Hydroides dianthus</i>	10	0.4	6	0.3
<i>Lepidonous sublevis</i>	612	21.6	688	31.2
<i>Sabellaria vulgaris</i>	90	3.2	47	2.1
<b>Mollusca</b>				
<i>Corambe obscura</i>	78	2.8	ND	
<i>Crepidula convexa</i>	318	11.2	ND	
<i>Crepidula fornicata</i>	2	0.1	ND	
<i>Crepidula plana</i>	320	11.3	ND	
<i>Mytilus edulis</i> spat	213	7.5	ND	
<b>Pycnogonida</b>				
<i>Anoplodactylus (lentus)</i>	4	0.1+		
<b>Arthropoda</b>				
Barnacle spat***	34	1.2	ND	
<i>Trypetesa lampas</i>	75	2.6	163	7.4

\* ND = no data.

\*\* *Conopiium tenuissimum* (Canu), *Membranipora tenuis* Desor, *Schizoporella unicornis* (Johnston).

\*\*\* *Balanus eburneus* and *B. improvisus*.

Additional invertebrates that are only loosely associated with shells, primarily in silt accumulated in damaged apices: sea anemone; heteronemerteans, hoplonemerteans; polychaetes, *Polycirrus eximus* (Leidy), *Autolytus* sp., phyllocodids, spionids; amphipods, *Caprella* sp., *Corophium* sp., isopod, *Erichsonella filiformis* (Say); mollusc, *Anadara ovalis* (Bruguère). Living boring sponge *Cliona* sp. was found on one *Nassarius obsoletus* shell.

*Pagurus longicarpus* and *P. pollicaris* seem to prefer gastropod shells with *Hydractinia* colonies, while some other members of the genus and other genera may reject shells with this hydroid (Conover 1976, Mills 1976, Mercado & Lytle 1980). Other evidence suggests that *P. longicarpus* does not discriminate between shells with or without *H. symbiolongicarpus* Weissberger (1995).

The only turbellarian associated with *P. longicarpus* is the polyclad *Stylochus zebra*,

but it is much more commonly found in the lumen of shells inhabited by *P. pollicaris* (Lytwyn 1976, 1979; Lytwyn & McDermott 1976). Its rarity with *P. longicarpus* in the present study confirms that found previously in New Jersey by Lytwyn & McDermott (1976) and Lytwyn (1979). This polyclad has been recorded from three other species of hermit crabs from North Carolina [*Pagurus impressus* (Benedict), *Petrochirus diogenes* (Linnaeus) and *Dardanus venosus* (H. Milne Edwards)], all

with a lower prevalence than with *P. pollicaris* (Lytwyn 1979). It is an embryo predator of *P. pollicaris* (Lytwyn 1979), but also feeds on shell symbionts such as the white slipper limpet *Crepidula plana* (Lytwyn & McDermott 1976).

For many years the encrusting ctenostome bryozoan *Alcyonidium albescens* was known as *A. polyoum* (Hassall). However, Winston & Key (1999) have shown recently that the latter is a European species. *Alcyonidium albescens* is a common facultative inhabitant of the outer surfaces of *P. longicarpus*-inhabited *Nassarius obsoletus* shells, but is rarely associated with the shells of the living snail (Karlson & Cariolou 1982). It grows, however, on the shells of some other living snails and on shells occupied by *P. pollicaris*, as well as on brachyuran crabs and inanimate shell surfaces (Karlson & Cariolou 1982, Karlson & Shenk 1983, Key et al. 1999, McDermott pers. obs.). Buss & Yund (1988) found that it dominates *Hydractinia* spp. in competition for space on shells occupied by *P. longicarpus*.

The lumen of shells with *P. longicarpus* (and *P. pollicaris*) often contains the obligate polynoid polychaete symbiont, *Lepidonotus sublevis* Verrill (Pettibone 1963, Lytwyn 1979, Mercado 1983, McDermott pers. obs.). It was found in the lumen of approximately 25% of hermit crab shells in New Jersey (Table 3). This was about half of that recorded by Lytwyn (1979) in the 1970's from a much smaller sample. *Lepidonotus sublevis* was found to be 25 times more frequent in shells harboring male crabs, which may be related to crab size (males tend to be larger than females) rather than to sex per se (Mercado 1983). These scaled worms may occupy a considerable percentage of the shell's internal volume, and Mercado & Donaghy (1984) showed that *P. longicarpus* had more difficulty entering shells occupied by *L. sublevis*, i.e., they selected empty shells significantly more frequently than those with worms. Although Frothingham (1976) demonstrated

that *L. sublevis* consumed detached embryos of *P. longicarpus* in the laboratory, there is still no evidence that the worm is an embryo predator under natural conditions.

Five species of gastropods are associated with *P. longicarpus* (Table 2). Of the three slipper limpets (Calyptraeidae), *Crepidula fornicata* (Linnaeus), *C. plana* Say and *C. convexa* Say, only the last two seem to show some predilection for inhabiting *P. longicarpus* shells (Table 3) (Karlson & Cariolou 1982, McDermott pers. obs.). *C. plana* lives on the inside of the shells, while *C. convexa* and *C. fornicata* are on the outside. The geographical distribution of *C. plana* is from New England to Georgia, and it is distinct from *C. depressa* Say, an inhabitant of hermit crab shells from Florida to Texas (Collin, 2000). *Crepidula plana* has a distinct relationship with crab-inhabited shells and is rarely detected on other substrates. This applies to shells inhabited by *P. longicarpus* (Shenk & Karlson 1986, Table 3), as well as *P. pollicaris* (Shenk & Karlson 1986, McGee & Targett 1989). Although the veligers of *C. plana* may settle and metamorphose on a variety of substrates, including the outside of hermit crab shells, they are usually found only on the inside of these shells where they are more protected from predation (Shenk & Karlson 1986, Collin 2000, present study). In this location, however, the limpet may be vulnerable to predation if the polyclad *Stylochus zebra* is present (Lytwyn & McDermott 1976, Lytwyn 1979). Effluents from *C. plana* and *P. pollicaris* in *Busycon carica* shells attract competent larvae to settle and metamorphose (McGee & Targett 1989).

The shell morphology of *C. convexa* living on hermit shells is markedly different in its dimensions than those on other substrates, i.e., the shells are shorter and narrower but greater in height (Franz & Henderler 1970). Unlike *C. fornicata* and *C. plana* which release veliger larvae, *C. convexa* has direct development and thus has a greater problem in distributing juveniles to

new locations. Attachment of *C. convexa* to the mobile hermit crab along with the high mobility of juvenile snails, however, aids in the colonization of new substrates (Hendler & Franz 1971). Thus, this association is a distinct benefit to *C. convexa* populations.

Two nudibranchs are associated with the gastropod shell of *P. longicarpus*. Strong evidence is presented here that the doridacean *Corambe obscura* has a very close association with one of its prey species, the encrusting bryozoan *Alcyonidium albescens*. Because of the possibility that some nudibranchs were dislodged from shells while being isolated in the field, it is likely that their 10.7% prevalence on the bryozoan is a minimal value. In Delaware Bay, New Jersey, Franz (1967) found that this nudibranch was always associated with, and fed on, the following encrusting bryozoans: *Alcyonidium verrilli* Osburn, *Conopeum tenuissimum* and *Membranipora tenuis* (Dudley (1973) clarified the identity of the last two species). *Corambe obscura* was also found with a *A. albescens* colony on a *Neverita duplicata* shell harboring *Pagurus pollicaris* from the same New Jersey location (McDermott, pers. obs.). Karlson & Shenk (1983) did not recover *C. obscura* from *A. albescens* colonies living on 39 shells of *Busycon carica* with *Pagurus pollicaris* and 18 live snails collected at the mouth of Delaware Bay. *Alcyonidium verrilli*, an upright species capable of forming large masses, has not been identified on shells with *P. longicarpus*. Cory (1967) found that *C. obscura* fed and deposited its egg strings on the colonies of *C. tenuissimum* and *M. tenuis* in the upper part of the Chesapeake Bay, Maryland. Wass (1972) reported that this snail is "often abundant on *Alcyonidium*" (presumably referring to *A. verrilli*) in the lower Chesapeake Bay, Virginia. Perron & Turner (1977) found the coiled egg strings of the snail on its cheilostome prey *C. tenuissimum*, and also noted that its larvae metamorphose on the colony. Perhaps an obligate metamorphosis may be involved in the *C. obscura*-*A. al-*

*bescens* relationship. The geographic distribution of *C. obscura* ranges in the Atlantic Ocean from the eastern United States to Brazil, and is found along the coast of northwestern Europe. It was introduced into the Black Sea in the late 1980's (Roginskaya & Grintsov 1990), and has been found subsequently in many locations within the Sea where it has apparently found encrusting bryozoans to sustain its reproduction (Roginskaya & Grintsov 1995, 1997).

*Cuthona nana* (Alder & Hancock) is a predator of *Hydractinia polyclina*, which is found primarily on shells inhabited by *Pagurus acadianus* in New England (Harris et al. 1975, Rivest 1978, Lambert 1991, Folino 1987, 1993, 1997). An unidentified species belonging to the same genus was found on *Hydractinia symbiolongicarpus* colonies on three shells of *Nassarius obsoletus* occupied by *P. longicarpus* in April and May 1986, from the same New Jersey location but not part of the collections in Table 3. Egg strings of the snail were on two of the shells, and on one shell with two nudibranchs most of the hydroid colony was destroyed. Lengths of the living nudibranchs were 3.5 mm for a juvenile and 10, 12 and 13 mm for adults.

Four shells among 2838 (0.1%) with living crabs had pycnogonids associated with colonies of *Hydractinia* (July and August 1987, May 1988). Three of the shells were *Nassarius trivittatus* and the other was *N. obsoletus*. The maximum number per shell was five (total = 10). These symbionts were juveniles and belonged to the genus *Anoplodactylus* (probably *A. lentus* Wilson). *Anoplodactylus lentus* is a common species along the eastern coast of the United States, living among and feeding on hydroids (Cole 1906, Sumner et al. 1913, Hedgpeth 1950).

*Endolithic species* (Tables 2, 3).—The shell-boring, spionid polychaete *Dipolydora commensalis* is an obligate commensal of gastropod shells occupied by hermit crabs including: *Pagurus annulipes* (Stimp-

son), *P. longicarpus*, *P. pollicaris* and *Clibanarius vittatus* Bosc (Andrews 1891, Hatfield 1965, Radashevsky 1989, Dauer 1991). It occurred in approximately 40% of the shells inhabited by *P. longicarpus* in this study, which compares well with the 36.8% prevalence (186 of 506) in five species of shells occupied by four species of hermit crabs, 91.8% of which were *P. longicarpus*, in Virginia (Dauer 1991). The other species of gastropod shells bored by *D. commensalis* from New Jersey were *Urosalpinx cinerea*, *Eupleura caudata*, *Neverita duplicata*, *Littoraria irrorata*, *Littorina littorea*, and *Busycotypus canaliculatus*. Hatfield (1965) recorded the worm from the shells of *Euspira heros* and *Buccinum undatum* Linnaeus. Although the prevalence of *D. commensalis* was significantly greater in the shells of *Nassarius trivittatus* than *N. obsoletus*, I have no rationale to explain this difference, except for possible dissimilarities in mineralization that may make the one shell more favorable for boring. The polychaete bores into the columella of shells producing a tube which in some cases eventually enters the lumen of the shell near the apex (Andrews 1891, Hatfield 1965, Radashevsky 1989, Dauer 1991, Williams 1995). The anterior end of the worm is usually located at the opening of the tube in the columella which is located on the medial side of the shell aperture. Here the worm extends its palps and draws food particles into the mouth (Dauer 1991, Williams & McDermott 1997). J. D. Williams (per. comm.) found that worms whose burrows reach the shell lumen, prey on the developing embryos attached to the pleopods of *P. longicarpus* in Rhode Island. Williams (1999, 2000, 2001) also reported that *Polydora* spp. and *Trypetesa* sp. inhabiting gastropod shells with hermit crabs from the Indo-West Pacific are also embryo predators, so that this may be a more common phenomenon than previously recognized. *Pagurus longicarpus* living in shells bored by *D. commensalis*, rather than normal shells, may be more vulnerable to pre-

dation because these shells are less resistant to crushing forces (Buckley & Ebersole 1994).

Other spionid polychaetes are boring facultative symbionts of shells inhabited by *P. longicarpus*. *Polydora websteri* Hartman was reported in shells from Maine (Blake & Evans 1973), and *P. neoacaeca*, recently described by Williams & Radashevsky (1999), was recovered from shells in Rhode Island. Also in shells from this state was *Dipolydora socialis* (Schmarda) (Williams per. comm.). The superficial nature of the burrows of these species, however, suggests that they are not embryo predators.

The acrothoracican barnacle *Trypetesa lampas* burrows into gastropod shells occupied by hermit crabs (Tomlinson 1969a, 1969b), and was detected in approximately 5% of the 5041 shells examined in New Jersey. The significant difference in the prevalence of this barnacle between *Nassarius obsoletus* and *N. trivittatus* may be related to the larger size attained by the former, some difference in the calcereous composition of the shells, or the much greater abundance of *N. obsoletus* in the Hereford Inlet estuary. Barnacle burrows are detected only on the inner surfaces of the body whorl of cracked shells where slit-like openings allows the cirri to protrude into the lumen. Beyond this opening is the enlarged chamber harboring the barnacle. Other acrothoracican barnacles burrow into a variety of calcareous substrata (e.g., gastropod and bivalve shells, corals), but *T. lampas* is an obligate associate of hermit crabs. This association obviates harmful silting experienced by species living in uninhabited gastropod or bivalve shells (Tomlinson 1969a, 1969b). In New England waters, this barnacle is found in the shells of *Euspira heros* and *Neverita duplicatus* occupied by hermit crabs (Sumner et al. 1913, Zullo 1963). *Neverita duplicatus* shells inhabited by *Pagurus pollicaris* from New Jersey are also infested with *T. lampas* (McDermott pers. obs.). White (1969) found *T. lampas* in the shells of several spe-

cies of gastropods inhabited by *Pagurus bernhardus* (Linnaeus) in Wales. Some species of shells were heavily infested, e.g., 67.2% of 2249 *Buccinum undatum* Linnaeus shells were infested, and there were positive correlations between shell length and the prevalence and numbers per shell (White 1969).

Tomlinson (1969a) said that *T. lampas* "... in general does little if any harm to the host. All species of the order collect food without taking from or giving anything of value to the host," although the gastropod shell may be weakened by the presence of numerous barnacles. Recent studies by Williams (1999) may eventually modify Tomlinson's observations. He showed that a species of *Trypetesa* found in hermit crab shells from the Philippine Islands ingest crab embryos in nature.

*Found on or in the crab* (Tables 2, 3).—Two species of ciliated protozoans are ectosymbionts of *P. longicarpus*. One is the loricate peritrich *Lagenophrys eupagurus* Kellicott, 1893, (Lagenophryidae) that attaches to the crab's gills (Kellicott 1893, Clamp 1989, Fernandez-Leborans & Tato-Porto 2000). It is not specific for *P. longicarpus*, having been reported from thirteen other species of crustaceans, none of which was a hermit crab (Clamp 1989). Members of this genus are well-known as ectosymbionts of crustaceans. The gill filaments of hermits from New Jersey were not examined for this species. The unidentified ciliate (Table 2) is a heterotrichous folliculinid that was periodically found cemented to different parts of the crab's body and also on crab shells. The species appears to be a facultative commensal and is similar to *Platyfolliculina paguri* Andrews & Reinhard, 1943, which attaches to the body of *Pagurus pubescens* Kröyer, from the coast of Maine (Andrews & Reinhard 1943).

Plerocercoids of the tetraphyllidean cestode, *Calliobothrium verticillatum* (Rudolphi) are found in the tubules of the anterior midgut ceca of *Pagurus pollicaris* Say collected in the Woods Hole region of Mas-

sachusetts (Caira & Ruhnke 1991). Cherry et al. (1991) suggested that >95% of hermit crabs from this area were infected (it is not clear whether this value referred just to *P. pollicaris* or all three hermits from the region). Smolowitz et al. (1993) demonstrated in histological sections that these plerocercoids cause inflammation to the mid gut ceca of *Pagurus* spp. (*Pagurus acadianus*, *P. longicarpus* and *P. pollicaris*). Unfortunately, although 39 crabs were sectioned for study, the authors did not record the identity of the crabs (R. M. Smolowitz, pers. comm.). The adult parasite is found in the spiral valve of the smooth dogfish *Mustelus canis* (Mitchill) (Caira & Ruhnke 1991).

The occurrence of *Mytilus edulis* spat attached to the body of *P. longicarpus* on a seasonal basis is not unprecedented, because such was reported more than a half century ago from Woods Hole, Massachusetts by Andrews & Reinhard (1943).

*Pagurus longicarpus* serves as an intermediate host for the acanthocephalan *Polymorphus* sp. in the Woods Hole area (Reinhard 1944). Cystacanths were found in the abdominal cavity on the outer walls of the gut or among the tubules of the digestive gland. Usually there was only one cystacanth per host, and approximately one percent of the crabs were infected. These cysts are glistening white, have a mean length and width of 2.6 and 1.3 mm, and are easily seen through the thin abdominal wall (Reinhard 1944). During the course of the present study only a small but unrecorded percentage of the live crabs were dissected, and no cystacanths were found.

*Pagurus longicarpus* harbors three epicaridean isopod parasites, two belonging to the Bopyridae and the other to the Entoniscidae (McDermott 1998). One of the bopyrids, *Stegophryxus hyptius* Thompson (subfamily Althelginae), lives on the abdomen of the crab. At the beginning of the past century it had a prevalence of 1.5–4.0% in the Woods Hole region of Massachusetts (Thompson 1902), and at mid-century Reinhard (1943, 1949) found the iso-



pods in 1.25–1.5% of the crabs examined. During the last part of the century crabs from the waters of New Jersey had a prevalence of 0.15% (14 of 9111) (McDermott 1998). This parasite is found at least as far south as Georgia and has little host specificity, parasitizing at least seven other species of related hermits (Markham 1974, 1988). *Stegophryxus hyptius* does not produce any noticeable changes in primary or secondary (pleopods) sex characters in *P. longicarpus* (Thompson 1902, Reinhard et al. (1947).

The other bopyrid, *Asymmetrione desultor* Markham, 1975 (subfamily Pseudioninae), is found along the southeastern coast of the United States, inhabiting the branchial chambers of *P. longicarpus* (Markham 1975). This parasite has been found on five other species of hermits (Markham 1988), but it was not seen in the hermits from New Jersey.

The hemocoel-dwelling entoniscid *Paguritherium alatum* Reinhard, 1945, was recovered from 38 of 4600 (0.8%) hermits collected in 1943 in the Woods Hole area (Reinhard 1943, 1945). In 1946, Reinhard & Buckeridge (1950) collected ~100 infected *P. longicarpus* from the same locale, for the purpose of documenting the effect of the parasites on the secondary sex characters of the hosts, but prevalence was not recorded. Adkinson and Heard (1978) found the entoniscids in 3% of ~300 crabs that they examined in North Carolina. An alternate host for *P. alatum* in North Carolina is *Pagurus annulipes*; two of ~250 crabs were parasitized (Adkinson & Heard 1978). In New Jersey the prevalence of *P. alatum* was only 0.11% (4 of 3703). *Paguritherium alatum* castrates its female host and causes a pronounced reduction in the length of endopodal rami and a reduction of endopodal hairs (Reinhard & Buckeridge 1950); the parasitized male is not modified externally. Simultaneous parasitism in *P. longicarpus* with *P. alatum* and *Stegophryxus hyptius* occurs, but is rare (Reinhard & Buckeridge 1950).

Rhizocephalans have never been reported from *Pagurus longicarpus*, but its congener *P. pubescens* Kröyer, 1838, from the waters of Maine harbors *Peltogaster paguri* Rathke (prevalence up to 25%), which also parasitizes the European *P. bernhardus* (Reinhard 1939, 1942, Walker & Pearse 1939). *Pagurus acadianus* Benedict, from the same locality as *P. pubescens* is not parasitized by this barnacle.

### Conclusion

Within this gastropod shell-*Pagurus longicarpus* complex are a number of biological relationships that deserve experimental study to further define their nature. This applies also to other species of hermit crabs whose associates are well known, e.g., the European *P. bernhardus* (Jensen & Bender 1973, Lancaster 1988). Such relationships involve a variety of predators and prey both on the outside and in the lumen of the shells, shell symbionts involved as crab embryo predators (a type of periodic parasitism involving only crabs of one sex), and host-parasite relationships involving the crabs as definitive or intermediate hosts. In all cases there is much to be learned about the factors involved in the establishment of all associates on and in the shell and with the crab itself. Just as the hermit crab is attracted to the physical nature of snail shells, so too is it likely that the associates may show preferences for attachment to shells with a particular topography or chemical composition. Likewise, predators are attracted by some means (e.g., chemical attraction) to certain prey species that precede them in their attachment to hermit crab shells.

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## A new species of *Exosphaeroma* Stebbing (Crustacea: Isopoda: Sphaeromatidae) from the Pacific coast of Mexico

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*Abstract.*—*Exosphaeroma bruscai* is described from the Pacific coast of Mexico. *Exosphaeroma bruscai* is most closely related to *E. diminuta* Menzies & Frankenberg, 1966 from the western Atlantic, from which it differs in having much longer antenna, an acute rostrum, a triangular first pleopod endopod, a transverse suture on exopod of pleopods 3–5, and a considerably longer and more slender appendix masculina. Specimens examined here define the geographic distribution of *E. bruscai* from the central Gulf of California to Los Arcos, in the southern part of Banderas Bay, Jalisco. Previously published records of an unidentified *Exosphaeroma* from the eastern tropical Pacific indicate that *E. bruscai* occurs from sandy beaches of the upper Gulf of California to Colombia.

Sphaeromatidae is the most speciose family of marine isopods. According to a recent survey it contains 633 species (Kensley & Schotte 2000) and they are often very abundant in intertidal and shallow water habitats. Their taxonomy is one of the most confused among isopods, in great part due to marked sexual dimorphism in some genera (Schultz 1969, Brusca 1980, Kensley & Schotte 1989) and to the difficulty in establishing generic relationships within the family (see Bruce 1995). The family has been formally divided into five subfamilies by Iverson (1982), who based his study on previous works by Hurley & Jansen (1977) and Bowman (1981). More recently, genera of Sphaeromatidae have been reviewed by Harrison & Ellis (1991) who presented an identification key to genera.

The genus *Exosphaeroma* is known from the Pacific coast of Mexico, but no identified species has been recorded. The first published record of *Exosphaeroma* for the area is by Dexter (1972) who recorded *E. diminuta* Menzies & Frankenberg, 1966, a west Atlantic sphaeromatid, from sandy beaches of the west coast of Panama. Dexter (1974, 1979) later reported the same

species for similar habitats in Costa Rica and Colombia. This identification, however, was considered doubtful by Brusca & Iverson (1985:26–28) who thought that Pacific records of Dexter (1974, 1979) belong to an undescribed species, probably extending from the upper Gulf of California, Mexico, to Parque Nacional Santa Rosa, Costa Rica. Brusca & Iverson (1985:26–28) provided some diagnostic characters of this undescribed *Exosphaeroma*, illustrated parts of an adult male, but did not give it a new name.

Since Brusca and Iverson's 1985 note on this genus, another report of an *Exosphaeroma* sp. was published by Ríos & Ramos (1990) from specimens collected in Malaga Bay, Colombia. These authors refer to the data presented by Brusca & Iverson (1985). No further reports on *Exosphaeroma* from the Pacific coast of America have been published. Recent collecting along the Pacific coast of Mexico, including sampling on sandy beaches, led to the discovery of an undescribed species similar to those of Brusca & Iverson (1985) in several localities. The purpose of the present paper is to formalize the description of this apparently

abundant species, the first of the genus *Exosphaeroma* reported for the Pacific coast of America.

Abbreviations used in this paper are: St., sampling station; TL, total length; NS, unsexed specimen; coll., collector; EMU, Unidad Académica Mazatlán UNAM Invertebrates Reference Collection.

Sphaeromatidae H. Milne-Edwards, 1840

*Exosphaeroma* Stebbing, 1900

*Exosphaeroma bruscai*, new species

Figs. 1–5

*Exosphaeroma diminutum*.—Dexter, 1972: 425; 1974:54; 1979:547 (Pacific records only).

*Exosphaeroma* sp.—Brusca & Iverson, 1985:26–28, fig. 10b–d.—Ríos & Ramos, 1990:86–87, fig. 2.

*Type material*.—Holotype, 1 male (TL 4.6 mm), Los Arcos (20°32.5'N, 105°18.4'W), Jalisco, Mexico, 12 Apr 1996 (EMU-4745). Paratypes, 3 females (TL 1.9–2.8 mm), Los Arcos (20°32.5'N, 105°18.4'W), Jalisco, Mexico, 12 Apr 1996 (EMU-5357).

*Additional material*.—El Tesoro (24°18.0'N, 110°19.0'W), La Paz, Southern Baja California, Mexico, 17 Jul 1996, 2 ovigerous females (TL 1.6–2.6 mm) and 1 unsexed, unmeasured specimen (EMU-4743). Piedras Pintas (27°56.5'N, 111°05.5'W), Sonora, Mexico, 24 Mar 1997, 1 female (TL 4.7 mm) (EMU-4742). Piedras Pintas (27°56.5'N, 111°05.5'W), Sonora, Mexico, 24 Mar 1997, 2 females (TL 2.9–3.4 mm) and 1 ovigerous female (TL 2.4 mm) (EMU-4744). Bacochibampo Bay (27°54.3'N, 110°57.6'W), Guaymas, Sonora, Mexico, 26 Mar 1997, 1 ovigerous female (TL 2.4 mm) collected by diving (EMU-5376).

*Description of male*.—Body ovate (Fig. 1A, C), about twice as long as wide; dorsal surface smooth. Head wide, rostrum short, acute. Length of holotype 4.6 mm. Pereonite 3 longest, pereonites 1–2 and 4–5 subequal in length; pereonite 7 more than half as long as pereonite 6. Coxae smooth (Fig.

2), not ventrally directed, without suture, not narrowed. Pleon with 3 incompletely fused pleonites. Pleotelson smooth, wider than long, regularly curving towards posterior margin in lateral view (Fig. 1B, D); wider anteriorly, posteriorly rounded in dorsal view. Epistome scarcely visible in dorsal view; elongate in ventral view (Fig. 1E), about twice as long as wide in its middle part, apex truncate, posterior arms shorter than anterior portion. Antennular peduncle with 3 articles; flagellum with 8–9 articles. Antennal peduncle with 4 articles; flagellum with 11–12 articles, twice as long as antennular flagellum (Fig. 1E). Mandibular palp of 3 articles; 2 distal articles with 9 and 14 spines. Left mandible with incisor 4-dentate and lacinia mobilis (3-dentate); setal row of 4 serrate setae; molar process serrate. Right mandible similar in shape, with a 4-dentate incisor; setal row of 4 serrate setae; molar process with dentate margin and a seemingly rugose surface (Fig. 3A, B). Apex of the lateral lobe of maxillula (Fig. 3C) with 6 serrate setae, and 3 slender non-plumose, non-serrate setae; mesial lobe with 4 plumose setae, and a short non-plumose seta. Maxilla (Fig. 3D) lateral lobe with 6 serrate setae, middle with 7, and mesial lobe with 7 plumose setae and a much longer, slender, mesial plumose setae. Maxilliped palp (Fig. 3E) with 4 articles; 11-10-11-8 setae on articles 1–4, respectively; endite with 1 retinaculum, 9 plumose setae, 4 stout non-plumose setae and about 7 setules.

All pereopods with setules, simple spines, composed spines (stout spines with basal part tipped with a slender seta), and diminutive scales on margins. Pereopod 1 (Fig. 4A) merus slightly shorter than half ischium length; ischium with 4 setae at superior distal angle; merus with 3 setae at superior distal angle; carpus triangular, short, slightly longer than half merus length; propodus shorter than ischium; dactylus about half propodus length, with 1 subterminal seta on the lower margin; composed spines, scales and serrate scales pre-

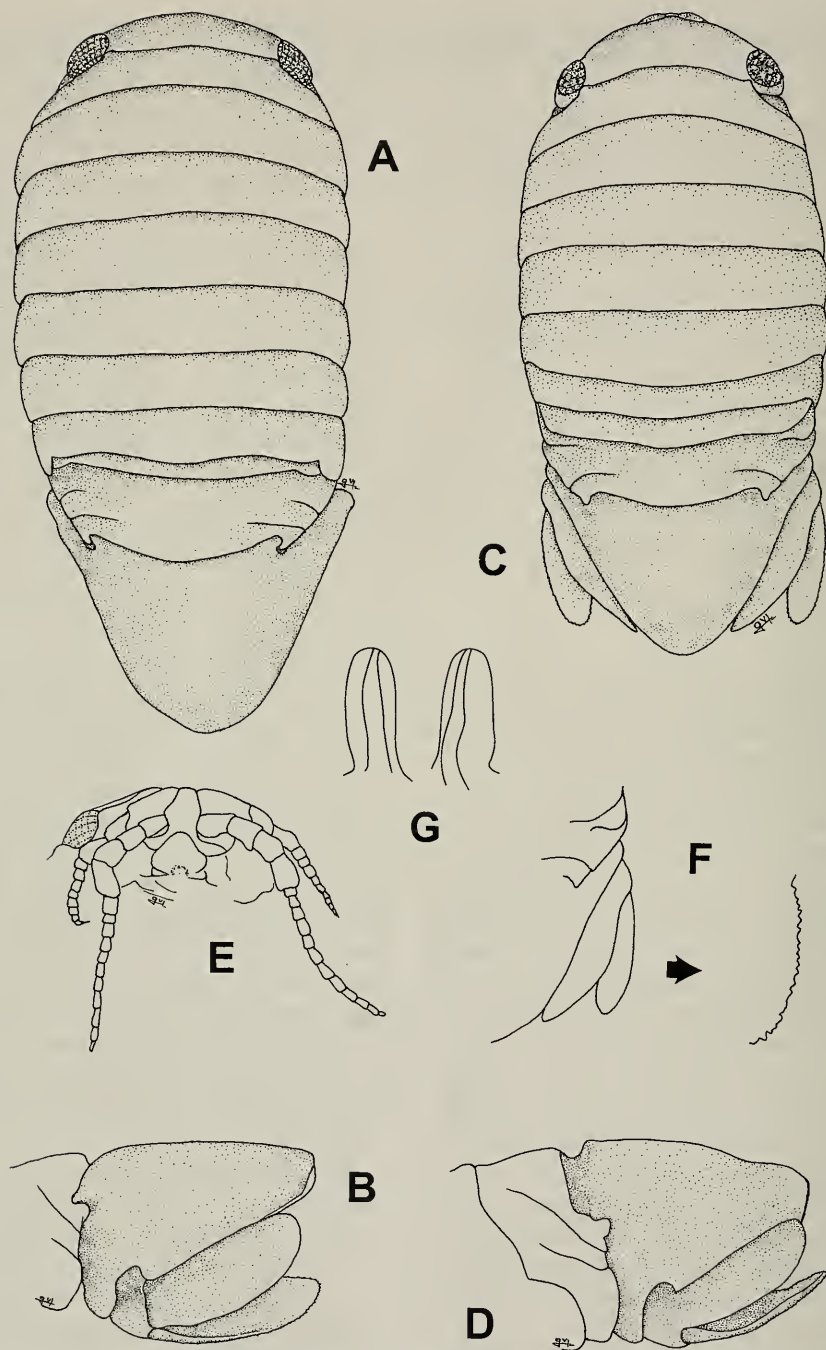


Fig. 1. *Exosphaeroma bruscai*, new species. A, Holotype, male, dorsal view (EMU-4745); B, pleotelson, male, lateral view; C, Paratype, female, dorsal view (EMU-5357); D, pleotelson, female, lateral view; E, cephalon, male, ventral view; F, uropods, dorsal view, detail; G, penes, male.





Fig. 2. *Exosphaeroma bruscai*, new species, male holotype (EMU-4745). Schematic drawing of body in lateral view; appendages not illustrated.

sent on articles as illustrated. Pereopods 2–3 similar, 3rd slightly longer than 2nd. Pereopod 3 (Fig. 4B) merus slightly longer than half ischium length; ischium with 5 spines near superior distal angle and 1 shorter proximal spine; merus with 6 spines at superior distal angle; carpus subcylindrical, similar in length to merus; propodus shorter than ischium; dactylus about half length of propodus, with 1 subterminal spine on the lower margin; composed spines, spines, scales and serrate scales present on articles as illustrated. Pereopod 7 (Fig. 4C) longer and more slender than pereopods 1–3; merus with 4 spines at superior distal angle; carpus distal margin with 2 inferior and a row of 5 superior serrated spines; propodus with 1 bifid spine and 1 subterminal serrate seta at superior angle; composed spines, spines and scales present on joints as illustrated. Pereopods 5–6 similar in shape and spination to pereopod 7; these pereopods slightly increasing in size from 5th to 7th.

Penes not fused, about twice as long as basal width (Fig. 1G).

Pleopods 1–3 (Fig. 5A–C) endopod and exopod with long, plumose marginal setae on pleopods as follows (endopod and exopod): pleopod 1, 16 and 26; pleopod 2, 18 and 27; pleopod 3, 13 and 30; protopod with 3 coupling spines. Distal margin of pleopod 1 exopod slightly curved; endopod triangular. Appendix masculina of pleopod 2 elongate, slender, distally minutely serrate and curving, tip rounded, overreaching en-

dopod of pleopod 2 by about half length of the latter. Pleopod 3 as illustrated. Exopod of pleopods 3–5 with complete transverse suture. Pleopod 4 (Fig. 5D) endopod with distinct thickened ridges, 3 short plumose marginal setae on ventral margin of exopod and 1 on endopod; a row of short non-plumose setae on the inner margin of exopod. Pleopod 5 (Fig. 5E) endopod with distinct thickened ridges, a row of short, non-plumose setae on inner margin of exopod and 6 similar setae near ventral margin of endopod; exopod with a deep cleft along inner margin, and 5 small lobes with scales close to inner distal and ventral margins.

Uropod exopods of similar length, endopod slightly longer and acute, exopod with rounded tip.

*Female*.—Body ovate, about twice as long as wide. Pleotelson slightly more inflated than in male, with a weak depression near posterior margin. All characters, including all pereopods, very similar to male.

*Etymology*.—This species is named for Richard C. Brusca, from the BIOSPHERE-2 Center, Tucson, Arizona, in recognition of his contribution to knowledge of the Isopoda, and for his support of our work.

*Habitat*.—In the eastern Pacific, previous records of *Exosphaeroma* are usually from sandy beaches. On Panamanian beaches, the species was collected in substrate composed of quartz sand, fine sand and calcareous shell fragments (Dexter 1972). Ríos & Ramos (1990) recorded specimens from sandy beaches of Colombia. *Exosphaeroma*

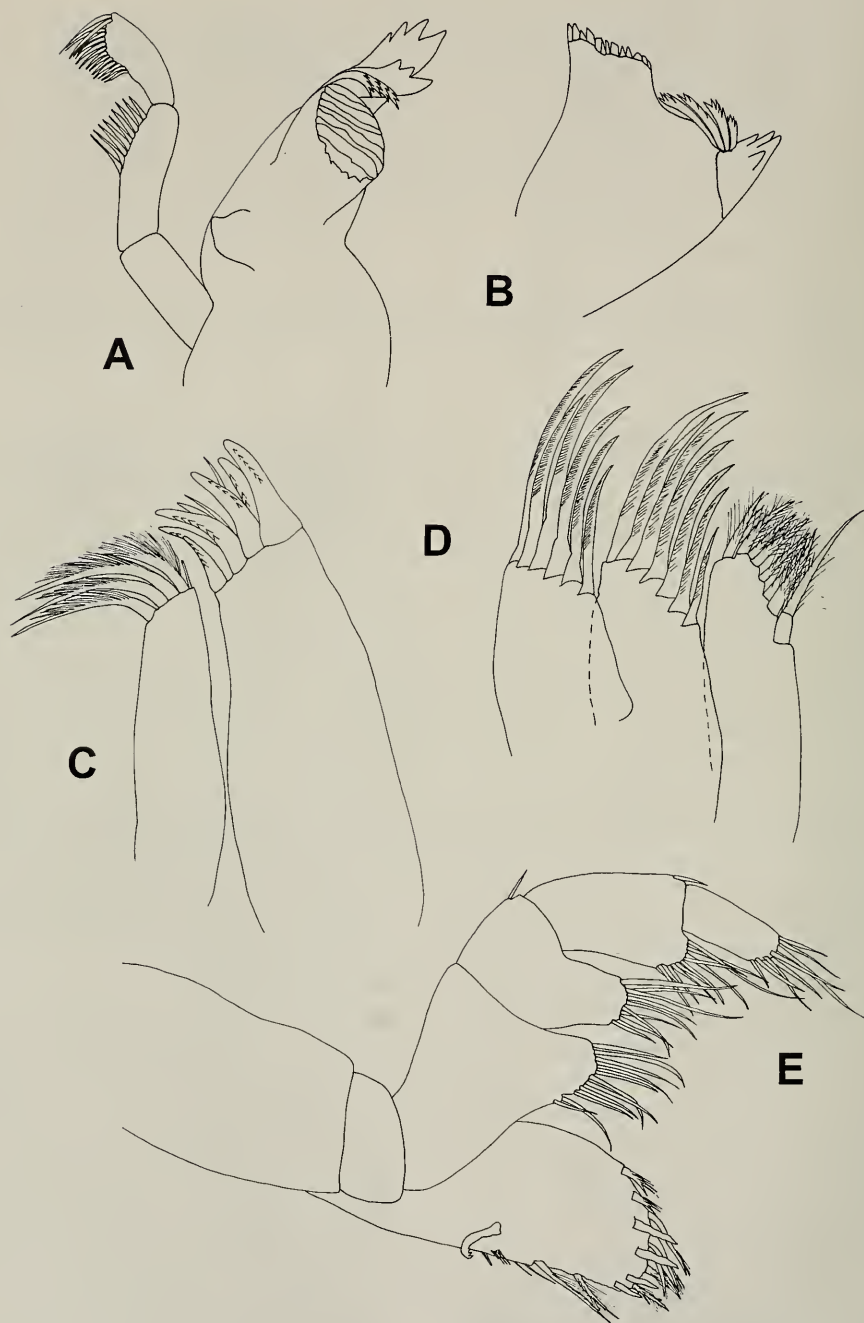


Fig. 3. *Exosphaeroma bruscai*, new species, male holotype (EMU-4745). A, left mandible; B, right mandible; C, right maxillula; D, right maxilla; E, right maxilliped.

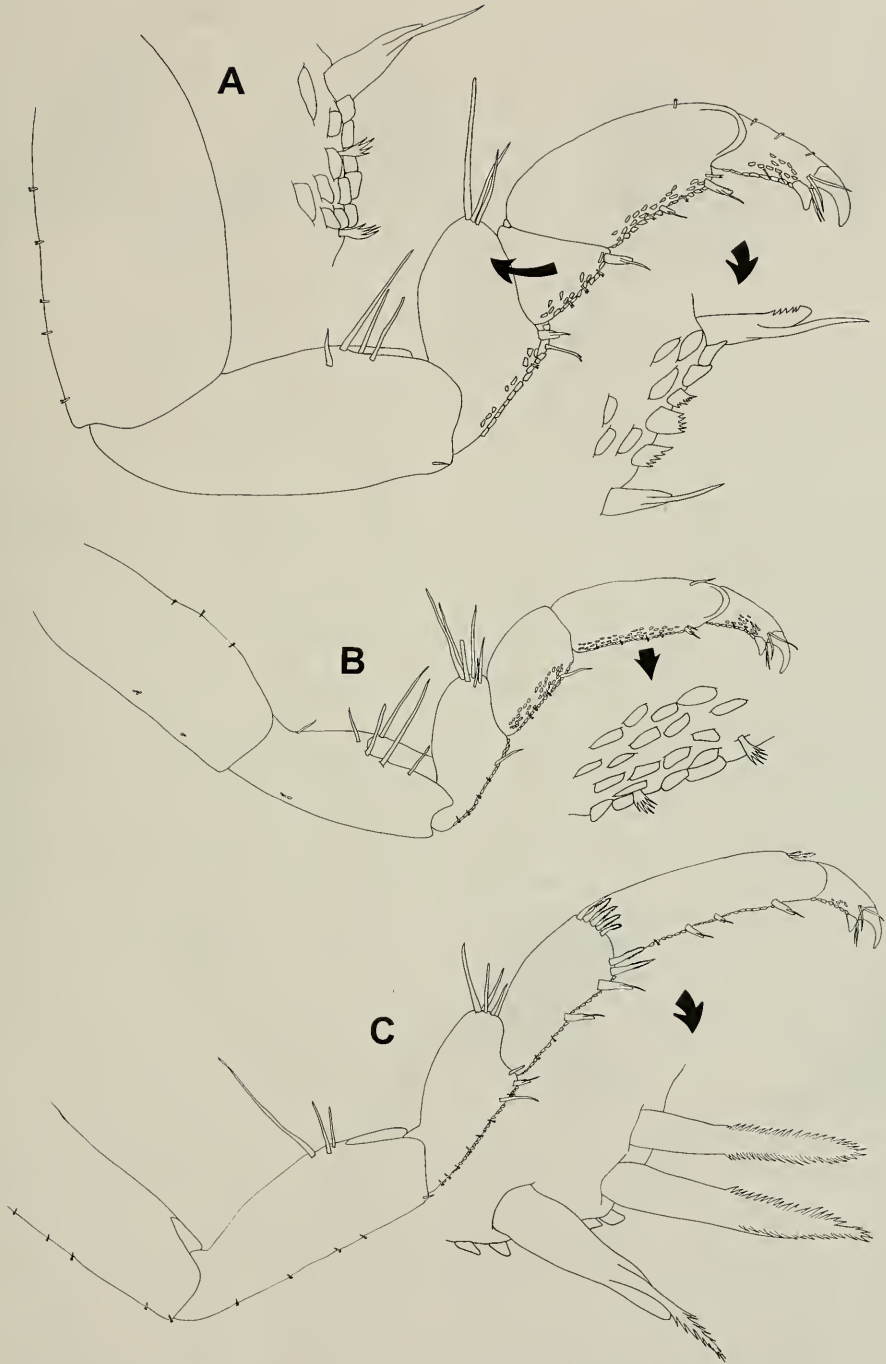


Fig. 4. *Exosphaeroma bruscai*, new species, male holotype (EMU-4745). A, right pereopod 1; B, right pereopod 3; C, right pereopod 7.

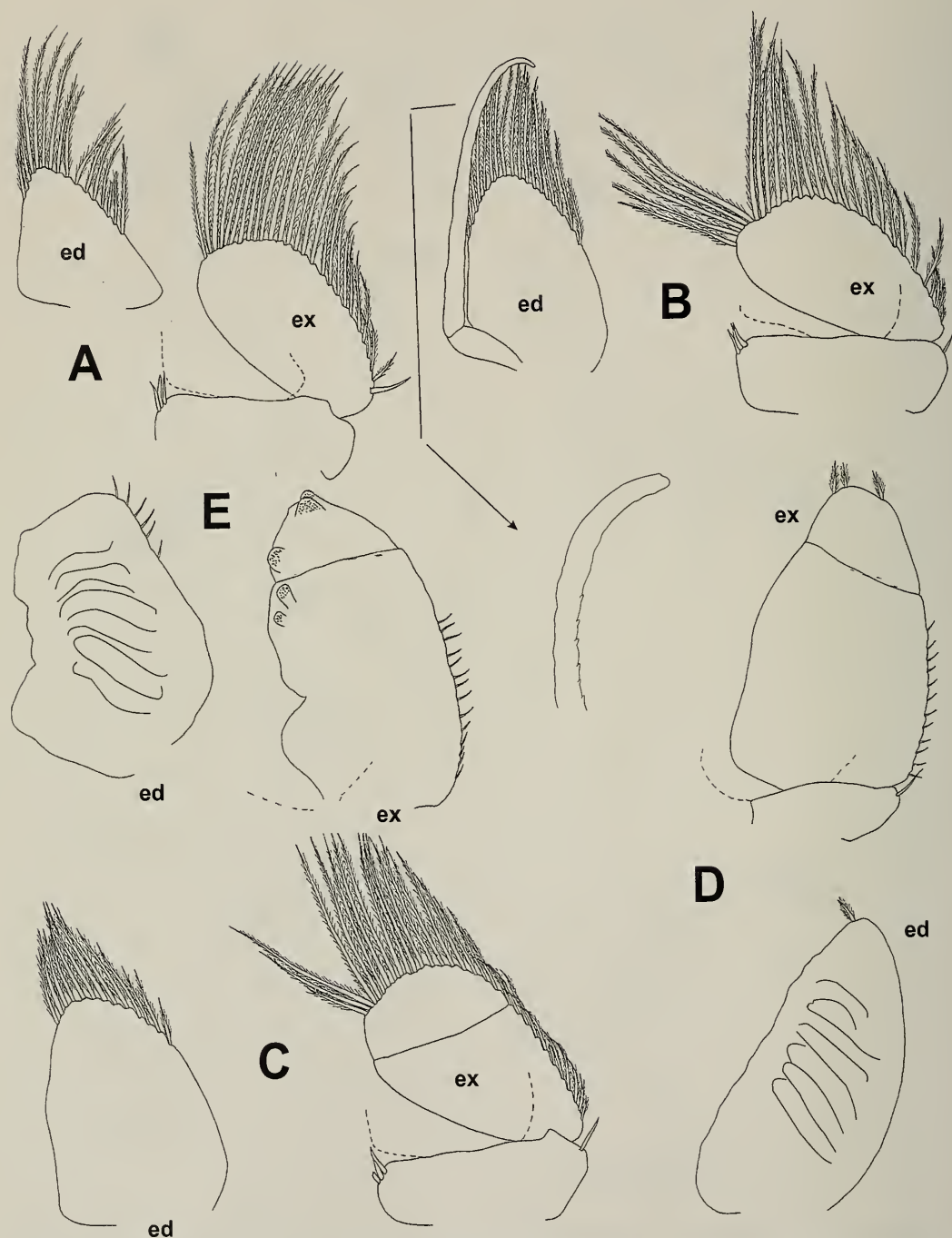


Fig. 5. *Exosphaeroma bruscai*, new species, male holotype (EMU-4745). A, right pleopod 1; B, right pleopod 2; C, right pleopod 3; D, right pleopod 4; E, right pleopod 5 (ed = endopod; ex = exopod).

has also been registered in gravels, off mangrove lagoons in Costa Rica (Brusca & Iverson 1985). In the Gulf of California, Mexico, *Exosphaeroma* has been taken under shell fragments on sandy stretches of tidal flats (Brusca & Iverson 1985). Records for *E. bruscai* are from algae on rocky beaches from intertidal zone to at least 3 m; environmental data available at the time of sampling indicate epibenthic temperature range from 20.3 to 28.0°C.

Although it seems reasonable to assume that all specimens of *Exosphaeroma* previously reported from the region belong to *E. bruscai*, the habitat of specimens described here differs from the typical sandy beach habitat reported previously by Dexter (1974, 1979) and Brusca & Iverson (1985). Furthermore, three species of *Exosphaeroma* from the Caribbean are known from sand (*E. diminuta*) or from algae on rocks (*E. alba* Menzies & Glynn, 1968 and *E. productatelson* Menzies & Glynn, 1968), but none has been reported from both habitats (Kensley & Schotte 1989). Although we believe that previous reports of *Exosphaeroma* from Panama, Costa Rica and Colombia correspond to *E. bruscai*, a comparison of specimens from these localities to type specimens of *E. bruscai* is desirable.

*Distribution.*—The species is known with certainty from Sonora (27°56.5'N, 111°05.5'W) to Los Arcos (Banderas Bay), Jalisco, on the east coast of the Gulf of California, and from La Paz, South Baja California. It is also known from the west coast of Costa Rica to Colombia.

*Remarks.*—The type species of *Exosphaeroma*, *Sphaeroma gigas* Leach, 1818, was recently redescribed (Brandt & Wägele 1989). *Exosphaeroma bruscai* expresses the typical generic characters considered by Brandt & Wägele (1989), in particular the ridges or folds of pleopods 4 and 5, and the two posteriorly directed submedian flat lobes on pleonite 1 (see Bruce 1994). *Exosphaeroma bruscai* is very similar to *E. diminuta* which occurs in the western Atlantic and with which is was originally con-

fused. The illustration of the dorsal habitus provided by Brusca & Iverson (1985: fig. 10, B) differs somewhat from our specimens; the Costa Rica specimens have an anteriorly inflated pleon, a character not so clearly marked in our specimens. This may be due to overshadowing of the original illustration, as demonstrated by the lateral view of the same pleon (Brusca & Iverson, 1985: fig. 10 D) provided by these authors, which is much more similar to our illustration (see Fig. 1). Comparison of original illustrations of *E. diminuta* by Menzies & Frankenberg (1966) with the new species show the following variations: antenna and antennula are similar in size in *E. diminuta*, while the antenna of *E. bruscai* is almost twice as long as the antennula; the rostrum is rounded in *E. diminuta*, acute in *E. bruscai*; endopod of first pleopod is triangular in *E. bruscai*, narrowly oval in *E. diminuta*; a transverse suture is present on exopod of pereopods 3–5 in *E. bruscai*, present only on pereopod 4 in *E. diminuta*; appendix masculina slender, much longer than pleopod 2 endopod in *E. bruscai*, stouter, just reaching apex of the endopod in *E. diminuta*; distal 2 articles of maxilliped palp slender in *E. diminuta*. According to Menzies & Frankenberg (1966: fig. 21 B), clypeus of *E. diminuta* is almost rectangular but it is figured by Kensley & Schotte (1989: fig. 100 H) as being widest in middle length, as in *E. bruscai*.

*Exosphaeroma bruscai* also differs from other American species of *Exosphaeroma* reported by Kensley & Schotte (1989). *Exosphaeroma alba* has a notched, and *E. yucatanum* (Richardson, 1901) a trilobate, margin of the posterior pleotelson; the pleotelson of *E. antillense* Richardson, 1912 bears two rounded submedian tubercles; *E. productatelson*, features broad lateral patches of pigment on pleotelson, not observed on any specimen of *E. bruscai*.

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**A review of *Pseudionella* Shiino, 1949 (Crustacea: Isopoda: Bopyridae), with the description of a new species parasitic on *Calcinus* hermit crabs from Easter Island**

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*Abstract.*—Two pairs of bopyrids collected on Easter Island, from the hermit crab *Calcinus imperialis* Whitelegge, belong to the genus *Pseudionella* Shiino (= *Pseudasymmetrione* Adkinson & Heard, new synonymy) and are described as *P. akuaku* n. sp. This is the first record of any bopyrid isopod from Easter Island and the first *Pseudionella* known to parasitize hermit crabs of the genus *Calcinus*. A review of the species of *Pseudionella*, with keys to males and females, is provided and includes a significant range extension for *P. deflexa* Bourdon.

Bopyrid isopods found in the branchial chambers of hermit crabs are restricted to the subfamily Pseudioninae. Seven genera have been erected exclusively for species of hermit crab branchial parasites, including *Pseudionella* Shiino, 1949, with one Pacific and one Atlantic taxon, and *Pseudasymmetrione* Adkinson & Heard, 1978, with one Atlantic species. Additionally, nine species of the heterogeneous (and probably paraphyletic) genus *Pseudione* Kossman, 1881, are known from hermit crabs; other *Pseudione* spp. occur on a broad range of decapod taxa, including carideans, nephropids, thalassinoids, galatheoids, and lithodids.

One of us (CBB) collected a series of hermit crabs from Easter Island (Rapa Nui) during August 1999. Two of these crabs contained mature female bopyrids, each with a male attached to the ventral side of the pleonites. Provisional identification of these specimens indicated that they appeared to belong to the genus *Pseudasymmetrione* Adkinson & Heard. However, an examination of *Pseudasymmetrione* type

material showed that genus to be a synonym of *Pseudionella* Shiino, and our specimens cannot be placed into any of the three described species now placed in that genus. These specimens are described as a new species of *Pseudionella* which is most closely related to an Atlantic congener, *P. markhami* (Adkinson & Heard).

#### Methods

Hermit crabs inhabiting gastropod shells were collected intertidally on Easter Island during August 1999. The data label in the vial containing the parasitized specimens was badly damaged during shipping of specimens from Easter Island to New York and, consequently, no specific locality can be determined. Specimens were preserved in 70% ethanol. The shells were cracked using a vise and the crabs removed and examined for parasites. Collection of a single female *Pseudionella deflexa* was made on Andros Island, Bahamas in September 2000 using methods identical to those above.

Drawing tube sketches made of the spec-

imens were scanned into a Macintosh<sup>™</sup> computer. Images were then prepared using the programs Adobe Photoshop<sup>™</sup> and Adobe Illustrator<sup>™</sup>.

Shield length (SL) is provided as an indicator of size for the host crabs. Isopod size is given as total body length (anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.01 mm using an ocular micrometer.

Specimens of the new species and *P. deflexa* are deposited in the Division of Invertebrate Zoology, American Museum of Natural History, New York, U.S.A. (AMNH). Specimens of *Pseudasymmetrione markhami* were borrowed from the National Museum of Natural History (Naturalis), Leiden, the Netherlands (RMNH) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Family Bopyridae Rafinesque, 1815

Subfamily Pseudioninae Codreanu, 1967

Genus *Pseudionella* Shiino, 1949

*Pseudionella* Shiino, 1949:60–61 (type species by monotypy: *Pseudionella attenuata* Shiino, 1949).

“Undescribed genus” Markham, 1978:110.

*Pseudasymmetrione* Adkinson & Heard, 1978:409, 412 (type species by monotypy: *Pseudasymmetrione markhami* Adkinson & Heard, 1978) (new synonymy). not *Pseudionella*, Shiino, 1958:41 (= *Bopyrissa* Nierstrasz & Brender à Brandis, 1931).

*Diagnosis*.—Female with seven pereonites and five pleonites plus pleotelson, all laterally distinct. Frontal lamina entire. Lateral plates very short. Marsupium enclosed by well-developed oostegites. Five pairs of lamellar pleopods, anterior two pairs biramous with exopodite distally bilobed; posterior three pairs uniramous. Uropoda uniramous. Male with seven distinct pereonites and five distinct pleonites plus pleotelson, pleonites markedly reduced in width from pereonites. Five pairs of uniramous tuberculiform or flap-like pleopods.

*Remarks*.—The addition of the new taxon described below to *Pseudionella*, and the synonymy of *Pseudasymmetrione*, requires some modifications to the original diagnosis of Shiino (1949). The frontal lamina is entire, although Shiino (1949) called it rudimentary in the type species. The first two pairs of pleopods in the female are biramous with the endopodite bilobed at the tip, while the last three pairs are uniramous. Both Shiino (1949) and Adkinson & Heard (1978) considered the coalescence of the head with the first pereonite in the male to be of great importance, but this character can vary between individuals within a species (e.g., *Stegophryxus hyphalus* Markham, 1972:38) and we are unconvinced in its reliability as a diagnostic feature. The pleotelson of the male is either a simple cone (as in *P. attenuata* and *P. deflexa*) or has lateral projections (as in *P. markhami* and the new species) which may represent reduced lateral plates on the sixth pleonite (=pleotelson).

The synonymy of *Pseudasymmetrione* with *Pseudionella* was suggested, but not formally proposed, by Bourdon (1979). Bourdon (1979) noted that the one, perhaps significant, difference between the two taxa was the form of the male pleotelson (simple in *Pseudionella* and with fused lateral plates in *Pseudasymmetrione*) but wondered if this was sufficient for the establishment of a separate genus. We agree that the four characters given as diagnostic for *Pseudasymmetrione* by Adkinson & Heard (1978) do not appear to warrant separation of the genera: the female dorsal segmentation is medially indistinct in both *P. markhami* and the new species, but is variable between the specimens of the new species, and therefore not a good character; the frontal lamina of *Pseudionella* is not reduced or absent, as stated by Shiino (1949), and there is little difference in this character between the four species; the coxal plates of *P. markhami* are well developed, but are reduced in the other taxa including the new species; and contrary to the statement of



Adkinson & Heard (1978), males of *P. markhami* do possess pleopods, but of a form more reduced than those seen in *P. attenuata* and *P. deflexa*. The only character left to discriminate between the two genera is the shape of the male pleotelson which, as noted by Bourdon (1979), was not included in the original diagnosis of *Pseudasymmetrione*. In our opinion, this single difference does not warrant separate generic status for these species. We propose that *Pseudionella* contains two species-groups, each with one Atlantic and one Pacific taxon: *P. attenuata* and *P. deflexa*; *P. markhami* and the new species from Easter Island. Note that *Pseudionella pyriforma* Shiino, 1958, does not belong in this genus, but to *Bopyrissa* Nierstrasz & Brender à Brandis, 1931 (see Bourdon 1979, Markham 1982). *Pseudionella* appears closely allied to the diverse genus *Pseudione* which contains species with very similar female morphology, but with five pairs of biramous pleopods in the females (e.g., Nierstrasz & Brender à Brandis 1931, Shiino 1933). The males of *Pseudionella* also resemble those of *Pseudione*, but have more laterally constricted pleonites. Although *Pseudionella* contains several clearly apomorphic characters (e.g., uniramous pleopods 3–5 in females, narrowed pleonites in males) as compared to *Pseudione*, a detailed phylogenetic analysis is needed to fully understand the relationships between these genera and the others in the subfamily.

*Pseudionella attenuata* Shiino, 1949

*Pseudionella attenuata* Shiino, 1949:62–63, fig. 2.

*Material examined*.—unavailable.

*Type locality*.—Seto, Wakayama Prefecture, Japan (Shiino 1949, type specimens (if extant) in National Science Museum, Tokyo).

*Distribution and host*.—Japan, on *Pagurus* sp. (Shiino 1949, as *Eupagurus* sp.).

*Remarks*.—No specimens have been reported subsequent to the two type speci-

mens. Unfortunately it has not been possible to directly examine the types, nor to even confirm if they are still extant, as Shiino's material is in a very poor state of organization (M. Takeda, pers. commun. 15 Jun 1999). The female type was dextral, which suggests that it came from the right branchial chamber of the host.

*Pseudionella markhami* (Adkinson & Heard, 1978), new combination

“Undescribed . . . species” Markham, 1978: 110.

*Pseudasymmetrione markhami* Adkinson & Heard, 1978:412–414, figs. 1–3.—Markham, 1988:8–9, fig. 2.

“*Pseudasymmetrione* . . . undescribed species” Adkinson & Heard, 1978:417.

*Material examined*.—Holotype: sinistral female (3.14 mm) infesting left branchial chamber of *Pagurus annulipes* (Stimpson) (sex and size unknown), Morehead Channel, Carteret County, North Carolina, U.S.A., R. W. Heard coll., 26 Aug 1963 (USNM 170590). “Allotype”: male (0.99 mm) same data as holotype (USNM 170590). Paratypes: female (2.14 mm) and male (0.89 mm) infesting male host (1.7 mm SL), female (2.00 mm) and male (0.78 mm) infesting male host (1.7 mm SL), female (2.86 mm) and male (0.87 mm) infesting female host (2.1 mm SL), all females sinistral and infesting left branchial chambers of *P. annulipes*, Morehead Channel, Carteret County, North Carolina, U.S.A., R. W. Heard coll., 25 Jun 1970 (USNM 170593); non-types: dextral female (3.14 mm), and male (0.99 mm), infesting [presumed right] branchial chamber of *Iridopagurus iris* (A. Milne Edwards) (sex and size unknown), Sta. P-757, 11°41'N, 69°21'W, off Peninsula de Paraguaná, Venezuela, 161–187 m, R/V *Pillsbury* coll., 27 Jul 1968 (USNM 172224); sinistral female (3.14 mm), male (1.57), sinistral female (1.26 mm), male (0.72 mm) infesting *Pagurus brevidactylus* (Stimpson) (host sexes, sizes and infested branchial chambers un-

known), Punta de Betin, Santa Marta, Dept. Magdalena, Colombia, under stones, 1–2 m, coll. H. G. Müller, 4 Feb 1986 (RMNH 7042); sinistral female (1.26 mm), infesting *Pagurus stimpsoni* (A. Milne Edwards & Bouvier) (host sex, size, and infested branchial chamber unknown), Punta de la Aquia, ca. 4 km east of Santa Marta, Dept. Magdalena, Colombia, on coral rubble, 17–19 m, coll. H. G. Müller, 9 Jan 1986 (RMNH 7058).

*Type locality*.—Morehead Channel, Carteret County, North Carolina, United States (Adkinson & Heard 1978, type specimens in USNM, Zoologiske Museum Copenhagen, and the collection of D. Adkinson).

*Distribution and hosts*.—North Carolina, U.S.A., on *Pagurus annulipes* (Stimpson) (Adkinson & Heard 1978, herein); Venezuela, on *Iridopagurus iris* (A. Milne Edwards) (Markham 1978, Adkinson & Heard 1978, herein); Colombia (Atlantic), on *Pagurus brevidactylus* (Stimpson) and *P. stimpsoni* (A. Milne Edwards & Bouvier) (Markham 1988, herein).

*Remarks*.—The pereonites and pleonites of male *P. markhami* are much more compacted than in the other three taxa in the genus, but the shape of the male pleotelson and the form of the male pleopods are very close to the new species from Easter Island. Although Adkinson & Heard (1978) did not designate an allotype, the male accompanying the female holotype is of equivalent status. Markham (1988) correctly identified the above cited specimens of *Pseudionella markhami* from Colombia, but inaccurately drew the male pleotelson of RMNH 7042 as having two slender projections; the shape is identical to that of the male allotype and of the other specimens in RMNH. Adkinson & Heard (1978) indicated that Markham's (1978:110) "undescribed new genus and species" from Venezuela appeared to be an undescribed *Pseudasymmetrione* (= *Pseudionella*). However, examination of those two specimens indicated no notable differences from *P. markhami*, other than the unique dextral orientation of the female.

*Pseudionella deflexa* Bourdon, 1979

*Pseudionella deflexa* Bourdon, 1979:139–141, fig. 1.

*Material examined*.—sinistral female (2.5 mm, with one female and three male *Cabirops* cryptoniscid isopods in the brood chamber), infesting male *Pagurus brevidactylus* (Stimpson) (2.1 mm SL), Station 409R, 24°53'13.3"N, 77°54'47.2"W, sand/algal plain, 1.2–1.8 m, Andros Island, Bahamas, coll. C. B. Boyko, 1 Sep 2000 (AMNH 18204).

*Type locality*.—24°35'5"S, 46°31'W, 45 m, Brazil (Bourdon 1979).

*Distribution and hosts*.—Brazil, on *Pagurus criniticornis* (Dana) (Bourdon 1979); Bahamas, on *Pagurus brevidactylus* (Stimpson) (herein).

*Remarks*.—The Bahamas specimen represents a new host record and a significant range extension for the species, which was previously known only from Brazil. The females of this species are extremely close to those of *P. markhami*, but can be distinguished by more delineated segmentation of the pereonites, less pronounced coxal plates (especially on the posterior pereonites), and less pronounced lateral projections on the pleotelson. The males of the two species are easily distinguished by the presence (*P. markhami*) or absence (*P. deflexa*) of lateral projections on the pleotelson and by the different forms of the pleopods.

*Pseudionella akuaku*, new species

Figs. 1–4

*Material examined*.—Holotype: sinistral female (1.44 mm), infesting left branchial chamber of male *Calcinus imperialis* Whitelegge (2.0 mm SL; AMNH 18187), inhabiting shell of *Planaxis akuana* Rehder, Easter Island, intertidal, coll. C. B. Boyko, Aug 1999 (AMNH 18201). Allotype: male (0.91 mm), same data as holotype (AMNH 18202). Paratypes: sinistral female (1.75 mm), male (1.26 mm) infesting left branchial chamber of male *Calcinus imperialis*

(2.0 mm SL; AMNH 18187), inhabiting shell of *Planaxis akuana* Rehder, Easter Island, intertidal, coll. C. B. Boyko, Aug 1999 (AMNH 18203).

*Type locality*.—Easter Island, territory of Chile, Pacific Ocean.

*Description*.—Female (Figs. 1, 2), based on holotype: Body length 1.44 mm, maximal width 1.19 mm, head length 0.48 mm, head width 0.52 mm, pleon length 0.45 mm. Pereon weakly S-shaped; head deflected to the right and pleon weakly to the left. Body outline broad at pereon, narrow at pleon and elongated (Figs. 1A, B). Dark spot or band of pigmentation at junction of all coxal plates and pereonites (in dorsal view).

Head weakly produced with anterior lamina raised and recurved along distal margin. Eyes present, large relative to cephalon, occurring near posterolateral corners of raised lamina edge (but absent in paratype female). Antenna (Fig. 2A) of three articles; antennule (Fig. 2A) of three articles, all segments with fine scales bearing setae on distal margins, distal margins of segments with setae. Maxilliped (Fig. 2B) with elongate rounded spur; palp subcircular with distal narrow, rounded projection; posterior margin setose. First oostegite proximal lobe ovate, distal lobe subtriangular, internal ridge smooth (Figs. 2C, D).

Pereon broadest across pereonite 4, tapering anteriorly and posteriorly. Coxal plates on sides of pereonites all similar but larger on left side of body. Oostegites sparsely covered in minute tubercles; posteriormost oostegite with fringe of setae on posterior margin. Pereopods 3–6 of about same size; pereopods 1, 2, and 7 (Fig. 2E, F) slightly smaller and shorter. Dorsal margins of dactylus and basis, and ventral margins of propodus, carpus, and merus with numerous plate-like scales bearing setae on distal margins; short setae at distal tip of propodus. First two pereopods surrounding head region; no large gaps between any pereopods.

Pleonites 1 and 2 with extended lanceo-

late, distally rounded, biramous pleopods and uniramous short lateral plates; exopodite of pleopod 1 bilobed, endopodite smaller and entire; exopodite and endopodite of pleopod 2 entire; pleonites 3–5 with lanceolate, uniramous pleopods and uniramous short lateral plates (Fig. 2G); lateral plates slightly reduced and pleopods markedly reduced in size from anterior to posterior; pleotelson (Fig. 2H) appears trifold distally as a result of incomplete fusion of segment with sixth pair of lateral plates, all projections subequal in length and width, with pair of large broad lanceolate, distally rounded, uropods. Lateral plates and uropods with dense covering of scales bearing setae on distal margins (Fig. 2I).

Male (Figs. 3, 4), based on allotype: Length 0.91 mm, head length 0.13 mm, head width 0.28 mm, pleon length 0.21 mm. Occurring on ventral side of pleon of female; directed anteroposteriorly.

Head suboval, widest posteriorly, distinct from with first pereonite (Figs 3A, B). Large eyes (relative to cephalon) near posterolateral margin. Antenna of five articles, distally setose; extending posterolaterally from head; antennule of three articles; antennae and antennule with scattered small scales bearing setae on distal margins (Fig. 4A).

Pereonites 3 and 4 broadest, tapering anteriorly and posteriorly. All pereonites directed laterally. Irregular dark pigmentation pattern at junction of body and pereonite lateral projections and on first three pleonites. All pereopods (Figs. 4B, C) subequal, all articles distinctly separated, no scales apparent on dorsal or ventral surfaces.

Pleonites tapering posteriorly and directed laterally. All pleonites distinctly segmented, weakly produced laterally and markedly narrower than pereonites. No midventral tubercles (Figs. 3B, 4D). Pleotelson (Fig. 4D) notched medially with minute anal cone, produced distolaterally into rounded lobes, distolateral corners of lobes with scales and setae; uropods absent.

*Distribution and host*.—On hermit crabs,

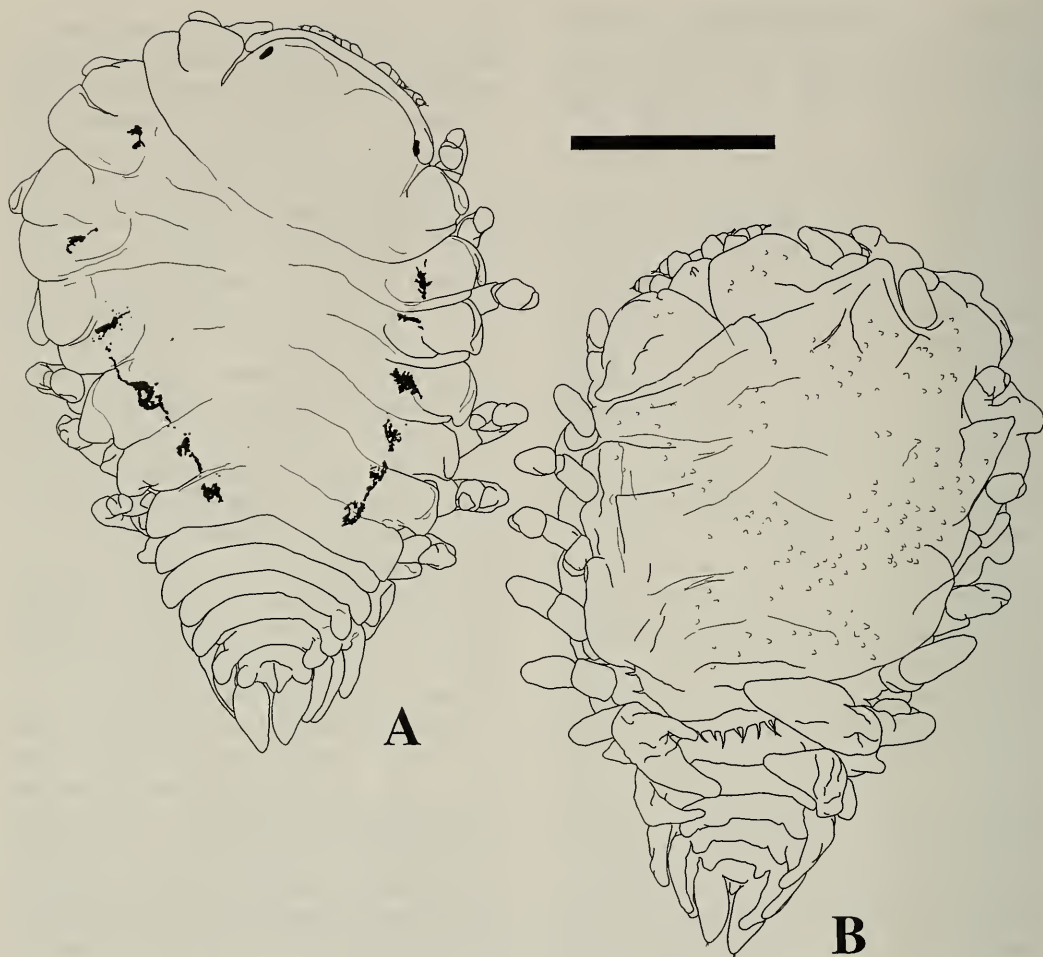


Fig. 1. *Pseudionella akuaku*, new species. Female, 1.44 mm, AMNH 18201, holotype. A, dorsal view; B, ventral view. Scale = 500  $\mu$ m.

*Calcinus imperialis* from Easter Island; intertidal.

*Etymology*.—The specific name *akuaku* is derived from the Rapa Nui word for supernatural beings who sometimes assumed animal shapes (Blixen 1993). The name is used as a noun in apposition.

*Remarks*.—The pleopodal formula of the female, the attenuated width of the pleonites of the male as compared with the pereonites, and the presence of uniramous pleopods in the male, clearly place this taxon in *Pseudionella*. Additionally, females of all species of *Pseudionella* possess small

lobes on the ventral surface of each pereonite mesial to the pleopods. The nature of these lobes is unknown but, as pointed out by Shiino (1949), they cannot be reduced pleopods as they occur alongside fully biramous pleopods. A comparison with the other three species now placed in this genus shows several important differences between the taxa. *Pseudionella akuaku* n. sp. has a “trilobed” appearance in the pleotelson of the female (i.e., a partly fused sixth pair of lateral plates), very broad uropods of the female, pronounced lateral lobes (fused sixth lateral plates) on the pleotelson

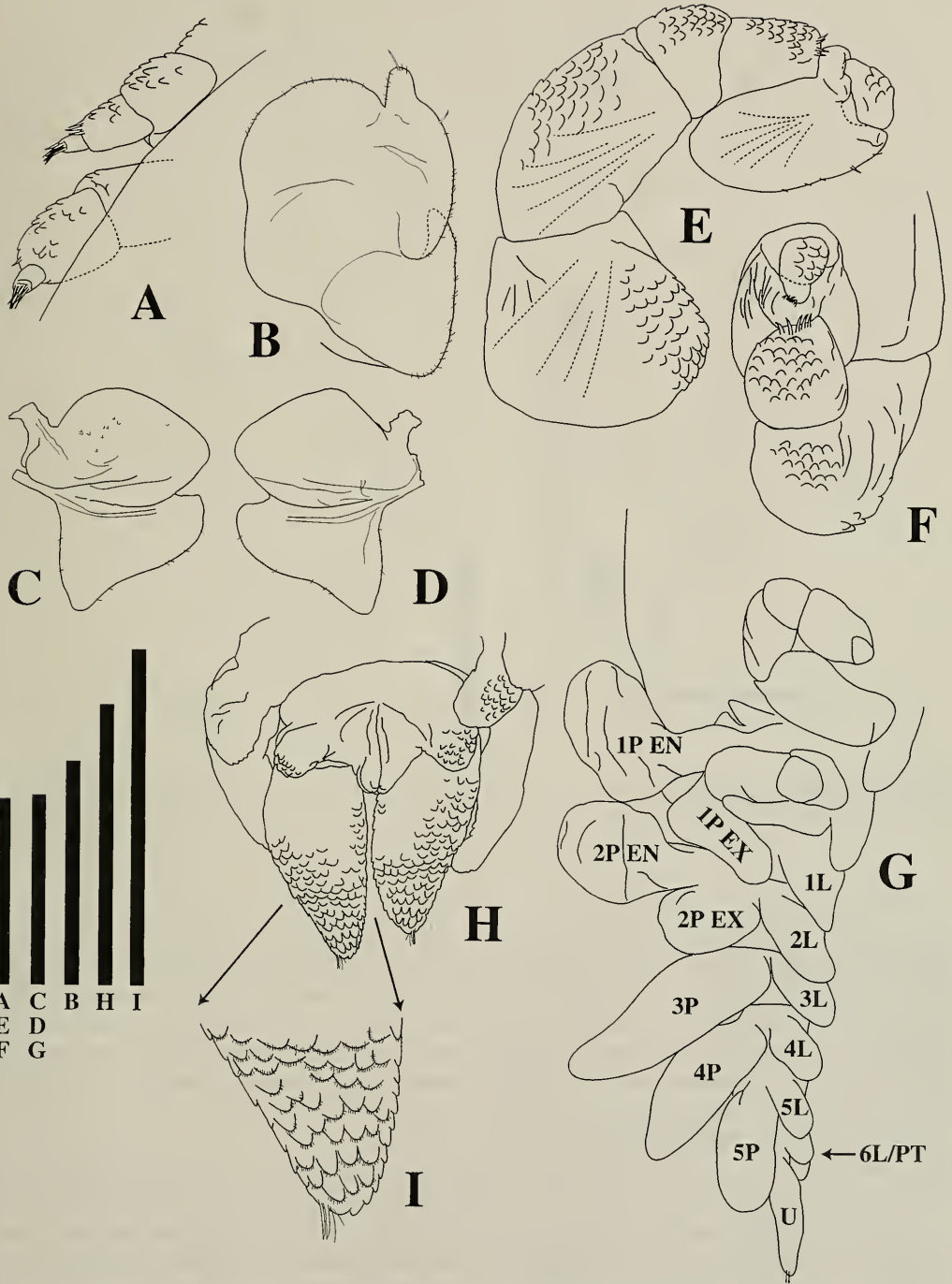


Fig. 2. *Pseudionella akuaku*, new species. Female, 1.75 mm, AMNH 18203, paratype (A–F): Female, 1.44 mm, AMNH 18201, holotype (G–I). A, left antenna and antennule; B, right maxilliped, external; C, right oostegite 1, external; D, right oostegite 1, internal; E, right pereopod 1; F, right pereopod 7; G, posterolateral view, left side; H, pleotelson and uropods; I, uropod detail (EN = endopod; EX = exopod; L = lateral plate; P = pleopod; PT = pleotelson; U = uropod; numbers indicate pleonite). Scale = 150  $\mu\text{m}$  (I), 200  $\mu\text{m}$  (A, E, F), 225  $\mu\text{m}$  (H), 250  $\mu\text{m}$  (G), 300  $\mu\text{m}$  (B), and 500  $\mu\text{m}$  (C, D).

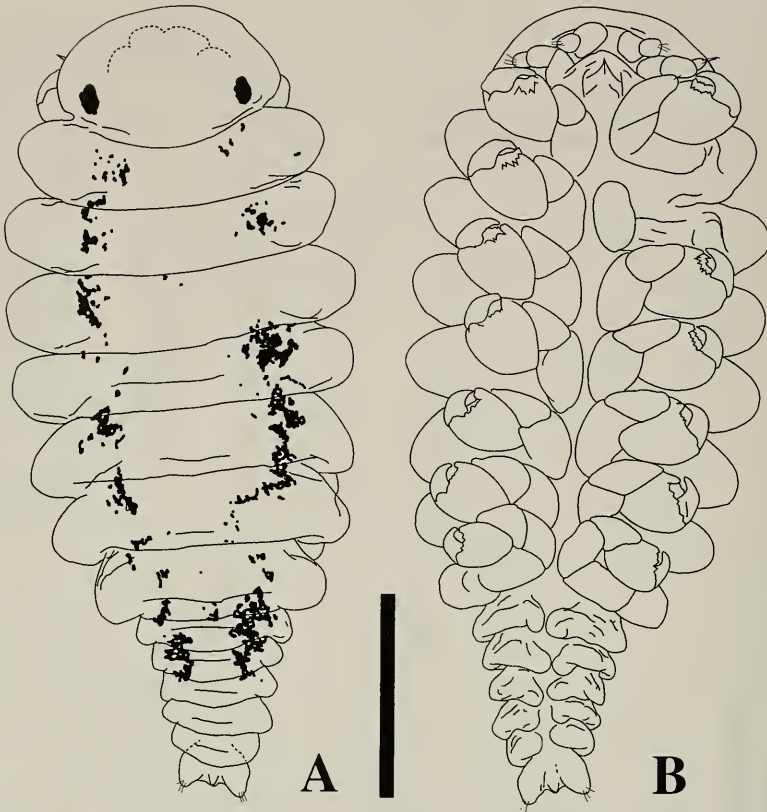


Fig. 3. *Pseudionella akuaku*, new species. Male, 0.91 mm, AMNH 18202, allotype. A, dorsal view; B, ventral view. Scale = 250  $\mu$ m.

of the male, and flap-like pleopods. In contrast, both *P. attenuata* and *P. deflexa* have slender uropods on the female, no lateral lobes on the pleotelson of the male, and tuberculiform pleopods. The pleotelson of *P. deflexa* does have a "trilobed" appearance, but it is less pronounced than that of *P. akuaku* n. sp. *Pseudionella markhami* possesses both flap-like pleopods on the male and broad uropods on the female, while the male has only weakly produced lateral lobes on the pleotelson. The antennae and antennules of female *P. deflexa*, *P. markhami*, and *P. akuaku* n. sp. are each composed of three articles, while those of *P. attenuata* are 2 and 3 segmented, respectively (Shiino 1949).

Female and male specimens of *Pseudionella* spp. possess plate-like scales bearing

setae on the distal margins of the antennae, antennules, and pereopods. Such scales have been noted in other bopyrids and their fine structure has been examined by SEM in *Heterocephon marginatum* Shiino, 1936, by Janssen & Brandt (1994), who suggested that these scales may aid in attachment to host crabs (for females) or female bopyrids (for males).

The shape of the female pleotelson in all of the nine species of *Pseudione* found on hermit crabs is nondescript, typically being a small rounded or slightly pointed lobe, as is true of *Pseudionella attenuata*. In marked contrast, the female pleotelsons of *Pseudionella deflexa*, *P. markhami*, and *P. akuaku* n. sp. are large and trifold with pronounced and rounded median and lateral lobes. These lateral lobes represent poorly devel-

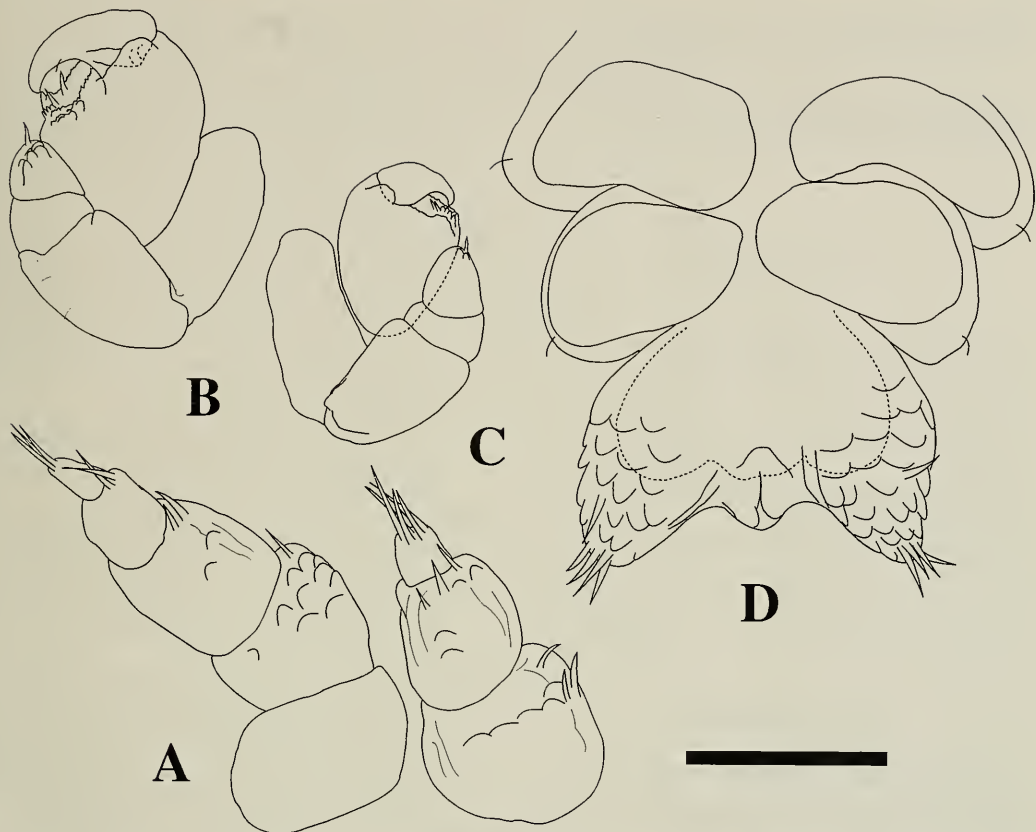


Fig. 4. *Pseudionella akuaku*, new species. Male, 1.26 mm, AMNH 18203, paratype (A); Male, 0.91 mm, AMNH 18202, allotype (B–D). A, right antenna and antennule; B, left pereopod 1; C, right pereopod 7; D, ventral view of posterior pleonites and pleotelson. Scale = 50  $\mu$ m (B, C), 100  $\mu$ m (A, D).

oped lateral plates partly fused with the pleotelson and are quite different from the lateral plates found on pleonites 1–5. *Pseudionella attenuata* may represent a transitional form between the hermit crab-infesting *Pseudione* and the other species of *Pseudionella*.

**Ecology.**—A total of 81 hermit crabs were collected from intertidal and subtidal locations on Easter Island from 22–31 August 1999. Examples of both previously known shallow water hermit crabs from the island were present in the collection: *Calcinus pascuensis* Haig (18 specimens) and *C. imperialis* (65 specimens), as well as a newly recorded species, *C. vachoni* Forest (1 specimen). Only two male hermit crab

specimens of *C. imperialis* were found to have bopyrid parasites (2.4% overall prevalence). This is the first report of a member of *Pseudionella* on a species of *Calcinus*, the other three species being known from *Pagurus* spp. (Shiino 1949, Adkinson & Heard 1978, Bourdon 1979).

Key to females of the species of *Pseudionella*

- 1. Pleotelson simple . . . . . *P. attenuata*
- Pleotelson “trifid” (with lateral plates) . . . . . 2
- 2. Medial pereonite segmentation entire . . . . . *P. deflexa*
- Medial pereonite segmentation indistinct . . . . . 3

3. Pleotelson lateral plates subacute, extending well beyond apex of pleotelson  
 ..... *P. markhami*  
 – Pleotelson lateral plates rounded, subequal to apex of pleotelson .....  
 ..... *P. akuaku* n. sp.

Key to males of the species of  
*Pseudionella*

1. Pleotelson with lateral projections . . . . 2  
 – Pleotelson simple, without lateral projections . . . . . 3  
 2. Pleotelson lateral projections large, distinct . . . . . *P. akuaku* n. sp.  
 – Pleotelson lateral projections small, indistinct . . . . . *P. markhami*  
 3. Pleotelson minute, shorter than pleonite 5  
 ..... *P. deflexa*  
 – Pleotelson elongate, longer than pleonite 5  
 ..... *P. attenuata*

Acknowledgments

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***Foliomolgus cucullus*, a new genus and species of Clausidiidae  
(Crustacea: Copepoda: Poecilostomatoida) associated with a  
polychaete in Korea**

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*Abstract.*—*Foliomolgus cucullus*, new genus and species, is described as an associate of the polychaete *Marphysa sanguinea* (Montagu) inhabiting the intertidal sands in Jeju Island in Korea Strait. The new genus possesses primitive features such as the complete segmentation and setation of rami on legs 1–4, 7-segmented antennule, 4-segmented antenna, and 5-segmented female urosome. It possesses also characteristic features such as a spatulate distal segment of the maxilla, foliaceous ventral elements and rudimentary dorsal claw on the mandible, atrophied distal segment of the antenna, and no maxilliped in the female.

The copepods of the family Clausidiidae have been considered to be the most ancestral group of the order Poecilostomatoida. They are found on/in various tubicolous invertebrates, including crustaceans, bivalves, and polychaetes.

The host of the new genus, *Marphysa sanguinea* (Montagu), is a cosmopolitan species of Polychaeta occurring in warm seas (Imajima & Hartman, 1964). Kim (2000) reported *Clausia lobata* as a new species of copepod associated with *M. sanguinea* from the Yellow Sea. During a recent field survey in Jeju Island, the largest island in Korea, a number of the same polychaete species were collected from the intertidal sands, and searched for copepod associates. At this island *C. lobata* was not found on the same polychaete, but, instead, a new species of Copepod belonging to a new genus of the family Clausidiidae was collected. Although only one female and two males were found, they were large enough to facilitate a thorough study, leaving type specimens available for future study.

Before microscopic observation and dissection, copepod specimens were cleared in

lactic acid. Dissections were done using the reversed slide method (Humes & Gooding, 1964). Drawing was done with the aid of a camera lucida. In the description of species, the body lengths were measured from the anterior tip of the cephalothorax to the posterior margin of the caudal rami, excluding the caudal setae. In the formula for the armature of legs 1–4 the Roman numerals indicate spines and the Arabic numerals represent setae.

Family Clausidiidae Embleton, 1901  
*Foliomolgus*, new genus

*Diagnosis.*—Clausidiidae. Body cyclopiform, relatively large, 9-segmented in female and 10-segmented in male. Prosome composed of cephalothorax and 3 metasomites. Fifth pedigerous somite of female with dorsal hood. Antennule 7-segmented; setation as for the species. Antenna 4-segmented; third segment with 1 claw and 3 setae; terminal segment atrophied, armed with 4 spiniform setae and 3 simple setae. Labrum reduced, incompletely covering oral appendages. Mandible with atrophied terminal process and 3 foliaceous subter-

mental elements. Paragnath encircling mouth, with 2 lobate processes on inner margin. Maxillule distally bilobed, with 3 and 5 setae on respective lobes. Maxilla 2-segmented, simplified, and armed with 1 seta on basal segment and 2 setae on digitiform distal segment. Maxilliped absent in female. Male maxilliped of well-developed and composed of 4 segments, including terminal claw. Legs 1–4 with 3-segmented rami; setation as for the species. Leg 5 with 1 seta on basal segment and 4 setae on distal segment. Basal segment of male leg 5 fused with fifth pedigerous somite. Male leg 6 represented by 1 seta on genital flap.

*Etymology.*—The generic name *Foliomolgus* is a combination of *folium* (=leaf in Latin) and *molgus* (the ending of many generic names of copepod associates). It alludes to the foliaceous subterminal elements on the mandible in both sexes. The gender is masculine.

*Type species.*—*Foliomolgus cucullus*, new species

*Foliomolgus cucullus*, new species

Figs. 1–3

*Type specimens.*—One female and two males found on the external surface of the polychaete *Marphysa sanguinea* (Montagu) collected from the intertidal coral sands at Sinhung-ri on the northern shore of Jeju Island (approximately 33°33'N, 126°39'E), on 3 Jun 2000. Holotype female (USNM 309082; left antennule, left antenna, and oral appendages dissected out and mounted on a slide) and allotype (USNM 309083; an intact male) have been deposited in the National Museum of Natural History, Smithsonian Institution. Dissected paratype (one male) is retained in the collection of the author.

*Female.*—Body (Fig. 1A) cycloform, 2.67 mm long. Greatest width 1.02 mm. Prosome composed of cephalothorax and three pedigerous somites. Rostral area of cephalosome produced anteriorly. Prosomal somites with well developed epimera. Epimera of second and third pedigerous so-

mites with pointed posterior corners. Epimeron of fourth pedigerous somite with rounded corners. Urosome (Fig. 1C) slender and five-segmented. Fifth pedigerous somite 405  $\mu\text{m}$  wide, characteristically with dorsal hood (487  $\mu\text{m}$  wide) covering most of dorsal surface of fifth pedigerous somite and anterior part of genital double-somite (Fig. 1B). Genital double-somite 335  $\times$  295  $\mu\text{m}$ , widest in anterior third, then tapering posteriorly. Genital area located laterally, invisible from dorsal and ventral views. Three abdominal somites 210  $\times$  165, 162  $\times$  142, and 115  $\times$  115  $\mu\text{m}$ , respectively. Anal somite with spinules along posteroventral border. Caudal ramus slender, divergent, 221  $\times$  40  $\mu\text{m}$  (5.53:1), with parallel lateral margins and 6 setae. Posteroventral border of caudal ramus armed with several denticles (Fig. 1D). All caudal setae naked. One of terminal setae distinctly larger than others, 1.05 mm long.

Egg sac not seen.

Rostrum wider than long, rounded posterior margin (Fig. 1E). Antennule (Fig. 1F) 7-segmented, 731  $\mu\text{m}$  long, with armature formula 5, 15, 6, 3, 4+1 aesthetasc, 2+1 aesthetasc, and 7+1 aesthetasc. Antenna (Fig. 2A) 4-segmented, elongate, with armature formula 1, 1, 3+1 claw, and 7. First and second segments slender, each about 3 times as long as wide. Seta on these segments relatively small and naked. Third segment armed with spinules on inner margin. Claw on this segment prominent, one of three setae very small. Fourth segment originating from proximal part of outer margin of third segment, wider than long, armed terminally with 4 spiniform setae and 3 simple setae, outermost seta plumose.

Labrum (Fig. 2B) reduced, distinctly shorter than wide, covering only part of oral appendages. Mandible (Fig. 2C) armed with 1 terminal fleshy, atrophied element tipped with a small claw-like process, and 3 long, very thin, foliaceous subterminal elements covered with minute spinules on all surfaces. Paragnath (Fig. 2D) with 2 hairy lobes on medial side. Maxillule (Fig. 2E) taper-

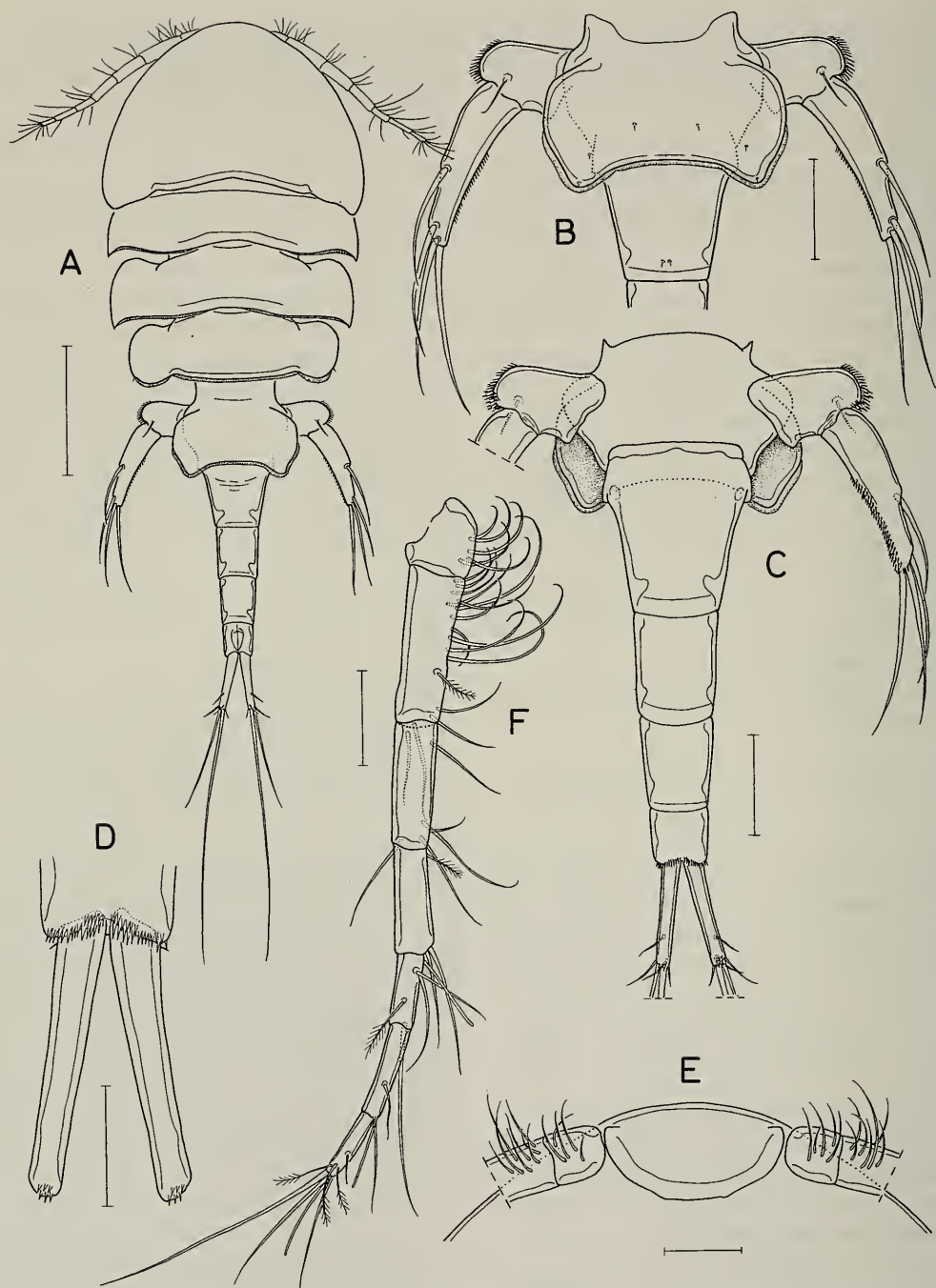


Fig. 1. *Foliomolgus cucullus*, new genus, new species, female. A, habitus, dorsal; B, anterior part of urosome, dorsal; C, urosome, ventral; D, caudal rami, ventral; E, rostral area, ventral; F, antennule. Scale bars: A, 0.5 mm; B, C, 0.2 mm; D-F, 0.1 mm.

ing, proximally with several setules, and terminally bilobed, with 5 setae (3 lateral ones larger) on anterior lobe and 3 setae on posterior lobe. Maxilla (Fig. 2F) 2-segmented. Basal segment greatly expanded proximally, roughly triangular, with 1 terminal seta. Distal segment terminally truncated and sclerotized, and armed with 3 unequal lateral setae; terminal portion of distal segment covered with numerous, minute spinules (Fig. 2G). Maxilliped absent.

Leg 1 (Fig. 2H), leg 2 (Fig. 3A), leg 3, and leg 4 (Fig. 3B) with 3-segmented rami. All these legs spiniferous. All legs with 1 large inner coxal seta; those of legs 1–3 plumose on one side and weakly spinulated on the other side. Inner spine on basis of leg 1 shorter than first endopodal segment of same leg. Posteromedian part of basis of legs 1–4 ornamented with spinules. Each leg with endopod distinctly longer than exopod. Formula of armature of these legs as follows:

- Leg 1:           coxa 0–1; basis 1–I;  
                  exp. I–0; I–1; I, 7  
                  enp. 0–1; 0–1; I, 5
- Leg 2 & 3:       coxa 0–1; basis 1–0;  
                  exp. I–0; I–1; II, 7  
                  enp. 0–1; 0–2; III, 3
- Leg 4:           coxa 0–1; basis 1–0;  
                  exp. I–0; I–1; I, 7  
                  enp. 0–1; 0–2; III, 2

Leg 5 2-segmented (Fig. 1B, C). Basal segment articulating with fifth pedigerous somite, distally armed with 1 small seta and spinules. Distal segment elongate, tapering, armed with 1 outer lateral and 3 terminal setae; all setae naked, and as long as or shorter than distal segment. Leg 6 not seen.

*Male*.—Body (Fig. 3C) similar to that of female. Length 2.20 mm. Urosome (Figure 3D) 6-segmented. Genital somite  $175 \times 317 \mu\text{m}$ , distinctly narrower than fifth pedigerous somite, without dorsal hood. Genital flap with numerous spinules near inner margin. Four

abdominal somites  $154 \times 187$ ,  $175 \times 155$ ,  $150 \times 135$ , and  $104 \times 113 \mu\text{m}$ , respectively. Caudal ramus  $198 \times 33 \mu\text{m}$  (6.0:1), more slender than that of female.

Antennule with 1 additional seta on distal portion of third segment. Antenna, labrum, paragnath, and maxillule similar to those of female. Mandible (Fig. 3E) with more prominent claw on tip of terminal element. Maxilla (Fig. 3F) with first segment not expanded, but distal segment as in female. Maxilliped (Fig. 3G) 4-segmented. First segment with 1 long distal seta. Second segment triangular, greatly expanded proximally, strongly tapering, with a flat, thin protrusion at inner proximal corner, and armed with 2 rows of thin, truncate spinules (one row shorter), 2 rows of epicuticular extensions and 2 small setae (one in the middle, the other smaller one in distal part) on inner margin. Third segment short and unarmed. Terminal segment forming a claw bearing proximally 2 setae and 1 distal membranous process.

Legs 1–4 as in female. Basal segment of leg 5 completely fused with fifth pedigerous somite, leaving only 1 distal seta. Free distal segment broader and shorter than that of female (Fig. 3D). Leg 6 represented by 1 stiff seta on terminal corner of genital flap.

*Etymology*.—The specific name *cucullus* (=hood in Latin) alludes to the hood-like dorsal coverture on the fifth pedigerous somite of the female.

## Discussion

The genus *Hemicyclops* best illustrates general features of the family Clausidiidae (Humes, 1987). The new genus *Foliomolgus* belongs to the Clausidiidae, because it shares with *Hemicyclops* the important characters such as the 7-segmented antennule, 3-segmented rami on legs 1–4, inner spine on the basis of leg 1, 4-segmented antenna armed with four and seven elements respectively on the third and terminal segments, and 5+3 setae on the maxillule.

Humes & Huys (1992) recognized seven

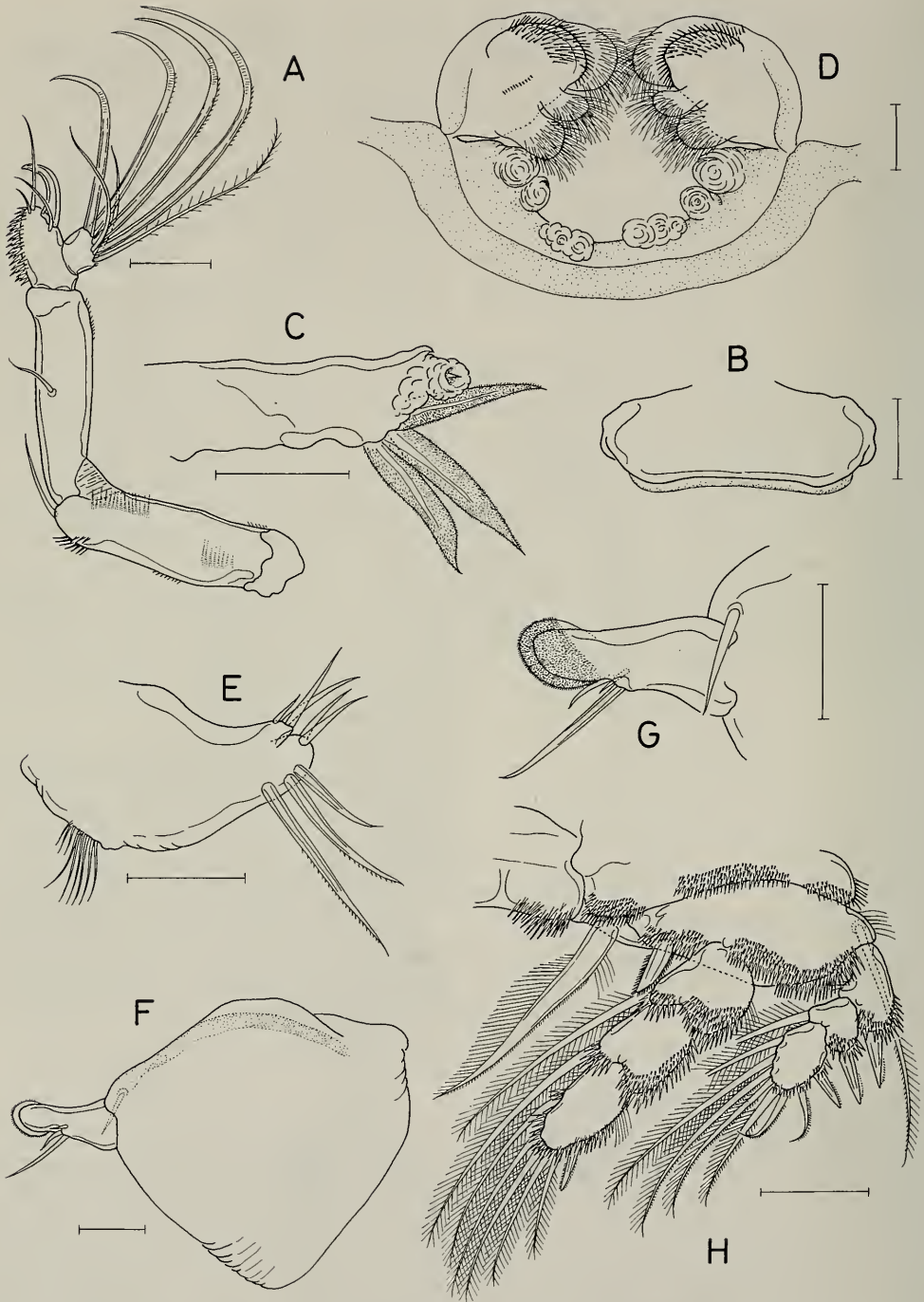


Fig. 2. *Foliomolgus cucullus*, new genus, new species, female. A, antenna; B, labrum; C, mandible; D, mouth area, including paragnaths; E, maxillule; F, maxilla; G, distal part of maxilla; H, leg 1. Scale bars: A-C, E-F, 0.05 mm; D, 0.02 mm; H, 0.1 mm.

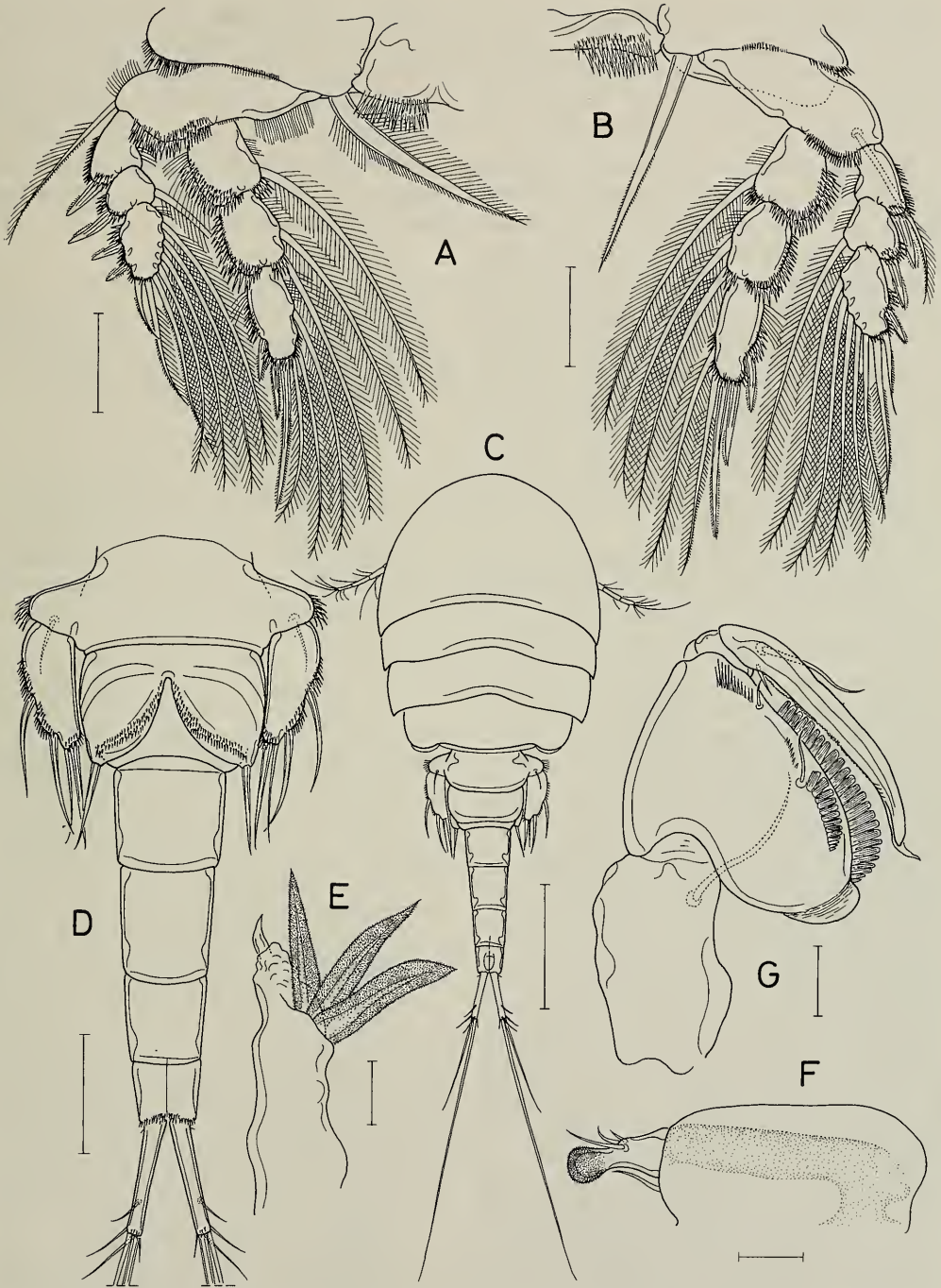


Fig. 3. *Foliomolgus cucullus*, new genus, new species. Female: A, leg 2; B, leg 4. Male: C, habitus, dorsal; D, urosome, ventral; E, mandible; F, maxilla; G, maxilliped. Scale bars: A, B, 0.1 mm; C, 0.5 mm; D, 0.2 mm; E, 0.02 mm; F, G, 0.05 mm.

genera as valid in the Clausidiidae: *Clausidium* Embleton, *Conchylurus* Bocquet & Stock, *Doviella* Rocha, *Hemicyclops* Boeck, *Hippomolgus* Sars, *Hyphalion* Humes, and *Leptinogaster* Pelseneer. In the same year, Ho & Wardle (1992) added a new genus *Pholadicola* to this family. Because one of these genera, *Doviella*, is a junior synonym of *Clausia* of the Clausiidae (Kim, 2001), the Clausidiidae currently consists of seven genera. In the absence of a maxilliped in the female and having a claw on the third segment of the antenna, *Foliomolgus* is comparable to the genera *Leptinogaster* and *Pholadicola*. However the latter two genera, both associates of bivalves, carry a 6-segmented antennule, and fewer setae on the antenna, maxillule and legs.

The morphology of the mandible, bearing the rudimentary dorsal (posterior) element (claw) and three well-developed foliaceous ventral (anterior) elements, is a unique feature of the new genus *Foliomolgus*. As far as the Clausidiidae and related families, the nereicoliform copepods of Gooding (1963), are concerned, the size reduction of mandibular elements usually involves the ventral ones. The extreme case of this armature reduction, where only the dorsal claw-like element is retained, is exhibited by some genera of Catiniidae, Clausiidae, and Synaptiphilidae. In contrast to this general trend of armature reduction, a mandible similar to that of the new genus may be seen in copepodid I of *Conchylurus* (see Kim, 1994; only three ventral elements are retained in the adult) and the adult of *Myzomolgus* where the dorsal claw is reduced and the ventral elements are developed.

In addition to the mandible, the antenna also is characteristic within the Clausidiidae and related families. In this appendage the third segment is produced distally along the main axis of the appendage; the fourth segment is displaced laterally.

The transformation of the maxilla in which the distal segment is a spatulate lobe,

one of the diagnostic features of the new genus, is a general feature observed in the Clausiidae, Nereicolidae and Serpulidicolidae, the copepods generally associated with the polychaetes. Therefore the similarity of the maxilla in these copepods may be a convergence resulting from the association with similar hosts.

#### Acknowledgement

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## Two new species of the *Canthocamptus mirabilis* group (Copepoda: Harpacticoida: Canthocamptidae) from South Korea

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*Abstract.*—Two new harpacticoid species belonging to *Canthocamptus mirabilis* species group, *C. odaeensis* and *C. incurvisetosus*, are described from South Korea, with an evaluation of the variability of several characters. Both species are assumed to be closely related in sharing the apomorphic characters of the triangular hyaline membrane on the anal operculum and the male-type caudal ramus in females. The occurrence of the *C. mirabilis* group in South Korea is also briefly commented. *Canthocamptus incurvisetosus* is most widely distributed and frequently occurs in mountain waters of South Korea, while *C. odaeensis* is a geographically isolated species. They co-occurred at only one location, where the reproductive isolation of these species is reinforced by character displacements, especially of the female caudal ramus and the ornamentation of the leg 5 exopod.

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The *Canthocamptus mirabilis* group, first identified as “*Attheyella*-like *Canthocamptus*” by Ito & Takashio (1980), was recognized in a series of faunistic studies on mountain harpacticoids in Japan (Ishida 1987, 1989, 1990, 1991; Kikuchi & Ishida 1988, 1994). It comprises several closely related species, occurring with great abundance and frequency in the various mountain water bodies of the Far East. Six species are currently known in this group: *C. mirabilis* Štěrba, 1968 from China; *C. morimotoi* Miura, 1969 from South Korea; and *C. prominulus* Kikuchi, 1993, *C. semicirculus* Kikuchi, 1993, *C. resupinatus* Ishida, 1993, and *C. tomikoeae* Ishida, 1993 from Japan.

In Korea, except for the record of *C. morimotoi* (Miura 1969, Chang 1998), the *mirabilis* group has not been studied in spite of its great abundance and frequent occurrence in the various mountain water bodies. We have fully re-examined the specimens belonging to the *C. mirabilis* group which were gathered from 120 lo-

calities in South Korea since 1986 by the senior author. We confirmed that they comprise five species: *C. semicirculus* Kikuchi; an unrecorded species, to be treated later in another paper, closely resembling *C. mirabilis* Štěrba from China; *C. morimotoi* Miura; and the two new species described here.

Collections were made with a dipnet with no. 10 mesh. All the specimens were dissected, drawn, and measured in lactophenol on a Cobb's hole slide. Figures were drawn with the aid of a camera lucida. Type material has been deposited in the U.S. National Museum of Natural History, Smithsonian Institution (USNM) and the Natural History Museum of Ewha Womans University, Seoul (EWNMH).

The caudal ramus, or furca, of species of the *C. mirabilis* group commonly show clear sexual dimorphism, but females in some populations have a furca similar to the males, a reversal of this secondary sexual character state (Ito & Takashio 1980, Ishida 1991). The normal furca and the male-type furca of females are abbreviated in the text

and figure legends to Fn and Fr, respectively. Abbreviations of enp 1–3 or exp 1–3 are used in the description to denote the first to third endopodal or exopodal segment of each leg.

*Canthocamptus odaeensis*, new species

Figs. 1–4

*Material examined.*—Twelve ♀♀, 7 ♂♂, foothill spring at Kangnung City (37°45' 59"N, 128°52'27"E), 23 Sep 1993, leg. C. Y. Chang, including: Holotype ♀ (USNM 310129), allotype ♂ (USNM 310130), and paratypes (3 ♀♀, USNM 310131; 8 ♀♀ & 6 ♂♂, EWNMH 60262).

*Additional material.*—Seven ♀♀, 3 ♂♂, streamlet at Mt. Odae, 2 Oct 1992, C. Y. Chang; 1 ♀, 3 ♂♂, spring at Kujeol-ri, Cheongseon, 23 Sep 1993, C. Y. Chang; 5 ♀♀, 3 ♂♂, Chodang Cave, Samcheok, 12 May 1995, H. S. Rho; 5 ♀♀, 2 ♂♂, same as type locality, 21 Jul 1995, C. Y. Chang; 3 ♀♀, 1 ♂, streamlet near Woljungs Temple, Mt. Odae, 28 Jul 1999, J. M. Lee & Y. H. Song; 5 ♀♀, 6 ♂♂, Mureung Valley, Mt. Duta, 9 Oct 1999, J. M. Lee & Y. H. Song; 3 ♀♀, 2 ♂♂, trickle near Hwansun Cave, Samcheok, 9 Oct 1999, J. M. Lee & Y. H. Song; 2 ♀♀, 2 ♂♂, Gongsujeon Valley, Yangyang, 6 Oct 2000, C. Y. Chang. All additional material is retained in the research collection of C. Y. Chang, except 5 ♀♀ and 3 ♂♂ from Mt. Odae (2 Oct 1992) in the collection of T. Ishida.

*Female.*—Body (Fig. 1A) length range 0.64–0.69 mm ( $0.66 \pm 0.04$  mm,  $N = 8$ ), excluding rostrum and furcal setae; broadest at posterior margin of cephalothorax, tapering posteriorly. Prosoma elliptical. Cephalothorax somewhat protruding anteriorly, slightly longer than succeeding 3 thoracic somites combined. Rostrum not prominent, directed anteroventrally, not distinct at base. Dorsal and lateral surfaces of thoracic somites with few sensilla; posterior part of cephalothorax bearing narrow hyaline membrane with 10–12 longitudinal folds along margin, each bearing 1 sensil-

lum at its tip. Genital double somite moderately expanded laterally and slightly broadened posteriorly, 1.25 times wider than long, subdivided by pair of lateral sutures, each suture with pair of sensilla near its dorso-medial end. Genital area T-shaped, flanks rather short. Each abdominal somite furnished with 1 row of spinules along laterodistal corner, and hyaline fringes with crenate posterior margins (Fig. 1B). Disto-medial corner of ventral side of anal somite bearing 3–4 sharp spinules (Fig. 1C), relatively undeveloped in comparison with those of *C. morimotoi* (cf. Chang 1998) or *C. mirabilis* sensu Ito & Takashio. Anal operculum convex; hyaline membrane (Fig. 1C) forming obtuse-angled triangle, its tip slightly passing dorsal seta of caudal ramus in lateral view (Fig. 1B).

Fr (Fig. 1C) shaped as an inverted bottle; about 1.5 times as long as wide, armed with 1 crescent row of slender spinules along medial surface; outer caudal seta ornamented with 2–3 pairs of sharp secondary spinules, directed outward and situated from proximal 1/5 to 1/3 of the seta (Figs. 1B, C); terminal seta stout, slightly bent and constricted near base; inner caudal seta bare. Fn somewhat suboval (Fig. 1D), about 1.3 times as long as wide. About 6 spinules arranged obliquely at laterodistal corner of dorsal surface. Outer terminal seta rather straight, not bent, with 3 secondary spinules on inner margin and 4–5 acute spinules on outer margin.

Antennule (Fig. 2A) of 8 segments, bearing 1 aesthetasc on anterodistal margin of fourth article, its tip not reaching distal end of antennule. Exopod of antenna (Fig. 2B) distinctly 2-segmented; first segment markedly slender, bearing 1 plumose seta on inner distal edge with 1 spinule on laterodistal margin; second segment bearing 2+1 plumose setae. Labrum subtriangular, with blunt hirsute tip, furnished with 4 subdistal spinules. Mandible, maxillule, maxilla, and maxilliped (Fig. 2C–F) with typical characteristics of genus *Canthocamptus* and showing no significant discrepancy from re-

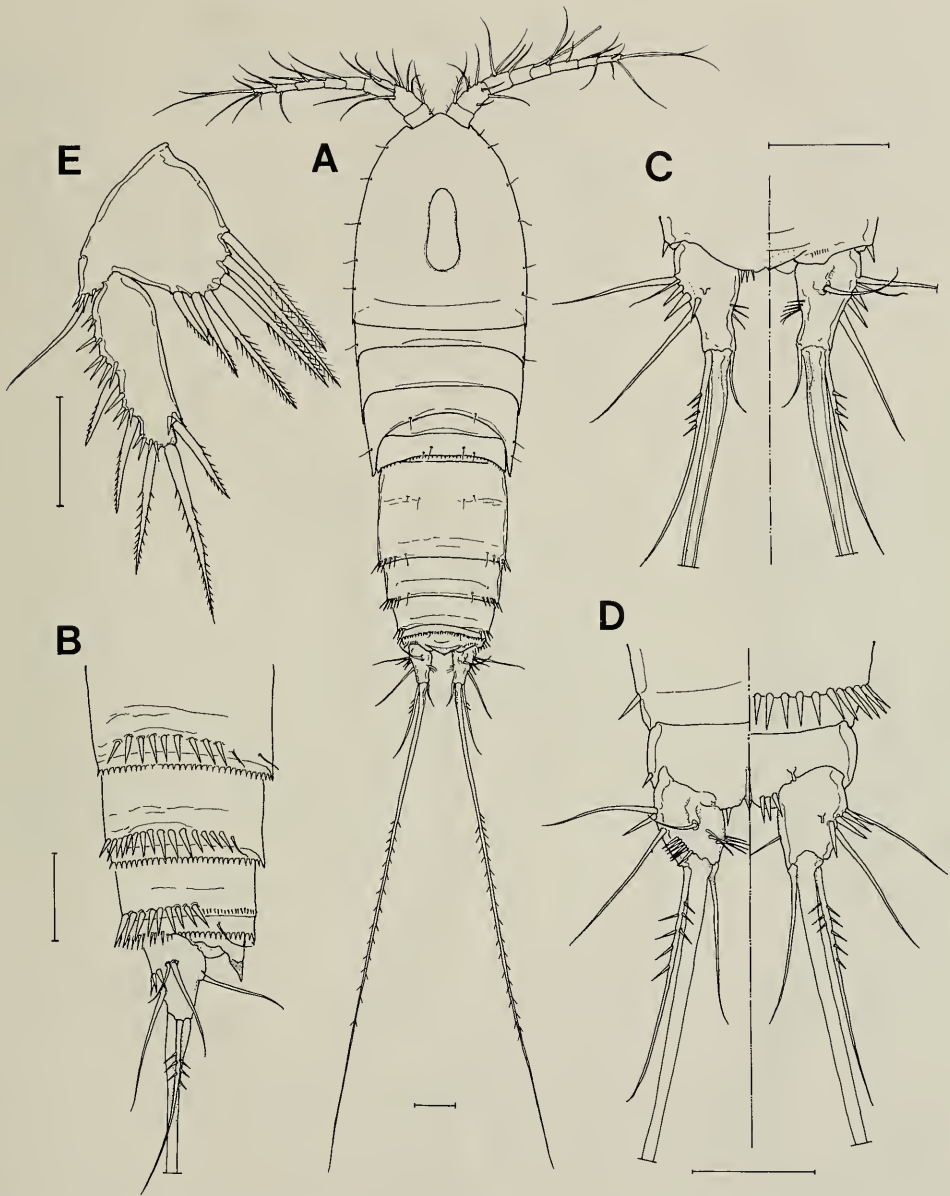


Fig. 1. *Canthocamptus odaensis*, Female. A, Habitus (dorsal); B, Urosome (lateral); C, Anal somite and caudal ramus, showing both ventral (left) and dorsal (right) sides (Fr type); D, Anal somite and caudal ramus (Fn type); E, Female leg 5. Scale bars = 0.05 mm.

lated members of *mirabilis* group (cf. Ito & Takashio 1980, Chang 1998).

Exopod and endopod of legs 1–4 each consisting of 3 segments, except endopod of leg 4 with 2 segments. Leg 1 (Fig. 2G) enp 1 as long as exopod, with 1 plumose seta on distal 1/5 of inner margin; enp 2

with 1 plumose seta on inner distal corner and 3 sharp spinules on outer edge; enp 3 slender, bearing 2 geniculate spines and 1 plumose seta. Exp 1 longer than next two segments; exp 2 with 1 inner seta and 1 outer spine; exp 3 bearing 2 outer spines and 2 geniculate setae. Distal edge of inter-

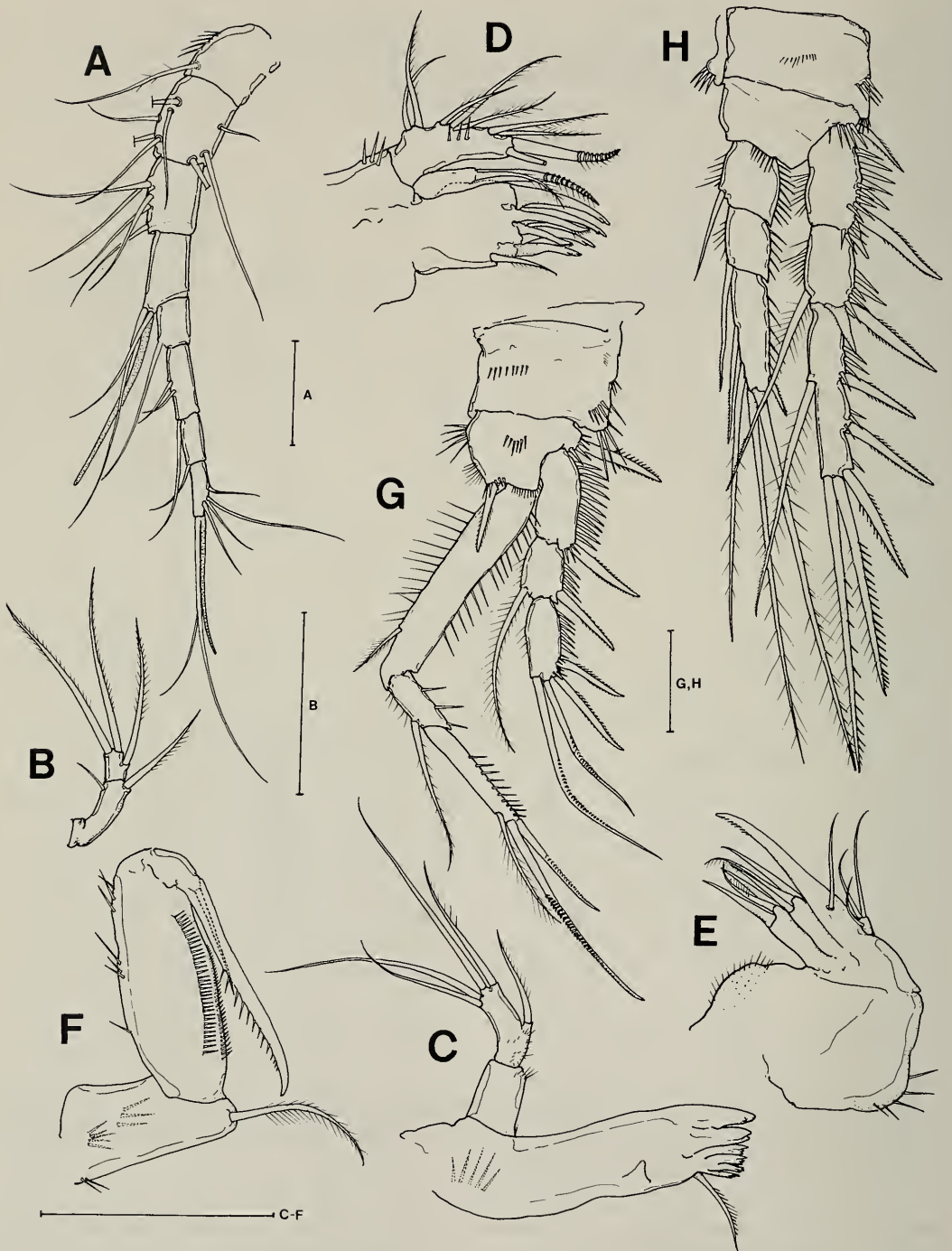


Fig. 2. *Canthocamptus odaeensis*, Female. A, Antennule; B, Exopod of antenna; C, Mandible; D, Maxillule; E, Maxilla; F, Maxilliped; G, Leg 1; H, Leg 2. Scale bars = 0.05 mm.

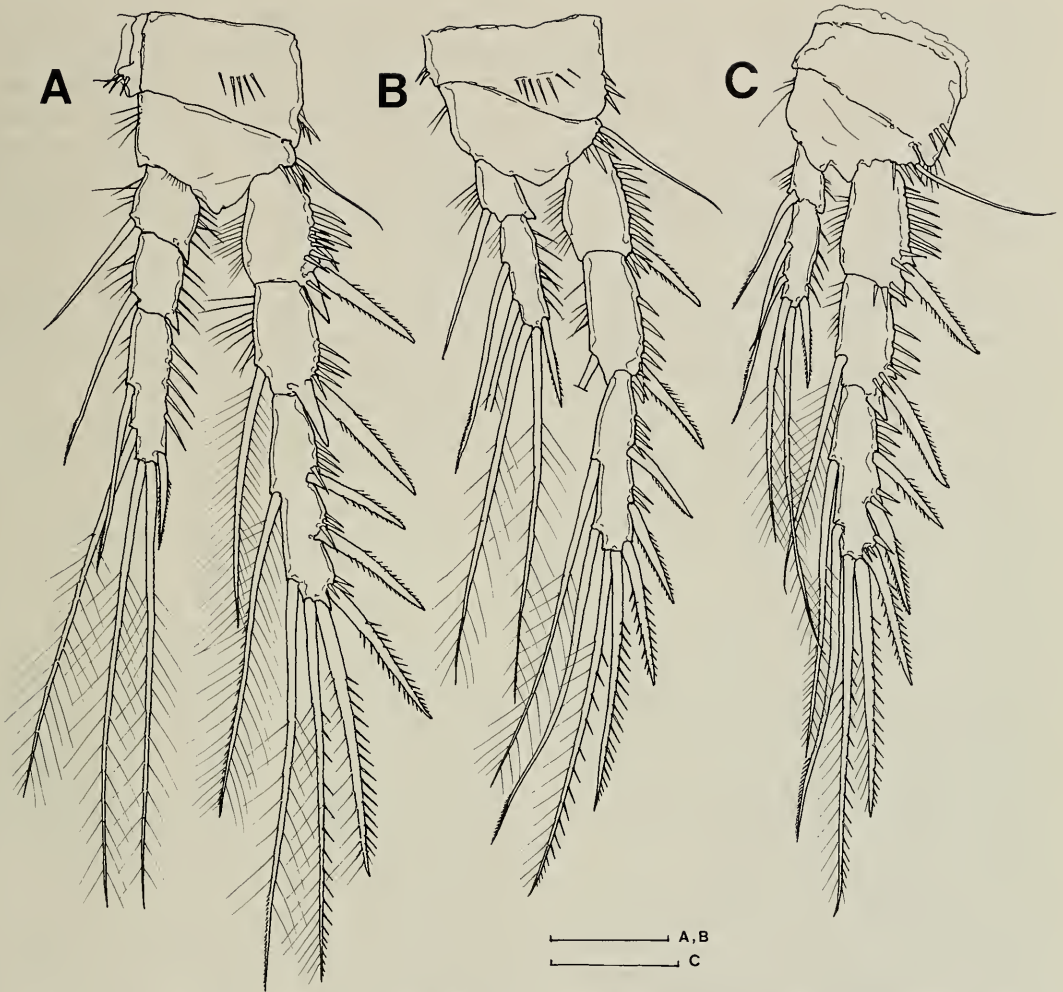


Fig. 3. *Canthocamptus odaensis*. A, Female leg 3; B, Female leg 4; C, Male leg 4. Scale bars = 0.05 mm.

coxal sclerites of legs 2–4 with several spinules. Ornamentation of legs 2–4 as follows (in armature formula, Roman numerals indicate spines and Arabic numerals represent setae):

Leg 2: basis I-0; exp I-0; I-1; III, 2, 1  
 enp 0-1; 0-1; I, 2, 2

Leg 3: basis 1-0; exp I-0; I-1; III, 2, 2  
 enp 0-1; 0-1; I, 2, 2

Leg 4: basis 1-0; exp I-0; I-1; III, 2, 2  
 enp 0-1; I, 2, 2

Distal end of leg 5 baseoendopod (Fig.

1E) not reaching middle of exopod; baseoendopod not confluent at its base, connected by intercoxal sclerite; bearing 6 spiniform setae, of which outermost two setae shortest and next innermost seta longest. Exopod rather oblong, slightly tapering distally, about 2.7 times as long as broad; inner margin slightly swollen; armed with 5 setae, distalmost seta of which slightly longer than exopod; 2 spinules usually present on distomedial corner on ventral side of exopod near base of inner seta.

*Male*.—Body (Fig. 4A) length from 0.63–0.68 mm ( $0.64 \pm 0.04$  mm,  $N = 6$ ). Overall appearance like female, except with

more slender caudal ramus. Hyaline membrane on anal operculum (Fig. 4B) triangular with convex margin, its tip reaching level of dorsal seta. Leg 2 (Fig. 4C), enp 1 with 1 inner seta; enp 2 bearing 3 inner, 2 long terminal setae, with outer spinules; 2 inner setae of enp 2 and inner seta of exp 3 modified with pectinate tip. Leg 3 (Fig. 4D), enp 2 armed with 1 acute spiniform seta and 1 process (apophysis) with terminal barbs, not extending beyond exp 3; enp 3 elongate, slightly longer than combined lengths of two proximal segments, tapering distally, ending with 2 plumose setae; exp 2 armed with stout spiniform process on outer distal corner, its tip usually not reaching or rarely reaching slightly beyond distal margin of exp 3; exp 3 with 2 inner setae, distal one bent with pectinate tip. Leg 4 (Fig. 3C) nearly same shape as that of female, including outer terminal seta on exp 3 armed with more than 18 spinules on outer margin of seta; distal inner seta of exp 3 modified with pectinate tip. Baseoendopodal lobe of leg 5 (Fig. 4E) triangular, not reaching middle of exopod; bearing 2 spiniform setae, inner seta about 1.3 times longer than outer; inner margin bare. Exopod 2.1 times longer than broad, armed with 6 setae in total, consisting of 1 weak plumose seta at about middle of medial margin, 1 inner distal, 2 terminal, and 2 outer spiniform setae. Leg 6 (Fig. 4B) represented by small plate bearing 1 spine and 2 slender setae.

*Variability.*—Females with normal-type caudal ramus (Fn) were rarely observed (fewer than 1% of all specimens examined). No significant variation was observed in the caudal ramus among the specimens examined, except that about 8% of Fr lacked the medial spinules (while all males examined had the spinules). The spiniform process on the male leg 3 exp 2 usually did not reach or reached only slightly beyond the tip of the leg 3 exp 3. Most females (78% of specimens examined) had two spinules on the inner distal edge of the ventral surface of the leg 5 exopod.

The ornamentation of the outer terminal caudal seta was characteristic and consistent in all the specimens examined, as was the unmodified outer terminal seta (armed with about 18 or more secondary spinules on outer margin of the seta) on the male leg 4 exp 3. No particular difference was detected in the major ornamentation of legs 2–4.

*Etymology.*—The specific name is taken from Mt. Odae, because the distribution of this new species is confined to Mt. Odae and the surrounding area.

*Remarks.*—Affinities with related species are discussed together with the next species.

*Canthocamptus incurvisetosus*, new  
species  
Figs. 5–6

*Material examined.*—Eleven ♀♀, 5 ♂♂, mountain streamlet in Seonamsa Valley, Mt. Jogye (34°59'26"N, 127°19'53"E), 13 Jan 2000, leg. C. Y. Chang, J. M. Lee & Y. H. Song, including: holotype ♀ (USNM 310132), allotype ♂ (USNM 310133), and paratypes (3 ♀♀, USNM 310134; 7 ♀♀ & 4 ♂♂, EWNMH 60261).

*Additional material.*—Eleven ♀♀, 9 ♂♂, spring, Ssangyesa Temple, Mt. Chiri, 21 Jan 1987, C. Y. Chang; 3 ♀♀, streamlet, Mt. Wolchul, 7 Feb 1987, C. Y. Chang; 9 ♀♀, 4 ♂♂, spring, Mt. Namdogyu, 8 Aug 1987, C. Y. Chang; 5 ♀♀, 4 ♂♂, trickle in Seonamsa Valley, Mt. Jogye, 31 Jan 1991, C. Y. Chang; 3 ♀♀, 2 ♂♂, Pongrae Fall, Ulung I., 3 Mar 1995, C. Y. Chang; 3 ♂♂, streamlet, Mt. Chiak, 27 Jun 1995, C. Y. Chang; 5 ♀♀, 4 ♂♂, streamlet, Mt. Sorak, 3 May 1998, S. M. Yoon; 4 ♀♀, 3 ♂♂, trickle in Naewonsa Valley, Mt. Chiri, 26 Oct 1999, C. Y. Chang & J. M. Lee; 10 ♀♀, 6 ♂♂, Mt. Seongju, Poryong, 20 Nov 1999, C. Y. Chang. All additional material is retained in the research collection of C. Y. Chang, except 3 ♀♀ and 2 ♂♂ from Mt. Chiri (21 Jan 1987) in the collection of T. Ishida.

*Female.*—Body length 0.69–0.73 mm

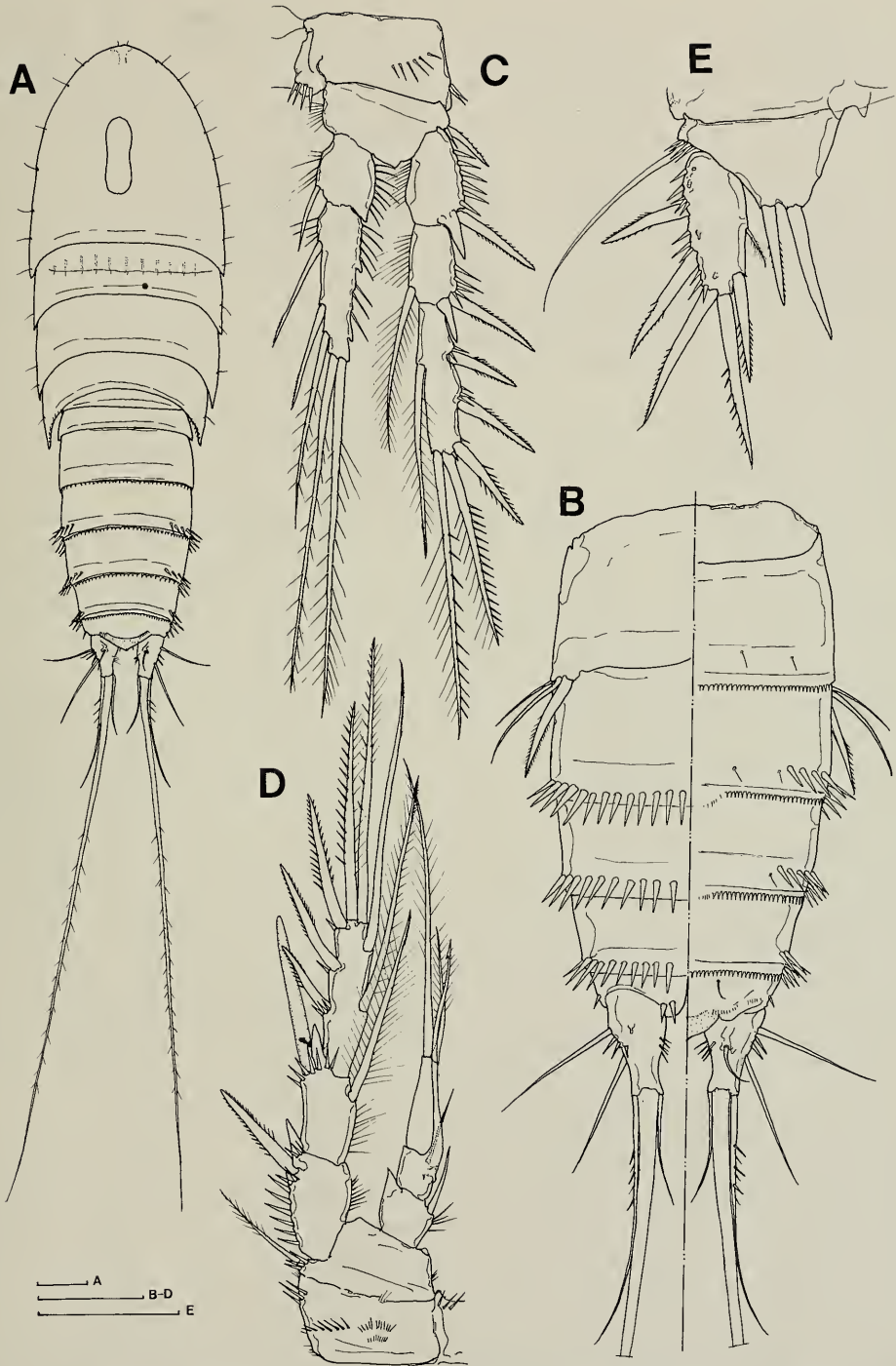


Fig. 4. *Canthocamptus odaensis*, Male. A, Habitus (dorsal); B, Urosome showing both ventral (left) and dorsal (right) sides; C, Leg 2; D, Leg 3; E, Leg 5. Scale bars = 0.05 mm.

( $0.71 \pm 0.02$  mm,  $N = 7$ ), excluding rostrum and caudal setae; overall appearance and mouthparts not showing significant differences from those of preceding species. Each abdominal somite bearing 1 row of spinules along laterodistal margin, and adorned with crenate hyaline frill (Fig. 5A). Posteromedial corner of ventral side of anal somite bearing 4–5 acute spinules. Anal operculum convex, furnished with hyaline membrane (Figs. 5B, C) forming obtuse-angled triangle with convex margin, but its tip projecting sharply.

Caudal ramus of normal type (Fig. 5B) ovoidal, about 1.76 times as long as wide, ornamented with crescent row of slender spinules along medial surface; laterodistal part of dorsal surface adorned with 6–9 spinules; dorsal keel over dorsal seta not prominent; outer terminal caudal seta twisted and curved inward, ornamented with 2–3 long, inward-directed secondary spinules on medial face of the seta; terminal seta slightly bent and constricted near base; inner caudal seta bare and strongly bent near its base. Fr (Fig. 5C) shaped as inverted bottle, about 1.5 times as long as wide, without spinules on outer distal part of dorsal surface; with or without crescent row of slender spinules along medial surface, this row sometimes present on only one ramus; other characters same as those of normal type ramus.

Segmentation and ornamentation of legs 1–4 exactly as those of preceding species. Leg 5 (Fig. 5D) exopod elongate, a little tapering distally, about 3.2 times as long as broad; inner margin slightly swollen; armed with 5 setae, of which inner distal seta always slightly shorter or as long as exopod; inner seta located near distomedial edge of exopod; spinules on distomedial corner of exopod usually absent, but sometimes 2–3 spinules present. Baseoendopod reaching about  $\frac{1}{4}$  length of exopod; baseoendopod not confluent at its base, connected by intercoxal sclerite; bearing 6 spiniform setae, two outermost setae smallest and two innermost longest.

*Male.*—Body (Fig. 6A) length from 0.54–0.63 mm ( $0.59 \pm 0.05$  mm,  $N = 5$ ). Hyaline membrane of anal operculum (Fig. 6B) triangular, its tip extending beyond level of dorsal setae of the caudal ramus. Distomedial corner of anal somite bearing 3–4 spinules, these relatively stronger than corresponding spinules of female. Caudal ramus (Fig. 6B) rather elongate, tapering posteriorly, about 1.76 times as long as wide, with no spinule row along medial surface; dorsal keel not prominent and dorsal surface smooth except for dorsal seta; outer terminal caudal seta normal, i.e., not twisted and not curved inward as in female, and ornamented with 2–3 outwardly directed secondary spinules; inner caudal seta unarmed. Leg 3 (Fig. 6D) exp 2 armed with stout spiniform process on outer distal corner, its tip extending far beyond distal end of exp 3. Leg 4 (Fig. 6E) exp 3 outer terminal seta with 3–4 sharp and strong spinules on outer margin. Other characters of legs 2–4 not showing significant discrepancies from preceding species. Baseoendopod of leg 5 (Fig. 5E) protruding, but not reaching  $\frac{1}{3}$  of exopod; bearing 2 terminal spiniform setae, inner seta about 1.43 times longer than outer seta; inner margin bare. Exopod 2.4 times longer than broad, armed with 6 setae in total, these consisting of 1 weak plumose seta on inner middle, 1 inner distal, 2 terminal, and 2 outer spiniform setae. Leg 6 (Fig. 6F) a small plate bearing 1 stout spine and 2 slender setae; spine 1.4 times longer than next seta.

*Variability.*—Fn always possesses the spinule array on the medial surface of the caudal ramus, while 38% of Fr (male-type caudal ramus) were unarmed, as were more than 95% of the males. 18% of Fr had spinules on one caudal ramus but not on the other. The spinule arrangement on the outer distal corner was absent in Fr, and sometimes also absent in Fn; rarely individuals possessed both the different types of ornamentation. Usually (in more than 95% of cases) the spiniform process on the outer distal edge of the male leg 3 exp 2 much



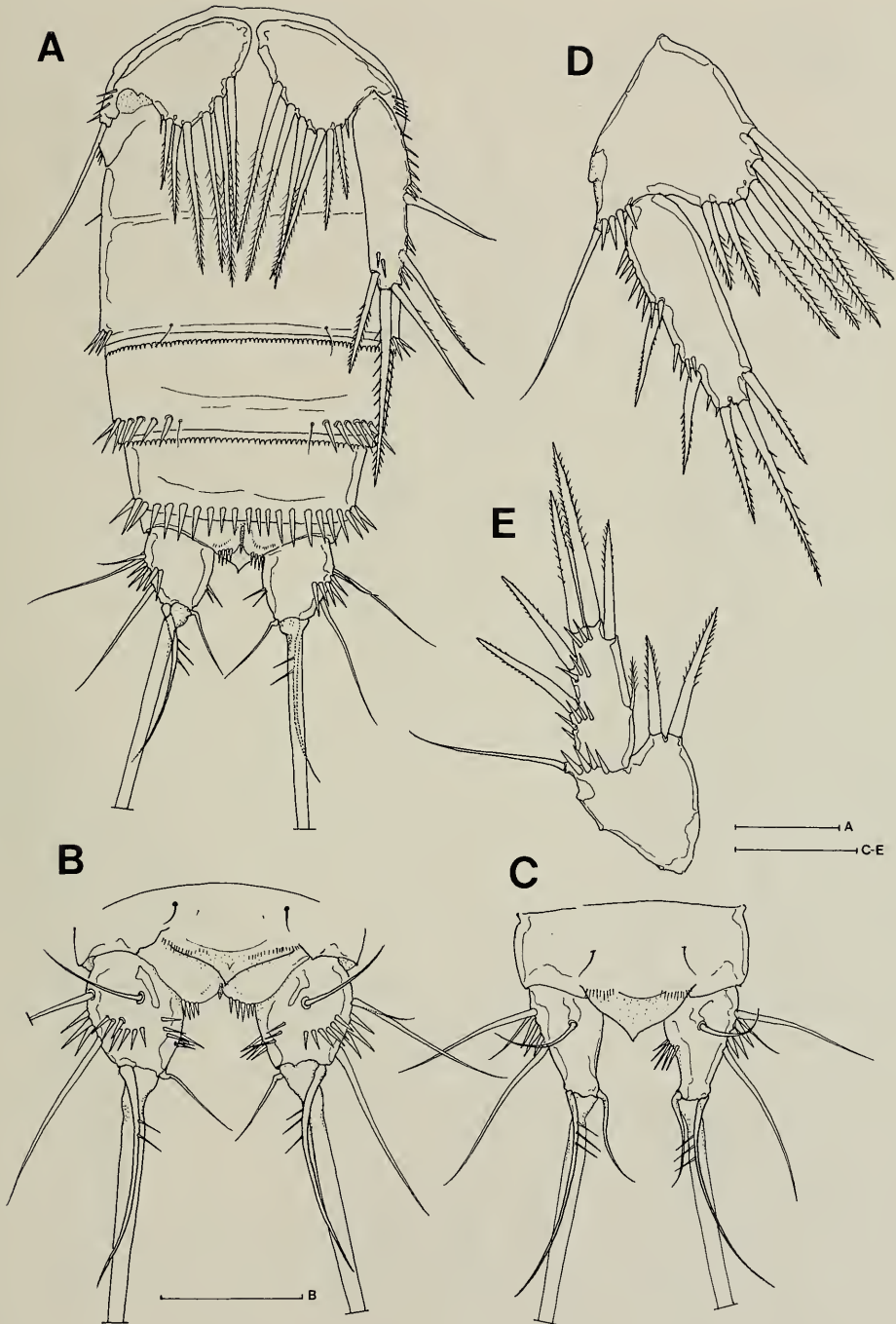


Fig. 5. *Canthocamptus incurvisetosus*. A, Urosome of female (Fn type, ventral); B, Anal somite and caudal ramus of female (Fn type, dorsal); C, Anal somite and caudal ramus of female (Fr type, dorsal); D, Female leg 5; E, Male leg 5. Scale bars = 0.05 mm.

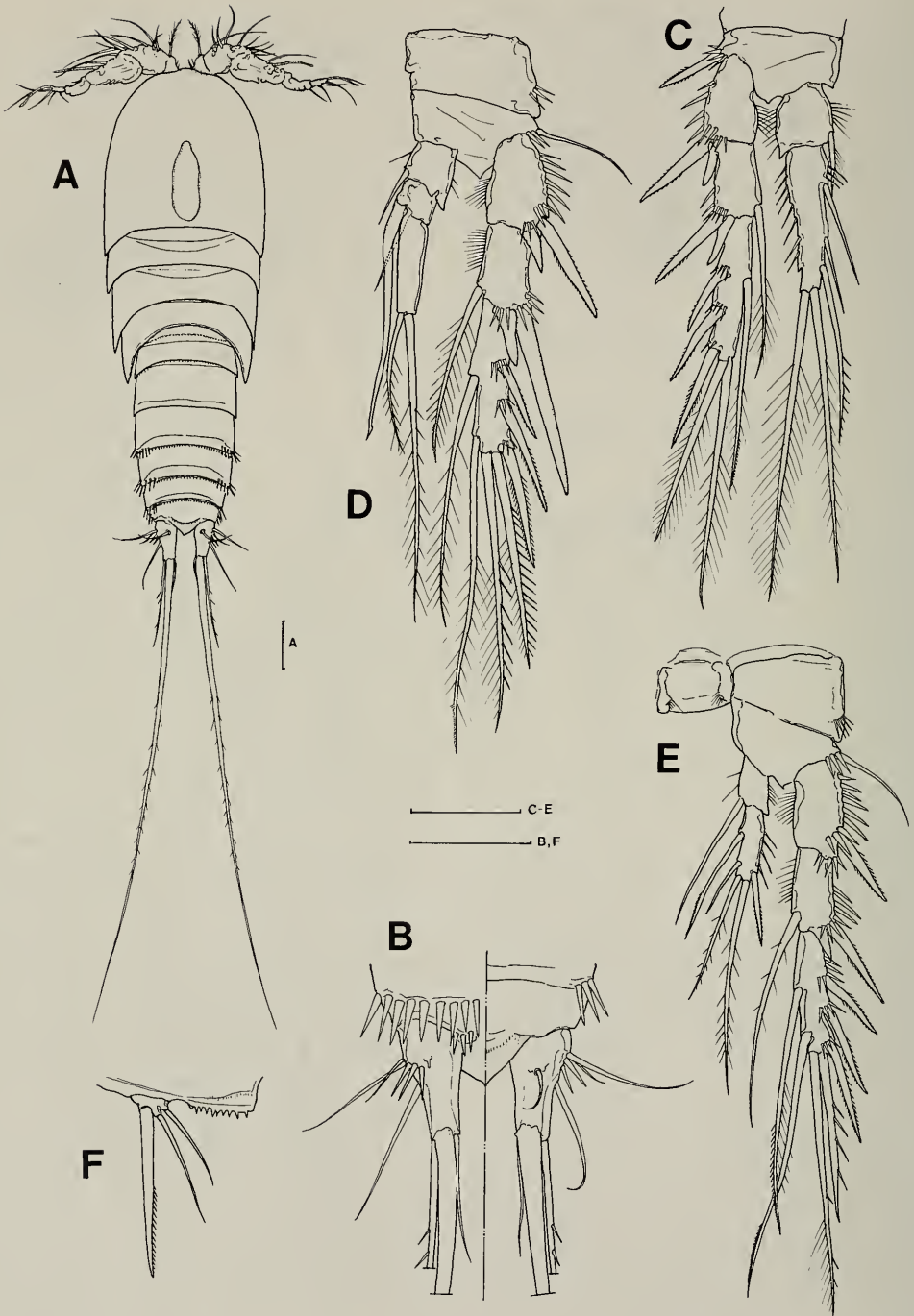


Fig. 6. *Canthocamptus incurvisetosus*, male. A, Habitus (dorsal); B, Anal somite and caudal ramus, showing both ventral (left) and dorsal (right) sides; C-E, legs 2-4; F, leg 6. Scale bars = 0.05 mm.

exceeded the tip of leg 3 exp 3. Only 28% of specimens examined had 2–3 spinules on the inner distal edge of the ventral surface of the female leg 5 exopod.

All individuals examined had the typical shape of twisted and inward-curved outer terminal caudal setae as described and illustrated above, with 2–3 secondary spinules, or exceptionally with 4 spinules. The outer terminal seta on male leg 4 exp 3 was also consistently furnished with 3–4 sharp strong spinules on its outer margin. No particular difference was detected in the major ornamentation of legs 2–4.

*Etymology.*—The proposed specific name is taken from the Latin *incurvus* (bent inward) and *setosus* (bearing seta), which alludes to the possession of the twisted and inward-curved outer terminal seta of the female caudal ramus, the distinctive characteristic of this species.

*Remarks.*—In having the apomorphic character-combination of the triangular hyaline membrane on the anal operculum and the male-type caudal ramus of the female, both these new species differ from *C. semicirculus* Kikuchi, *C. tomikoeae* Ishida, *C. mirabilis* Štěrba, and an undescribed species from Korea. They share these derived states with *C. morimotoi* Miura, *C. resupinatus* Ishida and *C. prominulus* Kikuchi. The affinities among the former group of four species will be discussed elsewhere, when *C. mirabilis* Štěrba is redescribed on the basis of the newly collected material from type locality near Beijing, China, together with the description of another new Korean species.

*Canthocamptus odaensis* n. sp. shares with *C. morimotoi* a well-developed triangular hyaline membrane on the anal operculum and the normal ornamentation of the outer distal seta of male leg 4 exopod 3 (i.e., not modified with 3–4 sharp and strong secondary spinules on outer margin, but armed with about 18 or more spinules on outer margin). However, females of *C. odaensis* may express one of two different kinds of caudal ramus, the normal-type fe-

male caudal ramus has a spinule row near the distolateral corner of dorsal surface, and the male caudal ramus has medial spinules. Females of *C. morimotoi* express only one kind of caudal ramus, which lacks the spinule row near the distolateral corner of dorsal surface, and the male caudal ramus has smooth medial face without medial spinules. However, it is distinct in showing Fr while the caudal ramus of both sexes are subconical in *C. morimotoi*. In possessing the terminal seta of leg 5 slightly longer than leg 5 exopod and the medial spinules on the caudal ramus of the male, *C. odaensis* is similar to *C. resupinatus*, but is distinguished from that species by the normal outer distal seta on the male leg 4 exopod 3, and the shape of the outer terminal caudal seta.

*Canthocamptus odaensis* resembles *C. prominulus* Kikuchi in having a relatively short spiniform process on the outer distal edge of the male leg 3 exopod 2, but the former species differs from the latter in having an unmodified terminal seta on the male leg 4 exopod 3, and in possessing the terminal seta on female leg 5 exopod slightly longer than the exopod. *Canthocamptus odaensis* is also distinguished from *C. incurvisetosus* by the shape of the outer terminal caudal seta, the presence of a setule array on the medial surface of male caudal ramus, and the relative length of the female leg 5 exopod with its terminal seta.

*Canthocamptus incurvisetosus* closely resembles *C. resupinatus* in the hyaline membrane of the anal operculum and in the ornamentation of the outer distal seta of the last exopodal segment of the male leg 4, together with the twisted and inward-curved outer caudal setae. It differs from *C. resupinatus* in having the male caudal ramus with a smooth medial surface and the female caudal ramus with several spinules near distolateral corner of dorsal surface, as well as in having the terminal seta on the exopod of the female leg 5 shorter than the ramus itself. The inward curvature of the outer terminal caudal setae of *C. incurvi-*

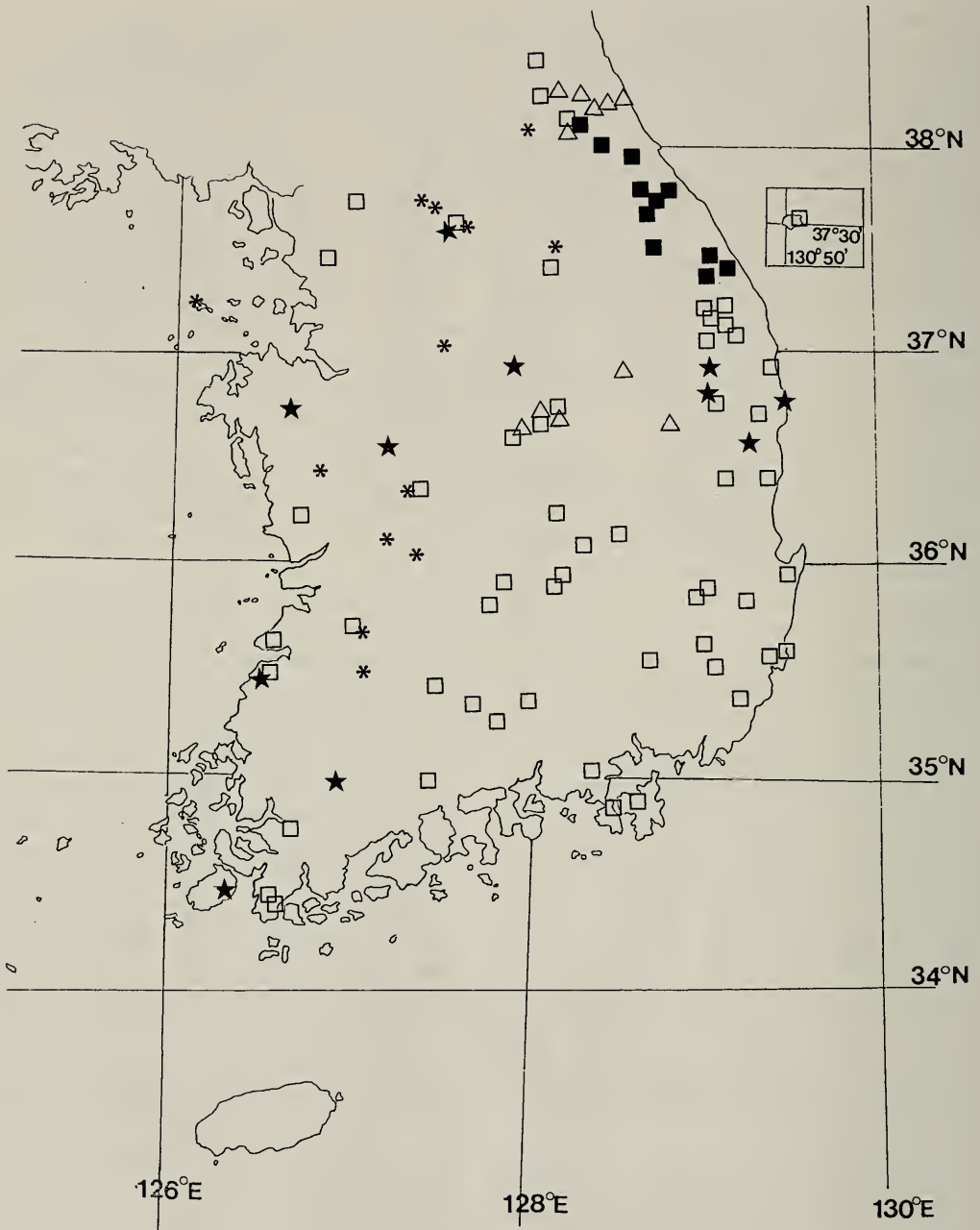


Fig. 7. Occurrence of species of the *Canthocamptus mirabilis* group in South Korea. Symbols as follows: ■ *Canthocamptus odaensis*, ★ *Canthocamptus semicirculus*, □ *Canthocamptus incurvisetosus*, \* *Canthocamptus* sp., △ *Canthocamptus morimotoi*.

*setosus* and *C. resupinatus* is the decisive feature distinguishing these two species from other congeners. These setae are the site of initial male mechanical contact with

the female during mating of the *C. mirabilis* group. The male always grasps the proximal portion of female's caudal setae (cf. Chang 2001, Fig. 4A, B). The ornamenta-

tion of the setae is somewhat different among the members of the species group, as indicated in the specific names, the inward curvature of the outer terminal caudal setae of *C. incurvisetosus* and *C. resupinatus*. However, morphological details of these setae differ between the two species: smoothly curved with 2–3 secondary spinules on the medial surface of the seta of *C. incurvisetosus*, and somewhat sharply bent like a sickle with 7 setiform spinules of *C. resupinatus*.

Four of five species occurring in South Korea are endemic, and only *C. semicirculus* Kikuchi is known to be widely distributed in Japan (below 37°N) and Taiwan (Kikuchi & Ishida 1994). *Canthocamptus incurvisetosus* n. sp. frequently occurs in mountain waters such as streamlets, trickles, and springs in South Korea (Fig. 7). It was collected from 63 of the 120 localities studied, and ranged throughout South Korea except where *C. odaeensis* was found. Thus it co-occurred with *C. morimotoi* over the area from Mt. Sorak (northeastern South Korea) to Mt. Joryeong (central South Korea), with *C. semicirculus* along the Sobaek Mountains (which run diagonally southwestward), and with an unrecorded species of the *mirabilis* group in western South Korea. Like *C. resupinatus* in Japan, *C. odaeensis* is geographically restricted. It is found within narrow limits from south of Mt. Sorak, the northern limit of its range, to north of Mt. Taebaek, the southern limit (from 37°15' to 38°10' N), along the eastern slope of the Taebaek Mountains. This species co-occurred with *C. incurvisetosus* and *C. morimotoi* at only one location, Hangeoryong of Mt. Sorak at the northern border of its range. There, all female *C. odaeensis* were Fn type while all *C. incurvisetosus* were Fr type, and *C. incurvisetosus* possessed the elongated female leg 5 exopod bearing one seta on the medial edge as in the male, as well as several fine setules as in *C. semicirculus*. This suggests that reproductive isolation among these species where they co-occur is reinforced by

character displacement, especially of the female caudal ramus and the ornamentation of the leg 5 exopod.

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## Exopod and protopodial endite III of the maxillae of Sarsiellinae (Crustacea: Ostracoda: Myodocopa)

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*Abstract.*—The number of bristles on the exopod and, also, the number and distribution of bristles and claws on protopodial endite III of the maxillae of species of the Sarsiellinae (Ostracoda) are of value in discriminating species, and should be described and illustrated in descriptions of new species.

Poulsen (1965:46) stated, “Most of the species of the family Sarsiellidae differ from one another in only a few characters and the differences themselves are not very conspicuous.” The purpose of the present study is to evaluate the possible importance in taxonomic discrimination within the Sarsiellinae of two characters of the maxilla: 1, the number of bristles on the exopod; and 2, the number and distribution of bristles and claws on endite III of the protopod.

The number of exopodial bristles generally have been noted in species descriptions enabling most of the data on exopodites in Table 1 to be obtained from a survey of the literature; however, the number and distribution of bristles and claws on endite III of the protopod seldom have been noted in descriptions, requiring that most of the data on endite III in Table 1 had to be obtained from examination of specimens.

The maxilla of the Sarsiellinae has a protopod with three endites: endite I, endite II (middle), endite III (distal) (Fig. 1B, D). Distally, the limb has a 2-jointed endopod, and a single jointed exopod (Fig. 1A). The maxilla of the adult male is reduced (Fig. 1C).

When the maxilla is viewed in its natural position on the body, the basis and endopod have their broadest dimensions parallel to the carapace. The 2nd endopodial joint is curved inward towards the mouth. The short exopod is on the outer side of the limb

just posterior to the 1st endopodial segment. The endites form a diagonal row medial to the endopod with endite III lateral and slightly posterior to endites I and II. Because of its lateral location, the distribution of bristles on endite III is generally visible when the limb is viewed from the outside.

### Exopod

With the exception of some members of the *Cylindroleberididae*, which have maxillae with a quite different morphology than other families of the *Myodocopina*, the maxillae of the *Myodocopina* are biramous. The exopods of the maxillae of members of the families *Cypridinidae*, *Philomedidae*, and *Rutidermatidae* bear three bristles; whereas, the exopods of the *Sarsiellidae* bear either 1 (rarely), 2 (Fig. 2G), or 3 bristles (Fig. 2A–C, F) (Table 1).

The ontogeny of only a few species of *Sarsiellinae* are known. Three species (*Sarsiella japonica* Hiruta, 1977; *Sarsiella misakiensis* Kajiyama (Hiruta, 1978), and *Eusarsiella ryanae* Kornicker & Iliffe, 2000) have the same number of exopodial bristles on Instar I and the adult. Juveniles of both sexes have maxillae similar in type to that of the adult female.

The exopod of the adult male is smaller than that of the female and a lobe may be absent; however, the bristles of the exopod are well developed and ringed. Of the 28

Table 1.—Number of species in genera of Sarsiellinae having either 2 or 3 exopodial bristles and 4, 5, or 6 bristles and claws on endite III of the protopod. (The number of exopodial bristles is mostly from adult females, but includes a few adult males. The number of bristles on endite III is mostly from adult females, but includes a few instar IV males and females, which are believed to have the same number of bristles as on the adult; the list does not include all species in the subfamily.)

Genus	Exopod			Endite III		
	2 br.	3 br.	4 br.	5 br.	6 br.	
<i>Adelta</i>	1	—	—	—	—	
<i>Alphasarsiella</i>	—	2	—	—	1	
<i>Ancohenia</i>	—	1	—	—	1	
<i>Anscottiella</i>	—	2	—	2	—	
<i>Chelicopia</i>	6	1	—	—	3	
<i>Cymbicopia</i>	—	5	—	—	1	
<i>Eurypylus</i>	3	5	—	3	1	
<i>Eusarsiella</i>	25	34	3	4	34	
<i>Junctichela</i>	1	0	1	—	1	
<i>Metasarsiella</i>	0	2	—	1	—	
<i>Neomuelleriella</i>	2	1	—	—	3	
<i>Parasarsiella</i>	0	1	—	—	1	
<i>Sarsiella</i>	13	5	—	—	4	
<i>Spinacopia</i>	5	8	—	—	14	
<i>Tetrasarsiella</i>	—	3	—	—	—	

species considered herein of which adult males and females are known, 26 have the same number of exopodial bristles (two or three). The males of two species have three exopodial bristles compared to two on the females.

Adult females and juveniles of the Sarsiellinae are voracious predators, whereas, adult males are not. This is reflected in the reduced maxilla of the adult male (Fig. 1C); the reduction of the maxilla suggests that it is not used in feeding. The well developed exopodial bristles on the adult male maxilla suggest that they are mainly used for sensing.

If the species of the Cypridinidae, Philomedidae, and Rutidermatidae, were to be considered as outgroups, three bristles could be interpreted as the plesiomorphic character state. Then, the two bristles on some exopods of species of Sarsiellinae could be interpreted to be the apomorphic character state. However, because both two and three exopodial bristles occur on diverse genera of the Sarsiellinae, I interpret the loss of one bristle to be the result of convergence or parallelism, and probably

not of significance in discriminating genera of Sarsiellinae as presently defined.

In conclusion, the number of bristles on the exopod appears to be a useful character in defining some species.

#### Protopodial Endite III

The bristles of endite III of the reduced maxilla of the adult male are weakly developed and not considered further herein. Endite III of the adult female and juveniles of both sexes is broad and globose with well developed bristles. When the endite is flattened under a cover slip, the bristles generally appear to be along, or close to, an edge of the endite (Fig. 2). Endite III of the species studied herein bears a total of 4, 5, or 6 bristles and claws (Table 1). In the discussion below claws and bristles are not differentiated, both are included as bristles.

The number of bristles on endite III of juvenile instars was determined for only a few species (Table 2). The four species of instar I examined all have 4 bristles; the remaining instars and the adult females examined have a total of 4 to 6 bristles and

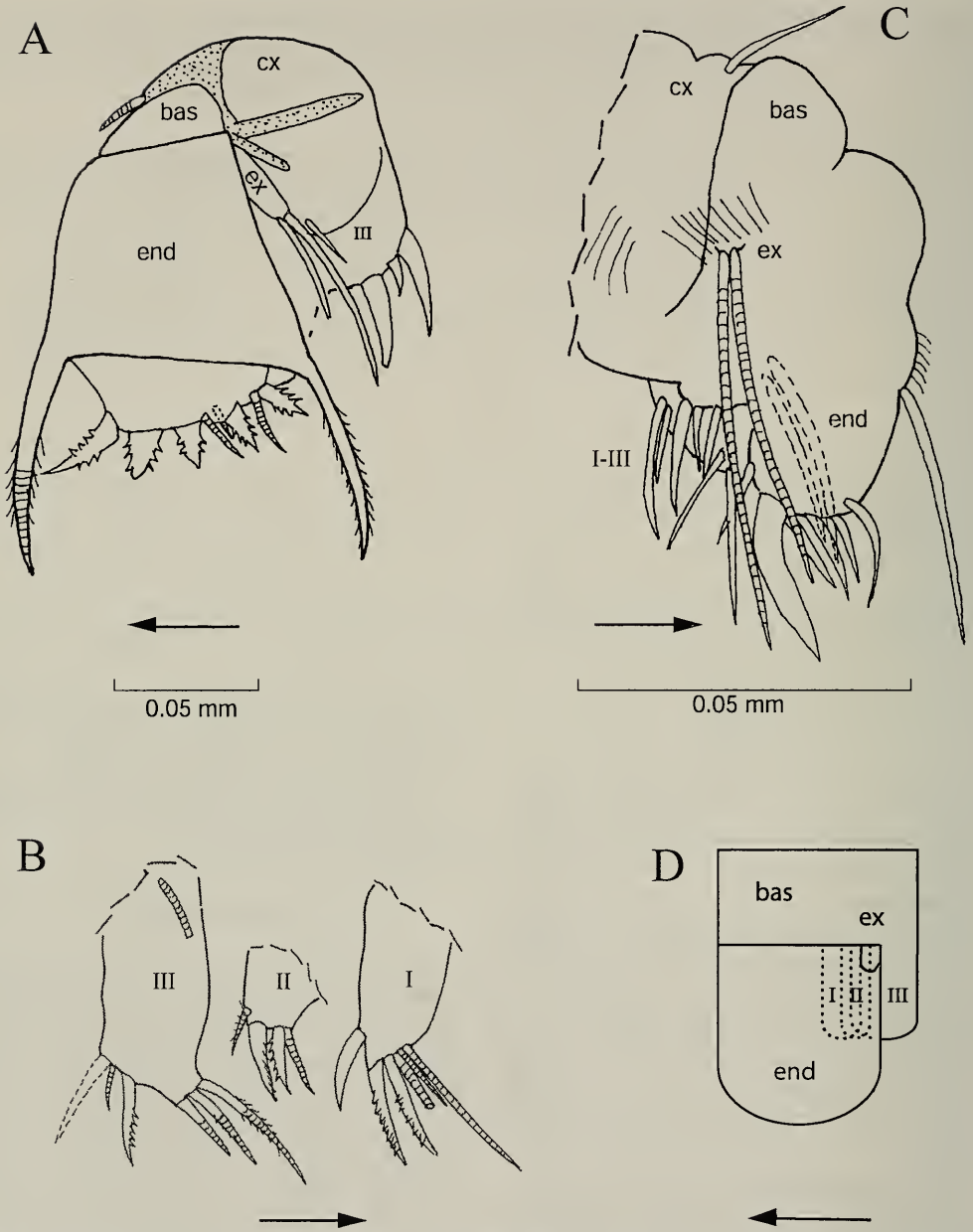


Fig. 1. *Eusarsiella ryanae* Kornicker and Iliffe: Adult female, holotype, USNM 194475. A, left maxilla, lateral view (endites I and II and 3 bristles of endite III not shown); B, endites left maxilla, medial view; C, adult male, paratype, USNM 194476, right maxilla, lateral view; D, stylized lateral view of female left maxilla. Illustrations A–C adapted from Kornicker and Iliffe (2000, figs. 18c, e and 20a, respectively.) (bas = basis; cx = coxa; end = endopod; ex = exopod; arrows indicate anterior; Roman numerals identify endites.)

claws. The species *Junctichela pax* has 4 bristles on all stages. The remaining species examined have 5 or 6 bristles on instars II–IV and the adult female, but the early in-

stars are known for only a few species. Endite III of instar IV and the adult female have the same number of bristles, except for endite III of *Eusarsiella radiicosta*,



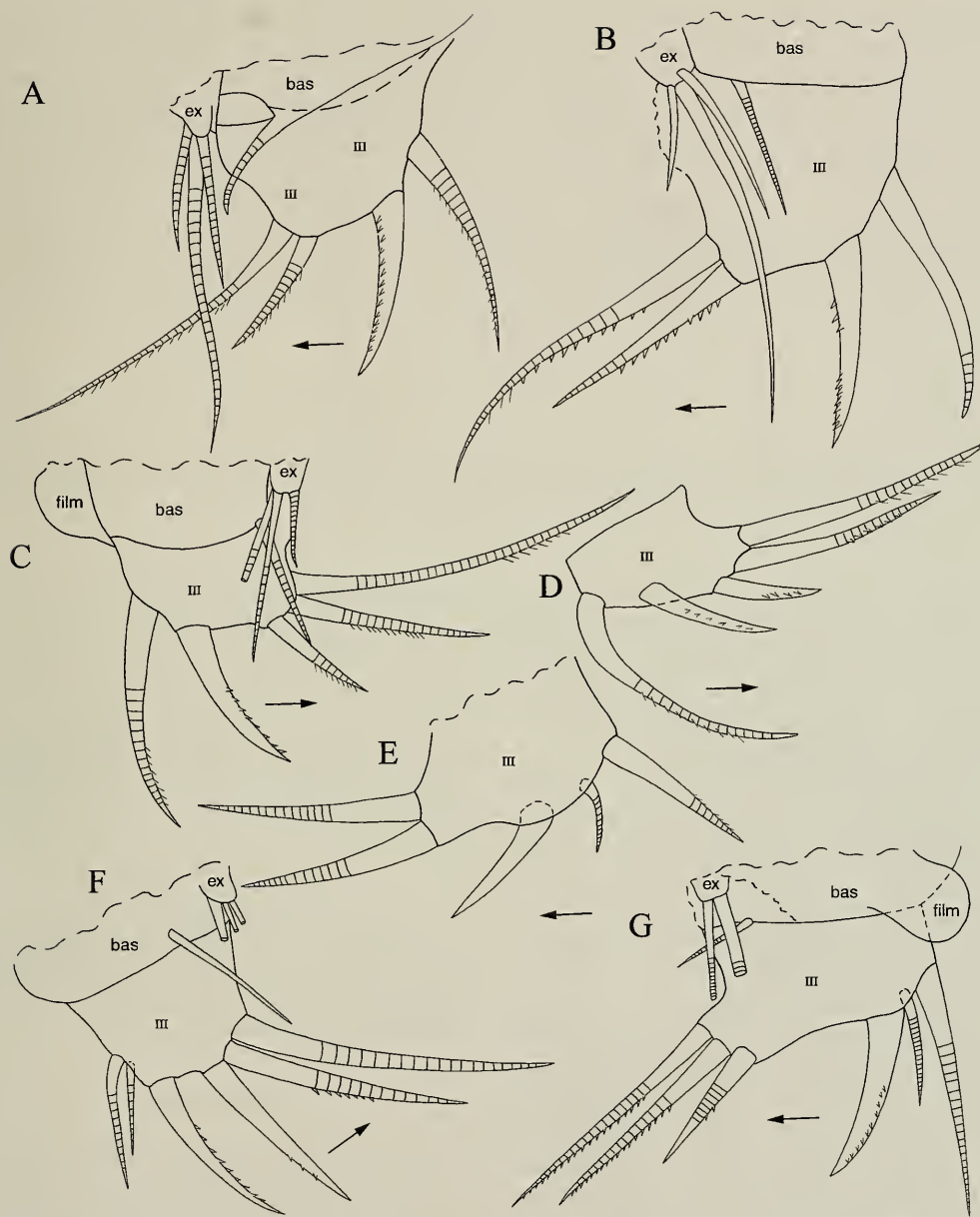


Fig. 2. Endite III of maxilla of species of Sarsiellinae: A, *Eusarsiella dispar* Kornicker, 1986, USNM 158033, adult female, left limb, lateral view; B, *Eusarsiella mawrae* (Kornicker, 1977), USNM 156739, adult or A-1 female, left limb, lateral view; C, *Eurypylus hapax* Kornicker & Iliffe, 2000, USNM 194494, instar IV male, right limb, lateral view; D, *Anscottiella vertex* Kornicker, 1991, USNM 159317, adult female, left limb, medial view; E, *Ancohenia robusta* (Brady, 1890), USNM 193623, instar III female, left limb, lateral view; F, *Spinacopia menziesi* Kornicker, 1969, USNM 122086, adult female, right limb, lateral view; G, *Eusarsiella styx* Kornicker & Iliffe, 1989, USNM 193367, adult female, left limb, lateral view. (Arrows indicate anterior.)

Table 2.—Number of bristles (includes claws) on endite III of the protopod of stages of selected species of Sarsiellinae (both sexes are combined for juvenile instars). (nd = no data)

Species	Stages				
	I	II	III	IV	Adult female
<i>Ancohenia robusta</i>	nd	nd	5	nd	nd
<i>Chelicopia obex</i>	nd	nd	nd	6	nd
<i>Chelicopia radix</i>	nd	nd	nd	6	nd
<i>Eurypylus hapax</i>	nd	nd	nd	5	nd
<i>Eusarsiella capillarus</i>	nd	nd	nd	6	nd
<i>Eusarsiella merx</i>	4	5	nd	5	nd
<i>Eusarsiella radiicosta</i>	nd	nd	nd	5-6*	6
<i>Eusarsiella ryanae</i>	4	6	6	6	6
<i>Eusarsiella thrix</i>	nd	nd	nd	6	nd
<i>Junctichela pax</i>	4	4	4	4	4
<i>Sarsiella capsula</i>	nd	nd	nd	6	6
<i>Spinacopia sandersi</i>	4	nd	nd	6	6

\* Specimen with 5 bristles on one limb and 6 on other limb.

which has 5 bristles on one limb of instar IV and 6 on the other; that species has 6 on the adult female. Because of the similarity in the number of bristles on endite III of both instar IV and the adult female, either stage is included in Table 1.

The number of bristles on endite III of 5 adult females and 2 instars IV of *Spinacopia sandersi* were counted. All had 6 bristles. Because of this it is tentatively assumed in this paper that the number of bristles is fairly constant in those two stages in species in the Sarsiellinae.

Endite III of seven species in five genera of Sarsiellinae are illustrated in Fig. 2. All were drawn with the limb flattened under a cover slip. Endite III is usually broader than either endites I and II. Endite III bears three to five ringed bristles and one or two unringed pectinate claws. On some species the anterior bristles of endite III are on a projection (Fig. 2D, E, G). The anterior bristles extend anteriorly towards the mouth, and the anterior of these is generally longer than other bristles (Fig. 2A-C). Claws are located between the anterior and posterior groups of ringed bristles and each curves anteriorly (Fig. 2). On some species two or three bristles form anterior and posterior groups separated from each other by a wide space (Fig. 2A-C, G).

In conclusion, the distribution of bristles and claws on endite III, as well as the lengths of bristles, vary considerably among species of the Sarsiellinae, and may be a valuable character for discriminating species. Therefore, I highly recommend that endite III be illustrated in species descriptions of the Sarsiellinae.

#### Acknowledgments

I thank Molly K. Ryan for inking the appendages in Fig. 2, and Elizabeth Harrison-Nelson (Smithsonian Institution) for assisting in preparation of the paper.

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***Cypridina olimoblonga* Kornicker, a new name for the junior primary homonym *Cypridina oblonga* Jones & Kirkby, 1874, and clarification of its authorship, and the authorship of the Palaeozoic genera *Cypridinella*, *Cypridellina*, *Sulcuna*, *Rhombina*, and *Offa* (Crustacea: Ostracoda)**

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*Abstract.*—A new name, *Cypridina olimoblonga* Kornicker, is proposed for the junior primary homonym *Cypridina oblonga* Jones & Kirkby 1874 (non *C. oblonga* Grube 1859), type species of *Sylvesterella* Kornicker & Sohn 2000. Authorship of the replaced species, as well as other species described as new in “A Monograph of the British Fossil Bivalved Entomostraca from the Carboniferous Formations” (1874), should be attributed to T. Rupert Jones & James W. Kirkby, not to Jones, Kirkby & Brady. It is concluded that the correct authorship of the genera *Cypridinella*, *Cypridellina*, *Sulcuna*, *Rhombina*, and *Offa* should be attributed to T. Rupert Jones.

Kempf (in litt., 24 Aug 2000) informed me that the species listed in Kornicker & Sohn (2000:20) as *Cypridina oblonga* Jones & Kirkby 1874, type species of *Sylvesterella* Kornicker & Sohn 2000, is a junior primary homonym of *Cypridina oblonga* Grube 1859. The illustrations of the species by Grube (1859: pl. 12: figs. 2–5) clearly identify it as a member of the *Cylindroleberidinae*. Therefore, I herewith rename *Cypridina oblonga* Jones & Kirkby 1874, as *Cypridina olimoblonga* Kornicker nom. nov. *Olim* is from the Latin meaning “formerly” or “once”.

In the same letter, Kempf (in litt., 24 Aug 2000) stated, “Authors of this species [the junior homonym *Cypridina oblonga*] are Jones, Kirkby, & Brady [see Kempf, 1986: 65] as is explicitly told by the ‘Table of Contents’ published with part 2 of that monograph in 1884, and not just Jones & Kirkby, as cited by many authors who perhaps did not know of the complete monograph.”

Kornicker & Sohn (2000:20) had fol-

lowed Sylvester-Bradley (1951:210; 1961: Q403) in attributing *C. oblonga* to Jones & Kirkby 1874, not Jones, Kirkby, & Brady 1874. The following discussion attempts to resolve which set of authors is correct. Because the Jones & Kirkby 1874 publication includes an additional 35 new species and several new varieties, any conclusion drawn herein concerning proper attribution of the junior homonym *Cypridina oblonga* should also apply to them (no attempt is made herein to determine whether or not some of the additional species are junior homonyms or junior synonyms).

For brevity, the 1874 and 1884 volumes of the Palaeontographical Society are simply referred to as “the 1874 volume” and “the 1884 volume”, respectively, throughout this paper.

#### Discussion

Fig. 1 is a copy of the title page of the 1874 volume of the Palaeontographical Society. It clearly states that “Part I, The Cypridinadae and their allies” containing pag-

A MONOGRAPH  
OF THE  
BRITISH FOSSIL  
BIVALVED ENTOMOSTRACA  
FROM THE  
CARBONIFEROUS FORMATIONS.

BY  
PROFESSOR T. RUPERT JONES, F.R.S., G.S., &c. &c.;  
JAMES W. KIRKBY, ESQ., &c. &c.;  
AND  
GEORGE S. BRADY, ESQ., C.M.Z.S., &c. &c.

PART I.  
THE CYPRIDINADÆ AND THEIR ALLIES.  
BY PROF. T. RUPERT JONES, F.R.S., G.S., AND J. W. KIRKBY, ESQ., &c. &c.  
CONTAINING  
PAGES 1-56; PLATES I-V.

LONDON:  
PRINTED FOR THE PALÆONTOGRAPHICAL SOCIETY.  
1874.

Fig. 1. Title page of the 1874 volume of the Palaeontographical Society.

es 1-56 and plates I-V, is the contribution of T. Rupert Jones & James W. Kirkby. On page 20 of that publication appears the description of *Cypridina oblonga* having the heading "13. *Cypridina oblonga*. Sp. nov. Plate V, figs. 12 a-c."

The names Jones, Kirkby, & Brady are listed as authors of the whole monograph on the title pages of both the 1874 (Fig. 1) and 1884 (Fig. 2) publications of the Palaeontographical Society, but in comparison

with the 1874 title page (Fig. 1) where Jones & Kirkby are listed as the authors of Part 1, no authors are specified for Part 1, No. 2 in the 1884 title page. However, "Directions to the binder" (Fig. 3) that presumably accompanied the distribution of the 1884 volume instructed the binder to "Cancel the Title-pages in the Palaeontographical volumes for the years 1874 [Fig. 1] and 1884 [Fig. 2], and substitute the General Title page (dated 1874 and 1884) provided in

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PART I. No. 2.

THE CYPRIDINADÆ AND THEIR ALLIES.

CONTAINING

PAGES i—iii, 57—92; PLATES VI, VII.

WITH TITLE-PAGE AND DIRECTIONS FOR BINDING.

LONDON:

PRINTED FOR THE PALÆONTOGRAPHICAL SOCIETY.

1884.

Fig. 2. Title page of the 1884 volume of the Palaeontographical Society.

the volume for 1884" (Fig. 4). The page with directions to the binder also gives the dates of publication of the various parts of the bound volume (Fig. 3). In the General Title page (dated 1874 and 1884) Jones, Kirkby, & Brady are listed as authors of the whole monograph, but no authors are listed under Part 1 (Fig. 4). Unlike the 1874 vol-

ume, the 1884 volume contains a Table of Contents (pages i—iii). In that table *Cypridina oblonga* and 35 additional species designated as new species in the 1874 volume are attributed to Jones, Kirkby, & Brady. Only one of the new species, *Cypridina Bradyana* (sic), is attributed to Jones & Kirkby. In 1874 (page 15) Jones & Kirkby

THE CARBONIFEROUS BIVALVED ENTOMOSTRACA.

PART I.

DIRECTIONS TO THE BINDER.

The Monograph of the Carboniferous Bivalved Entomostraca, Part I (the Cypridinadae and their Allies), will be found in the volumes of the Palaeontographical Society for the years 1874 and 1884.

~~Cancel the Title-pages (dated 1874 and 1884) in the parts issued in the Palaeontographical volumes for the years 1874 and 1884, and substitute the General Title-page (dated 1874—1884) provided in the volume for 1884.~~

ORDER OF BINDING AND DATES OF PUBLICATION.

PAGES	PLATES	ISSUED IN VOL. FOR YEAR	PUBLISHED
Title-page	—	1884	December, 1884
i—iii	—	"	
1—56	I—V	1874	July, 1874
57—92	VI—VII	1884	December, 1884

Fig. 3. "Directions to the Binder" in the 1884 volume of the Palaeontographical Society.

had explained the naming of that species as follows: "it is named after our accomplished friend, Mr. G. S. Brady of Sunderland, who has favoured us with much help in the study of these and other fossil Entomostraca." One species, *Bradycynetus Rankinianus* (*sic*), which is attributed to Jones & Kirkby 1867 in the 1874 volume, is attributed to Jones, Kirkby, & Brady in the Table of Contents of the 1884 volume. Another species, *Cypridina radiata*, which is attributed to Jones, Kirkby & Brady in the Table of Contents of the 1884 volume, is attributed to Jones & Kirkby in an "Addendum to the Cypridinadae" in the 1884 volume (page 81). The Table of Contents does not indicate which part of the volume was published in 1874, and which part in 1884.

Jones & Kirkby (1886:508, 509: Table II), in a table entitled, "The Genera and Species of Carboniferous Ostracoda, and their Occurrences in England, Scotland, and Ireland" attributed *Cypridina oblonga* to

Jones, Kirkby & Brady. Other species in the table that are also present in the Table of Contents in the 1884 volume are attributed to the same authors in both places. This indicates that Jones and Kirkby agreed in 1886 with the addition of Brady's name to *C. oblonga* in the 1884 volume.

The number of 1874 volumes that have not been bound to an 1884 volume appears to be sparse. The shared on-line catalog database, Online Computer Library Center, Inc. (OCLC), of January, 2000, lists only the University of Oxford as having an 1874 volume not bound to the 1884 volume. That 1874 volume, which is in the Oxford University Museum (Natural History) Library, has a title page identical to that of Fig. 1, which is a copy of the title page in an 1874–1884 bound volume in the Smithsonian Library (Parker, in litt., 4 Oct 2000). The 1874 volume at Oxford does not have a Table of Contents (Parker, in litt., 4 Oct 2000).

An abstract published by Jones (1873b:

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PART I.

THE CYPRIDINADÆ AND THEIR ALLIES.

LONDON :

PRINTED FOR THE PALÆONTOGRAPHICAL SOCIETY.

1874—1884.

Fig. 4. Substitute "General Title-page (dated 1874-1884)" of the combined 1874-1884 volumes of the Palaeontographical Society.

409) mentions *Cypridina oblonga* (page 410) and other new species that subsequently were described in the 1874 and 1884 volumes. A description of *C. oblonga* is not given; therefore, the species name is a *nomen nudum*. The abstract states (page 409):

"Numerous other specimens from Ireland, Scotland, Yorkshire, Derbyshire, and the Isle of Man, communicated by friends, have also been studied; and the results will be given in detail in a Monograph by Messrs. Jones and Kirkby, to be published by the



Table 1.—List of selected authors (arranged chronologically) showing attribution by them of authorship of five genera of Paleozoic Ostracoda. (B = George S. Brady, J. = T. Rupert Jones, K = James W. Kirkby, — = genus not mentioned; list does not include Jones, 1873a, b.)

Author	Attribution				
	<i>Cypridinella</i>	<i>Cypridellina</i>	<i>Sulcuna</i>	<i>Rhombina</i>	<i>Offa</i>
Jones & Kirkby (1874)	J & K	J & K	J & K	J & K	J & K
Jones, Kirkby, & Brady (1884)	J, K & B	J, K & B	J, K & B	J, K & B	J, K & B
Woodward (1877)	J & K	J & K	J, K & B	J, K & B	J, K & B
Jones & Kirkby (1887)	J	J	J	J	J
Gemmellaro (1890)	J & K	J & K	—	—	—
Bassler & Kellett (1934)	J, K & B	J, K & B	J, K & B	J, K & B	J, K & B
Neave (1939)	J, K & B	J, K & B	—	—	—
Neave (1940a)	—	—	—	—	J, K & B
Neave (1940b)	—	—	J	J, K & B	—
Sylvester-Bradley (1951)	—	—	—	J & K	—
Howe (1955)	J	J & K	J	J	J
Mertens (1958)	J	J & K	J	J & K	J
Pokorny (1958, 1965)	J	J	—	J, K & B	J
Sylvester-Bradley (1961)	J & K	J & K	J & K	J & K	J & K
Howe (1962)	J	J & K	J & K	J & K	J & K
Kempf (1986, pt. 1)	J, K & B	J, K & B	J, K & B	J, K & B	J, K & B
Kornicker & Sohn (2000)	J & K	J & K	J & K	—	—
Herein	J	J	J	J	J

Palaeontographical Society, and now in press.” The only importance of the abstract in the Quarterly Journal (Jones, 1873b) to the present study is that it contains a reference to the monograph by Jones & Kirkby then in press by the Palaeontographical Society.

Concerning the Palaeontographical Society archives, Paul Ensom (in litt., 12 Dec 2000) kindly sent the following:

“I checked all the Annual Reports (printed), which were present in the minute book, i.e., tabbed in. There was no reference to the problem [addition of Brady’s name]. The Printed annual reports only appear in 1875, 1976, then 1879 onwards; 1877 and 1878 are not present. The annual report for 1884 states ‘The other portions of the Volume for 1884 will be. . .the continuation of the Carboniferous Entomostraca by Messrs Prof. Jones, J.W. Kirkby, and Prof G.S. Brady, . . .,’ and that is all.”

While researching the above, I observed that five Paleozoic ostracode genera (*Cypridinella*, *Cypridellina*, *Sulcuna*, *Rhombina*, and *Offa*), which had been described by

Jones (1873a), were designated as new genera in both Jones & Kirkby (*in* Jones, Kirkby, & Brady 1874) and Jones, Kirkby, & Brady 1884. Since then various authors have attributed the genera to either Jones 1873, or Jones & Kirkby (*in* Jones, Kirkby, & Brady 1874), or Jones, Kirkby, & Brady 1884 (Table 1). The descriptions of the five genera in Jones 1873a are adequate to satisfy Article 12.1 of the International Code of Zoological Nomenclature, Fourth Edition (International Commission on Zoological Nomenclature 1999). Therefore, the genera should be attributed to Jones.

### Conclusions

The 1874 volume satisfies the “Criteria of Publication” (Chapter 3) and “Criteria of Availability” (Chapter 4) of the International Code of Zoological Nomenclature, Fourth Edition. The Abstract published by Jones (1873b:409) indicates that only Jones & Kirkby were intended to be authors of Part 1 of the 1874 volume, and the original title page of the 1874 volume should be ac-

cepted at face value, not withstanding contrary information issued 10 years later.

My interpretation of rules listed under "Date of Publication" (Chapter 5) in the Code and other provisions contained therein leads me to believe that only Jones and Kirkby are the authors of the junior homonym *Cypridina oblonga* in the 1874 volume.

### Acknowledgments

I wish to thank Eugen Karl Kempf for making me aware of this problem and for correspondence concerning it, including a suggestion for the new specific name. I also thank Andrew Richard Parker, Oxford University, for information mentioned above, and Elizabeth Harrison-Nelson, Smithsonian Institution, for assistance in preparation of the paper. Paul C. Ensom, John E. Whitaker, and C. Giles Miller, The Museum of Natural History, London, kindly answered correspondence concerning the 1874–1884 volumes, and Wendy Cawthorne, Geological Society Library, London, kindly answered correspondence concerning the Jones (1873b) abstract. I thank Frederic M. Swain, University of Minnesota, and several anonymous reviewers for criticizing the manuscript. I much appreciate the review of the manuscript by Brian Kensley (Smithsonian Institution). I also thank for their help Leslie Overstreet, David Steere, and Martha Rosen, Smithsonian Institution; Storrs Olson, Smithsonian Institution; and F. Christian Thompson, U.S. Department of Agriculture.

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***Seepiophila jonesi*, a new genus and species of vestimentiferan tube worm (Annelida: Pogonophora) from hydrocarbon seep communities in the Gulf of Mexico**

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*Abstract.*—*Seepiophila jonesi*, a new genus and species of vestimentiferan tube worm is described from material collected from hydrocarbon seep communities in the Gulf of Mexico, based on morphological and molecular characters. In these communities, individuals occur singly, in small groups or in association with large aggregations of a second vestimentiferan species, *Lamellibrachia* cf. *luymesii*. Tubes extend deeply into the sediment, and a relatively short apical portion normally projects above the sea floor. *Seepiophila jonesi* is most similar to vestimentiferan species in the genus *Escarpia* but differs from it and other vestimentiferan species by a combination of morphological characters that includes the number of types of branchial filaments associated with the branchial plume, the presence of an incision in the posteroventral margin of the vestimentum, the presence of a well-developed, medial obturacular structure, the relative position of the excretory pore and the presence of a variable number of broad collars associated with the tube. The divergence in the sequence of the cytochrome oxidase I gene between *S. jonesi* and other described vestimentiferan tube worms supports its placement in a new genus within the family Escarpiidae.

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With the description of *Lamellibrachia barhami*, Webb (1969) recorded the first vestimentiferan tube worm from a cold-water site in the northeastern Pacific Ocean. The discovery of hydrothermal vents and their associated fauna along the Galápagos Rift, East Pacific Rise and Juan de Fuca Ridge of the eastern Pacific Ocean and in various regions of the western Pacific has led to the description of ten additional vestimentiferan species from the Pacific Ocean (Jones 1981, 1985; Southward 1991; Miura et al. 1997; Southward & Galkin 1997; Southward et al. 2001).

In contrast to the Pacific Ocean, the Atlantic Ocean, including the Gulf of Mexico, at present, exhibits much less vestimentiferan diversity. Two species of *Lamelli-*

*brachia* are known from putative cold-water sites in the western Atlantic Ocean. Van der Land & Nørrevang (1975) described *L. luymesii* based on a single male specimen taken from about 500 m of water off Guyana, and *L. victori* was characterized by Mañé-Garzón & Montero (1985) based on several specimens dredged from about 300 m of water on the continental slope of Uruguay.

Paull et al. (1984) were the first to report the presence of vestimentiferan tube worms in the Gulf of Mexico. Diving in the submersible *Alvin* at a depth of more than 3000 m at the base of the Florida Escarpment, they observed clumps of specimens that varied in density from a few to more than 100 individuals per square meter. Speci-

Table 1.—Names, coordinates and depths of hydrocarbon seep sites on the Louisiana Slope, Gulf of Mexico sampled for the present study.

Lease block	Site name	Latitude	Longitude	Depth (m)
GC185	Bush Hill	27°47'N	91°31.5'W	540
GC233	Brine Pool	27°43.4'N	91°16.8'W	640
GC234	Green Canyon	27°44.1'N	91°15.3'W	540
TAMU-17	Tamu	27°43.8'N	91°18.2'W	560
GB425	Garden Banks	27°33.3'N	92°32.4'W	570

mens collected from this site were later given the name of *Escarpia laminata* by Jones (1985).

As part of an investigation of the possible effects of hydrocarbon release into overlying waters in the Gulf of Mexico, Kennicutt et al. (1985) performed deep-water trawls at two sites along the Louisiana Slope. One of the trawls contained vestimentiferan specimens which they identified as *Lamellibrachia* sp. Subsequent cruises and submersible dives to sites along the Louisiana Slope revealed the presence of dense assemblages of hydrothermal vent-type taxa, including large aggregations of the vestimentiferan *Lamellibrachia* cf. *luyesi* (see MacDonald et al. 1989, among others). Occurring in association with these aggregations, or sometimes occurring independently, is a second undescribed vestimentiferan species (CRF, SLG, EM pers. obv.). The purpose of the present study is to provide a description of this new species, using morphological features, and to examine its relationships with other vestimentiferans, using morphological and molecular analyses.

#### Materials and Methods

Specimens were collected by the manned submersibles *Johnson Sea Link I (JSL I)* and *Johnson Sea Link II (JSL II)* from five seep sites on the Louisiana Slope in the Gulf of Mexico, ranging from 540 to 640 m in depth: Bush Hill, GC234, Brine Pool, TAMU-17 and GB425 (Table 1). Specimens were brought to the surface in a temperature-insulated container and immediately placed in chilled water on board ship.

Animals collected for morphological studies were removed from their tubes, preserved in 10% buffered formalin in seawater and subsequently transferred to 70% ethanol. Specimens collected for molecular analyses were removed from their tubes, and a sample of the vestimentum was snipped and immediately frozen in liquid nitrogen. Frozen samples were transported on dry ice and subsequently stored at  $-80^{\circ}\text{C}$ .

To show the relationship of the Louisiana Slope vestimentiferans to other known vestimentiferans, we sequenced a portion of the mitochondrial cytochrome oxidase I gene (COI) and compared it with published data for other vestimentiferans (Black et al. 1997, Kojima et al. 1997, Feldman et al. 1998). The four specimens of the new species described herein were collected from four different sites within 65 km of each other on the Louisiana Slope (Bush Hill, GC234, TAMU-17 and GB425). Specimens were stored at  $-80^{\circ}\text{C}$  before and after DNA extraction. For these studies, total nucleic acids were extracted from vestimentum tissue by the classic phenol/chloroform extraction technique. The COI gene was amplified by PCR, at an annealing temperature of  $55^{\circ}\text{C}$ , with the following primers: COIf: TC(CA)ACTAATCA(CT) AA(GA) GA-(CT)ATTGG(ATGC)AC, COIr:CC(ATG)-CTTAG(TA)CCTA(GA)(GA)AA (GA)TG-TTG(ATCG)GG (Nelson & Fisher 2000). PCR products were visualized on a 1.5% agarose gel (GIBCO BRL) stained with ethidium bromide. Products were cleaned with a PCR Purification Kit (QIAGEN) before

sequencing. This primer pair amplifies an approximately 1250 base pair segment, from which a 1100 base pair fragment was sequenced with multiple primers, generating overlapping sequences from both strands.

Cycle sequencing PCR was done with a Beckman CEQ DTCS dye terminator reaction kit (BECKMAN), under manufacturer's suggested conditions. End labeled products were separated on a capillary autosequencer (Beckman CEQ 2000XL). Individual sequence runs were assembled and edited with SEQMAN (DNASTAR, Inc.). Consensus sequences generated in this study were aligned (MEGALIGN, DNASTAR Inc.) with those generated in previous studies available in Genbank (Table 2). Molecular evolutionary relationships among sequences were examined by the minimum evolution (ME) method of tree construction (Rzhetsky & Nei 1992) based on pairwise genetic distances estimated from the proportion of differences and corrected for multiple substitutions by the Kimura 2-parameter formula (Kimura 1980). Significance of branching order was evaluated by bootstrap analysis with 1000 replications. Both a pogonophoran from the study of vestimentiferans in Japan by Kojima et al. (1997) and *Galathealinum brachiosum*, a described pogonophoran species, were used as outgroup sequences. All analyses were performed with MEGA (Kumar, version 2.0 beta).

### Systematics

The systematic relationships of vestimentiferans (= subphylum Obturata sensu Jones 1981) to pogonophorans (= subphylum Perviata sensu Jones 1981) and to other invertebrate taxa such as the Annelida, as well as their placement in a taxonomic hierarchy, remain unsettled. It is not a purpose of the present study to provide an exhaustive historical account of these issues. Recent morphological, molecular and developmental studies suggest a close rela-

tionship between vestimentiferans and pogonophorans and also support an annelid affinity for both groups or place them within the Annelida or Polychaeta (Southward 1988, 1999; Gardiner & Jones 1994; Rouse & Fauchald 1995, 1997; Black et al. 1997; Kojima et al. 1997; McHugh 1997, 2000; Bartolomaeus 1998; Halanych et al. 1998; Rouse 2001). In spite of the seemingly convincing body of evidence provided by these studies, Salvini-Plawen (2000) questioned the reliability of characters used in determining possible relationships between vestimentiferans and pogonophorans and the Annelida-Polychaeta. He concluded that the current level of knowledge of characters of vestimentiferans and pogonophorans is insufficient to provide definitive relationships. Rather, he suggested that, depending on which characters are being analyzed, the two groups demonstrate possible affinities to the Annelida-Polychaeta, Annelida-Oweniidae and Oligomera. He stated that additional comprehensive studies of vestimentiferans and pogonophorans are required to refine better our understanding of their possible relationships with other taxa.

In order to maintain consistency with other recent descriptions of vestimentiferans (Southward 1991, Southward et al. 1995, Miura et al. 1997, Southward & Galkin 1997, Southward et al. 2001), we here adopt the classification proposed by Southward (1991) and consider vestimentiferans as comprising a subclass within the class Pogonophora of the phylum Annelida.

Subclass Obturata Jones, 1981

Order Basibranchia Jones, 1981

Family Escarpiidae Jones, 1985, amended

*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 or grouped in two types; plume lacking peripheral lamellar sheaths; anterior

face of obturaculum with moderate to thick crust and usually with variously developed medial structure arising from between obturacular halves; paired internal excretory ducts opening by single, dorsal medial excretory pore near base of obturaculum or more anteriorly, up to one-third distance of obturaculum from base. Anteroventral margin of vestimentum incised, posteroventral margin entire or incised. Opisthosome with setae in single to triple rows. Tube hard, tapering, with or without anterior funnel and variable number of broadly flared external collars and with or without variable number of rings along length.

*Remarks.*—The family Escarpiidae was amended by Southward et al. (2001) to allow for the inclusion of a new genus and species collected from deep water in the western Pacific Ocean.

The amended diagnosis of the family Escarpiidae provided above is constructed from observations by one of us (SLG) of type specimens of *Escarpia spicata* and *E. laminata* and the new genus and species described herein, together with characters of the new genus described in Southward et al. (2001). The significant morphological feature included in this amended diagnosis is the presence of only a single type of branchial filament associated with the obturacular plume.

Jones (1985) did not possess complete specimens of *Escarpia spicata* or *E. laminata*. Therefore, he was unable to characterize the opisthosome of *Escarpia*. Southward (pers. comm., Southward et al. 2001) describes the opisthosome of one specimen of their new genus as comprising about 15 segments with setae in single to triple rows. Setae are composed of an anterior smaller group of 2–3 teeth and a larger posterior group of teeth occurring in 3–4 rows.

#### *Seepiophila*, new genus

*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 lacking peripheral lamellar sheaths; anterior face of obturaculum with moderate crust and with conspicuous medial structure arising from between obturacular halves; paired internal excretory ducts opening by single, dorsal medial excretory pore situated on obturaculum approximately one-third distance anteriorly from base. Anteroventral and posteroventral margins of vestimentum incised. Opisthosome unknown. Tube hard, tapering, aperture surrounded by broadly flaring funnel, with variable number of broadly flared external collars anteriorly and with variable number of rings along length.

*Type species.*—*Seepiophila jonesi*, new species, by present designation.

*Gender.*—Feminine.

*Etymology.*—From English *seep* (= a place where water or petroleum oozes out slowly) + Greek *philia* (= affection, fondness), in reference to the strong preference of these worms to inhabit hydrocarbon seep communities in the deep sea.

#### *Seepiophila jonesi*, new species

Figs. 1–5

Unidentified vestimentiferan.—Childress et al., 1986:1307.

Undescribed family.—Brooks et al., 1987: 1139, table 1.

Escarpia-like [sic].—Brooks et al., 1987: 1140, table 2, 1141, table 3.

Undescribed member of the family Escarpiidae.—Fisher et al., 1988:230, 232.

*Escarpia*-like.—MacDonald et al., 1989: 239, 243, table 4.—Childress & Fisher, 1992:382.

The escarpiid.—MacDonald et al., 1989: 241, 245, fig. 3B.

*Escarpia* sp. [not *Escarpia* Jones, 1985].—MacDonald et al., 1989:235.—Young et al., 1996:514–516, figs. 1b, 2a, c, f-1.—Miura et al., 1997:455.—Southward, 1999:196.—Tyler & Young, 1999:197,

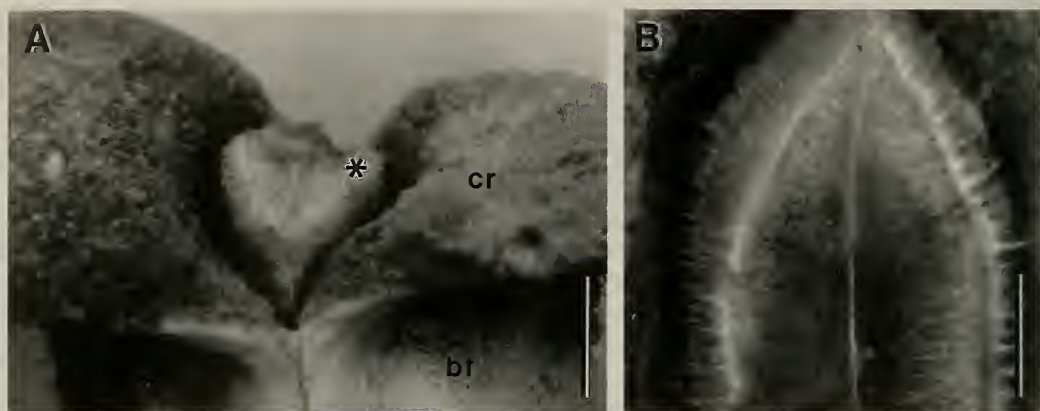


Fig. 1. *Seepiophila jonesi*, new species. Holotype (USNM 188519). A, Anterior face of obturaculum showing crust-like material (cr) and prominent medial process (asterisk). bf, branchial filaments. B, Enlargement of portion of medial process. Note numerous spines along lateral margins. Scale bars: A = 2 mm; B = 1 mm.

table 3, 198.—Salvini-Plawen, 2000:133, 134.

Undescribed genus.—Fisher, 1990:406, table 1, 410.

Unidentified escarpid.—Fisher et al., 1990: 1095, table 1.

*E. sp.* [not *Escarpia* Jones, 1985].—Fisher, 1995:307, table 4.

Escarpiidae species.—Nelson & Fisher, 1995:128, table 1.

*Escarpia spicata* [not *Escarpia spicata* Jones, 1985].—Feldman et al., 1997:270.

Escarpid-like.—Fisher et al., 1997:83–94, fig. 1b (as escarpids).—Nelson & Fisher, 2000:1–10.

Undescribed seep escarpid.—Scott et al., 1998:379, table 1.

*Type material.*—See Table 1 for coordinates and depths of hydrocarbon seep communities. Holotype, (USNM 188519), 6 paratypes (USNM 188520–188525), Bush Hill hydrocarbon seep community, *JSL I* Dive 3775, 8 Oct 1994, coll. S. L. Gardiner; 6 paratypes, Bush Hill hydrocarbon seep community, *JSL I* Dive 3530, 28 Jun 1993, coll. J. J. Childress. Additional type material is deposited in the Natural History Museum, London, the Canadian Museum of Nature, the National Science Museum, Tokyo and the Muséum National d'Histoire Naturelle, Paris.

*Additional material examined.*—See Table 1 for coordinates and depths of hydrocarbon seep communities. For morphological analyses: 14 specimens, Green Canyon hydrocarbon seep community, *JSL I* Dive 3525, 26 Jun 1993, coll. E. Nix; 2 specimens, Green Canyon hydrocarbon seep community, *JSL I* Dive 3526, 26 Jun 1993, coll. J. J. Childress; 8 specimens, Bush Hill hydrocarbon seep community, *JSL I* Dive 3530, 28 Jun 1993, coll. J. J. Childress; 17 specimens, Bush Hill hydrocarbon seep community, *JSL I* Dive 3775, 8 Oct 1994, coll. S. L. Gardiner. For molecular analyses: 1 specimen, Bush Hill hydrocarbon seep community, *JSL II* Dive 2853, 10 Jul 1997, coll. K. Nelson; 1 specimen, Green Canyon hydrocarbon seep community, *JSL II* Dive 2866, 16 Jul 1997, coll. K. Nelson; 1 specimen, Garden Banks hydrocarbon seep community, *JSL I* Dive 4053, 17 Jul 1998, coll. E. McMullin; 1 specimen, TAMU-17 hydrocarbon seep community, *JSL I* Dive 4049, 15 Jul 1998, coll. E. McMullin.

*Diagnosis.*—Characters of the genus.

*Etymology.*—The species is named in honor of the late Meredith L. Jones whose studies of vestimentiferan anatomy, morphology and development contributed greatly to our understanding of this enigmatic group of marine worms.



*Description.*—Measurements of selected specimens (length by diameter, in mm; obturacular: vestimental: trunk: opisthosomal regions; + = incomplete; - = change in diameter; — = missing); (USNM 188519): 9.5 by 7.5: 36.4 by 10.2: 415+ by 5.9–0.4: —; (USNM 188520): 12.1 by 7.8: 44.2 by 8.9: 330+ by 6.4–1.6: —; (USNM 188521): 11.5 by 6.1: 38.7 by 7.5: 100+ by 4.5–3.5: —; (USNM 188522): 10.7 by 6.1: 45.1 by 6.5: 380+ by 6.4–0.8: —; (USNM 188525): 11.2 by 5.6: 52.1 by 7.4: 350+ by 4.7–1.0: —. Measurements of selected tubes: (USNM 188519): 870+ by 12.4–1.0; (USNM 188520): 955+ by 9.6–0.8; (USNM 188523): 810+ by 11.6–0.6; (USNM 188524): 820+ by 10.9–2.7.

Anterior face of obturaculum with moderately developed crust, up to approximately 1 mm in thickness (Fig. 1A); cuticular axial rod between obturacular halves of distal one-third of obturaculum, extending beyond anterior face of obturaculum as prominent medial structure, laterally compressed, terminating bluntly, lateral margins provided with numerous small spines (Fig. 1A, B); measurements of selected medial structures (anteroposterior length above anterior face of obturaculum by dorsoventral height by lateral width) in mm: (USNM 188519): 1.5 by 5.9 by 3; (USNM 188521): 1.6 by 4.7 by 2.3; (USNM 188523): 1.5 by 5.5 by 2.5; (USNM 188525): 0.8 by 4.5 by 1.7. Obturaculum with approximately 45–50 pairs of branchial lamellae (Fig. 2A–D), lacking specialized sensory filaments; filaments comprising lamellae of one type, fused for greater portion of length, with single row of pinnules extending along free portion of filaments (Fig. 3A) and with two rows of ciliated cells (Fig. 3A, B); pinnules on filaments of lamella one (= oldest lamella) relatively inconspicuous, often irregularly spaced along distal length of filaments (Fig. 3C); pinnules on filaments of middle and posterior-most lamellae larger, regularly spaced along distal length of filaments (Fig. 3A, B); midventral face and distal sides of obturaculum bare; obturacu-

lum laterally compressed at base, oval to somewhat spindle-shaped in cross-section more distally (Fig. 4A), lacking dorsal groove, with poorly developed ventral ridge; paired internal excretory ducts (Fig. 4A) opening by single pore on dorsal medial ridge approximately one-third distance of obturaculum from base (Fig. 2D, arrow), dorsal medial ridge sometimes darkly pigmented; ratio of obturacular length to vestimental length variable, 1:2.8 to 1:6.6. Anterior margin of vestimentum forming short sheath around base of obturaculum (Fig. 2A), with shallow midventral incision often forming small lobes (Fig. 2C); posteroventral margin of vestimentum deeply incised, with two conspicuous lobes (Fig. 2C, large arrowhead, E); ratio of vestimental diameter to vestimental length highly variable, 1:3.1 to 1:12.6; ventral surface with tear-drop shaped ciliated field; plaques associated with epidermis ventrolaterally (Fig. 2E, arrowhead); males with paired dorsal ciliated grooves extending from gonopores to near anterior end of vestimentum, converging slightly anteriorly (Fig. 2D, arrowheads). Trunk very long in adult specimens, tapering to less than 1 mm in diameter; epidermis with numerous associated plaques (Fig. 2E, arrowhead). Opisthosome unknown. Tube hard, often somewhat darkly colored, tapering posteriorly, aperture with broadly flaring funnel (Figs. 4B, 5); diameter of aperture variable (6.6–11 mm;  $\bar{X} = 9.1 \pm 1.3$  mm,  $n = 34$ ), with variable number of collars posterior to aperture (0–10;  $\bar{X} = 3.2 \pm 1.9$ ,  $n = 34$ ); number of rings posterior to aperture highly variable (11–59;  $\bar{X} = 29.8 \pm 10.2$ ,  $n = 34$ ).

*Distribution.*—Presently known only in association with certain hydrocarbon seep communities in the Gulf of Mexico between 500 and 1000 m depth.

*Remarks.*—Seven vestimentiferan species in six genera possess a medial structure in association with the obturaculum: *Escarpia spicata* Jones, 1985, *E. laminata* Jones, 1985, *Oasisia alvinae* Jones, 1985, *Ridgeia piscesae* Jones, 1985, *Tevnia jerichonana*

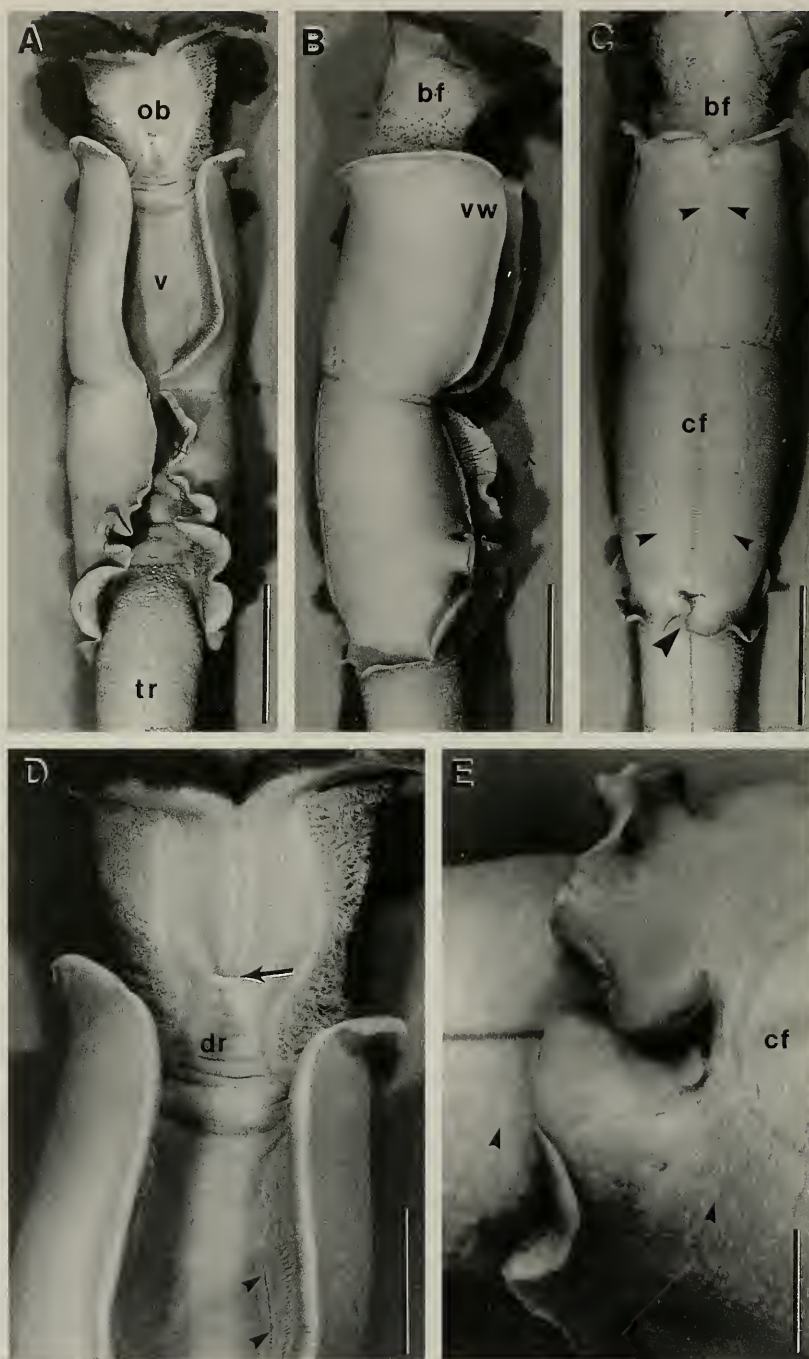


Fig. 2. *Seepiophila jonesi*, new species. Holotype (USNM 188519). A, Dorsal view of obturacular (ob) and vestimental (v) regions and portion of trunk region (tr). Note broadly splayed anterior face of obturaculum. B, Left lateral view of obturacular region showing branchial filaments (bf), vestimental region with vestimental wings (vw) and portion of trunk. C, Ventral view of obturacular region, vestimental region with tear-drop shaped ciliated field (cf) and portion of trunk region. Small arrowheads indicate position of intraepithelial nerve cords. Note deeply incised posteroventral margin of vestimentum (large arrowhead). bf, branchial filaments. D, Enlarged dorsal view of obturacular region showing prominent dorsal ridge (dr) at base of obturaculum. Arrow indicates

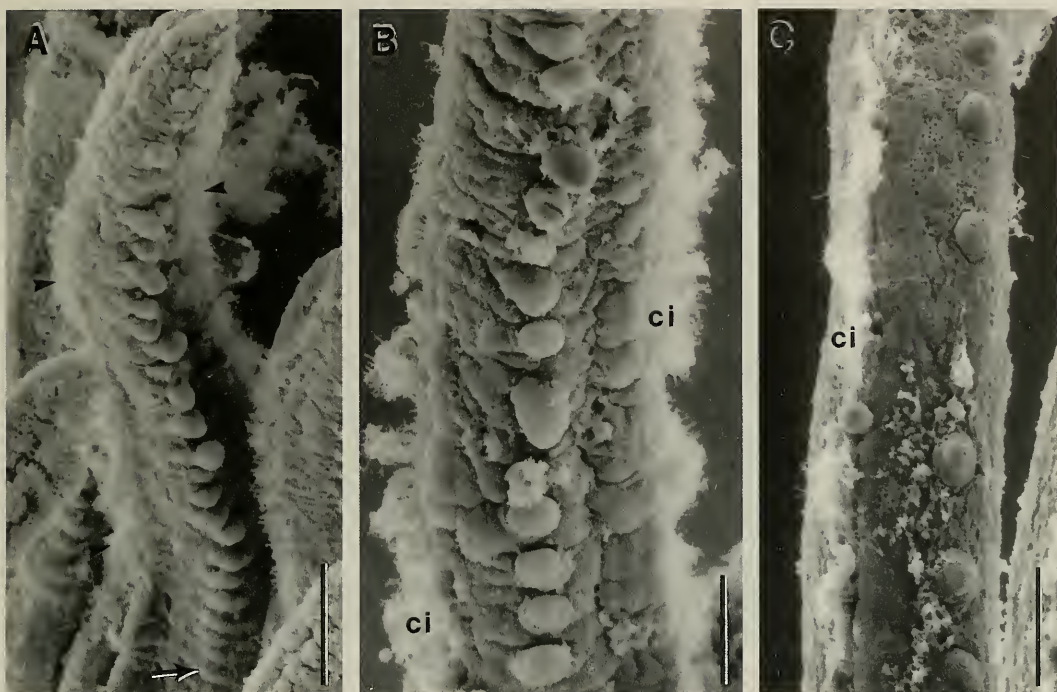


Fig. 3. *Seepiophila jonesi*, new species. Scanning electron microscopy. Non-type specimens. A, Branchial filament from middle lamella. Single row of pinnules extends from near tip of filament to region where filament fuses with adjacent filaments. Note diminished size of pinnules in region of fusion (arrow). Arrowheads indicate cilia. B, Branchial filament from basal lamella. Note well-developed pinnules and two rows of ciliated cells (ci). C, Branchial filament from lamella one (= oldest lamella). Note single row of small, somewhat irregularly spaced pinnules. ci, cilia. Scale bars: A = 50  $\mu\text{m}$ ; B = 25  $\mu\text{m}$ ; C = 30  $\mu\text{m}$ .

Jones, 1985, a new genus described in Southward et al. (2001) and *Seepiophila jonesi*, new species. *Seepiophila jonesi*, however, differs from all other species that possess an obturacular medial structure in having only a single type of filament comprising the branchial lamellae. In *S. jonesi*, all filaments possess a single row of pinnules, whereas other species that display an obturacular medial structure possess at least some filaments that lack pinnules.

A crust-like material on the anterior face of the obturaculum and a medial structure secreted by the obturacular halves are char-

acters shared by all species in the Escarpidae. The crust-like material appears to be about equally developed in the four species of the family. This is not the case, however, for the medial structure. Jones (1985) did not report dimensions for the medial structure of *Escarpia laminata*, presumably because of its small size. He reported, however, that the medial structure of *E. spicata* extends as much as 9.5 mm above the anterior face of the obturaculum. Southward (pers. comm.) indicates that one specimen of their new genus (Southward et al. 2001) possesses a medial structure that extends 20

←

approximate position of excretory pore. Note ciliated groove on dorsal surface of vestimentum (arrowheads). E, Enlarged view of posteroventral margin of vestimentum showing lobed condition. Arrowheads indicate plaques associated with epidermis of vestimentum and trunk. cf, ciliated field. Scale bars: A–C = 10 mm; D = 5 mm; E = 2 mm.

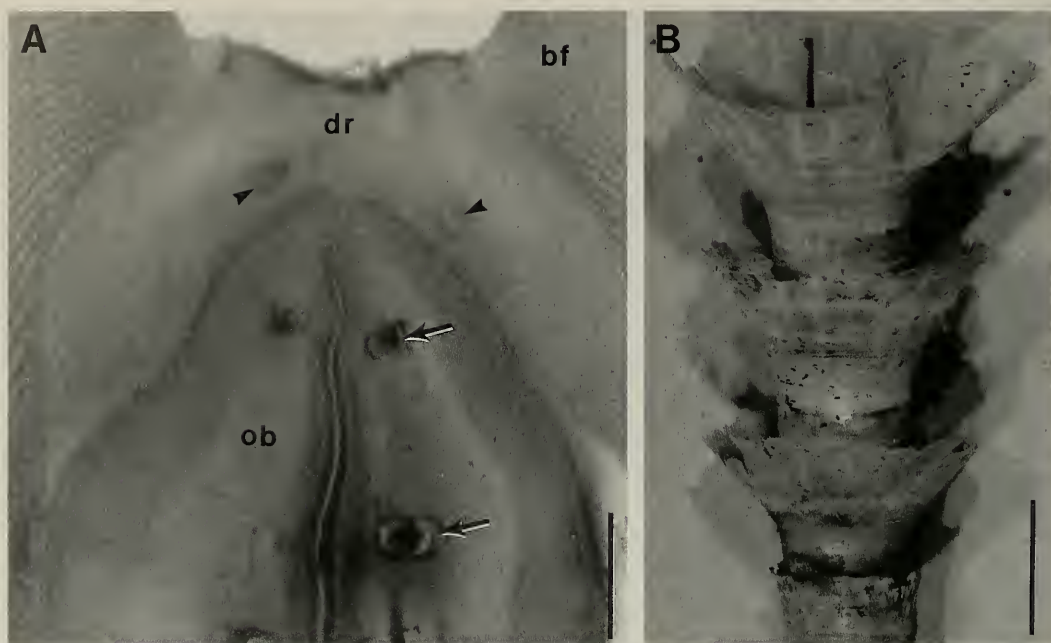


Fig. 4. *Seepiophila jonesi*, new species. A, Non-type specimen. Light microscopic view of transverse section through obturaculum region. Small arrowheads indicate positions of paired excretory ducts. Arrows indicate sections through obturaculum blood vessel. bf, branchial filaments; dr, dorsal ridge; ob, obturaculum half. B, Anterior region of tube showing aperture surrounded by broadly flaring funnel and two well-developed collars posterior to aperture. Scale bars: A = 0.5 mm; B = 10 mm.

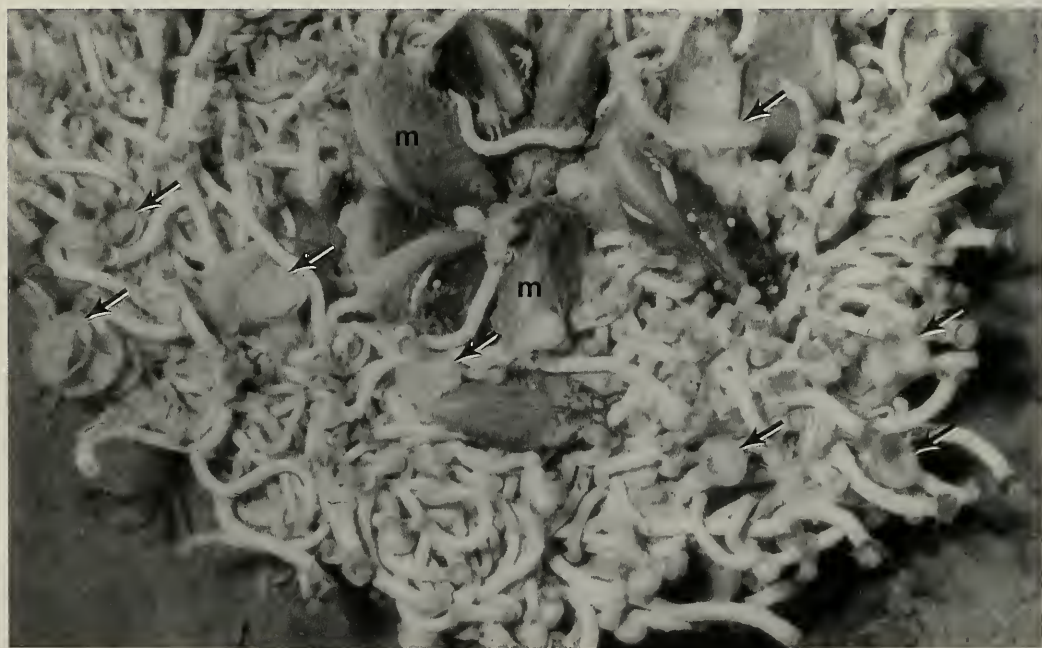


Fig. 5. Individuals of *Seepiophila jonesi* (arrows) within a clump of juvenile specimens of *Lamellibrachia* cf. *luynesi* and several seep mussels (m). No scale.

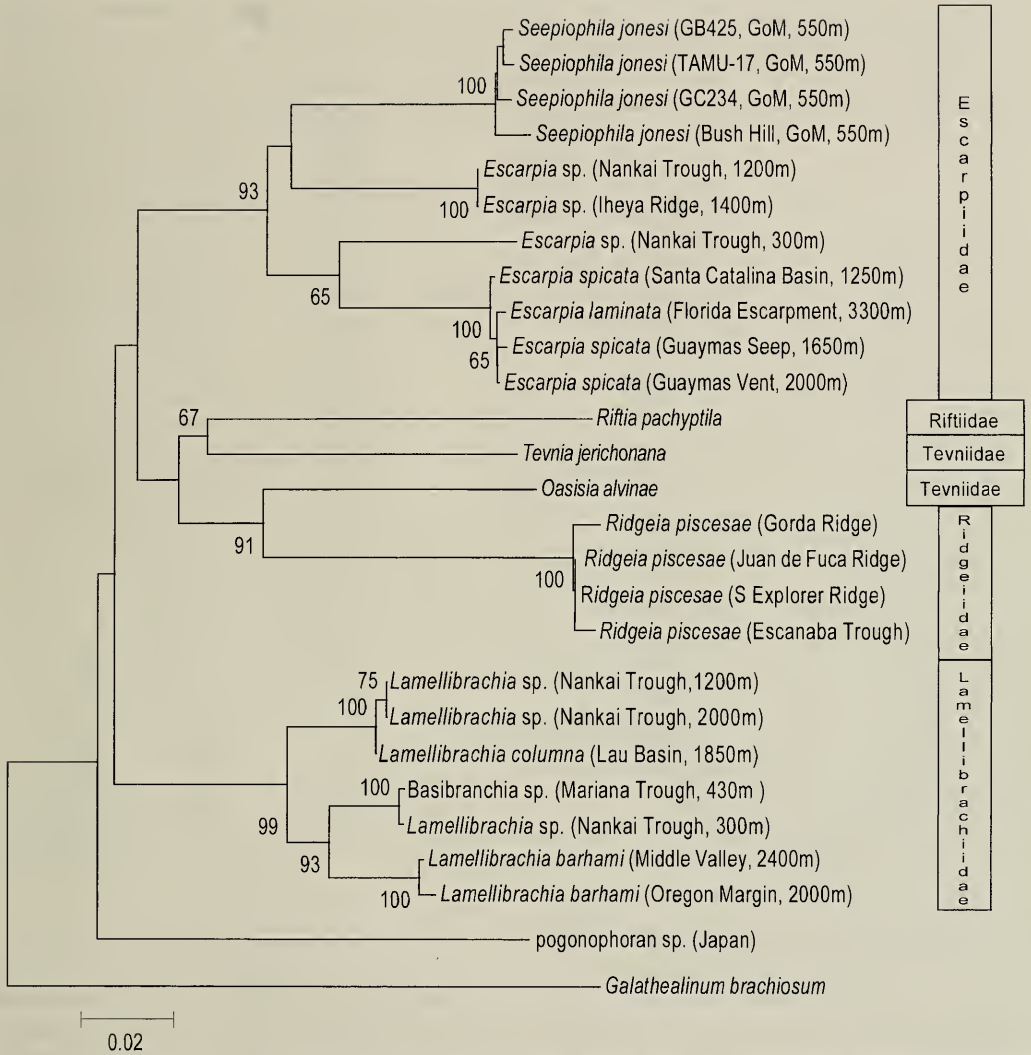


Fig. 6. Minimum evolution tree showing the relationships among tube worms based on a partial sequence (500 base pairs) of the mitochondrial cytochrome oxidase I gene, using the Kimura 2-parameter correction for multiple substitutions (references and Genbank accession numbers shown in Table 2). Numbers at nodes indicate the proportion of occurrences of a particular branching order in 1000 bootstrap replications. Bootstrap values below 65 not shown. GoM, Gulf of Mexico.

mm beyond the anterior face of the obturaculum. While the medial structure of *Seepiophila jonesi* is prominent and readily visible, it does not project a great distance beyond the anterior face of the obturaculum. The greatest distance recorded in specimens available for this study was 3.5 mm. Also, the medial structure of *S. jonesi* ends bluntly, whereas those of the new genus

(Southward et al. 2001) and *E. spicata* taper to a sharp point or terminate in a slightly bifid tip, respectively.

Paired internal excretory ducts opening through a single pore is a feature *Seepiophila jonesi* shares with other species in the Escarpiidae. However, in addition to having only a single type of filament associated with its branchial lamellae, the posteroven-

Table 2.—Collection locations, GenBank accession numbers and references for vestimentiferan specimens used in the present analysis of the COI gene.

Organism	Location	GenBank accession	Reference
<i>Escarpia laminata</i>	Florida Escarpment	U74063	Black et al. 1997
<i>Escarpia</i> sp.	Nankai Trough (300 m)	D50593	Kojima et al. 1997
<i>Escarpia</i> sp.	Nankai Trough (1200 m)	D50594	Kojima et al. 1997
<i>Escarpia</i> sp.	Iheya Ridge (1400 m)	D50595	Kojima et al. 1997
<i>Escarpia spicata</i>	Guaymas Basin seep	U74065	Black et al. 1997
<i>Escarpia spicata</i>	Guaymas Basin vent	U74064	Black et al. 1997
<i>Escarpia spicata</i>	Santa Catalina Basin whale fall	U84262	Feldman et al. 1998
<i>Basibranchia</i> sp.	Mariana Trough	U74078	Black et al. 1997
<i>Lamellibrachia barhami</i>	Middle Valley	U74055	Black et al. 1997
<i>Lamellibrachia barhami</i>	Oregon margin	U74054	Black et al. 1997
<i>Lamellibrachia columna</i>	Lau Basin	U74061	Black et al. 1997
<i>Lamellibrachia</i> sp.	Nankai Trough (1200 m)	D38029	Kojima et al. 1997
<i>Lamellibrachia</i> sp.	Nankai Trough (300 m)	D38030	Kojima et al. 1997
<i>Lamellibrachia</i> sp.	Nankai Trough (2000 m)	D50592	Kojima et al. 1997
<i>Oasisia alvinae</i>	21°N Eastern Pacific Rise	U74069	Black et al. 1997
<i>Seepiophila jonesi</i>	Gulf of Mexico, Bush Hill	AF317287	This study
<i>Seepiophila jonesi</i>	Gulf of Mexico, GB425	AF317288	This study
<i>Seepiophila jonesi</i>	Gulf of Mexico, GC234	AF317289	This study
<i>Seepiophila jonesi</i>	Gulf of Mexico, TAMU-17	AF317290	This study
<i>Ridgeia piscesae</i>	Southern Explorer Ridge	U74057	Black et al. 1997
<i>Ridgeia piscesae</i>	Juan de Fuca Ridge	AF022233	Black unpublished
<i>Ridgeia piscesae</i>	Gorda Ridge	U87978	Black et al. 1998
<i>Ridgeia piscesae</i>	Escanaba Trough	AF022235	Black unpublished
<i>Riftia pachyptila</i>	9°N Eastern Pacific Rise	U74074	Black et al. 1997
<i>Tevnia jerichonana</i>	9°N Eastern Pacific Rise	U74075	Black et al. 1997
pogonophoran sp.	Japan	D50598	Kojima et al. 1997
<i>Galathealinum brachiosum</i>	Oregon	AF178679	Boore & Brown 2000

tral margin of the vestimentum is deeply incised in *S. jonesi*, whereas this margin is entire in species of *Escarpia*. *Seepiophila jonesi* and species of *Escarpia* also differ in the relative position of the excretory pore. Jones (1985) states that the excretory pore is situated near the base of the obturaculum in *Escarpia*, whereas in *S. jonesi* it is positioned approximately one-third the distance from the base to the apex of the obturaculum.

Collars associated with tubes is a widespread feature among basibranchian vestimentiferans, and therefore, we believe this characteristic should not be emphasized in comparative accounts. However, it is worthy of note that the tubes of *Seepiophila jonesi* possess well-developed collars, whereas such collars are not present on tubes of species of *Escarpia*.

## Discussion

Presently, 15 species of vestimentiferan tube worms have been recognized and described (Webb 1969; van der Land & Nørrevang 1975; Jones 1981, 1985; Mañé-Garzón & Montero 1985; Southward 1991; Miura et al. 1997; Southward & Galkin 1997). *Ridgeia phaeophiale*, originally described by Jones (1985), was subsequently synonymized with *R. piscesae* by Southward et al. (1995). Of the remaining 14 species, eight species are reported only from hydrothermal vent communities, including *Riftia pachyptila*, *Oasisia alvinae*, *Tevnia jerichonana*, *Ridgeia piscesae*, *Alaysia spiralis*, *Lamellibrachia columna*, *L. satsuma* and *Arcovestia ivanovi*. Four species are known exclusively from cold-water communities, including *L. barhami*, *L. luy-*

*mesii*, *L. victori*, and *Escarpia laminata*. *Escarpia spicata* is reported from cold-water and hydrothermal vent sites (Jones 1985, Black et al. 1997). *Seepiophila jonesi*, at present, represents an additional species occurring only in cold-water communities.

The recognition of *Seepiophila jonesi* raises the number of vestimentiferan species known from the Gulf of Mexico to three. *Lamellibrachia* cf. *luymesi* and *S. jonesi* are sympatric in all of the shallow water hydrocarbon seep communities sampled for this study. The third species, *Escarpia laminata*, is currently recorded only from deep water at the base of the Florida Escarpment (Jones 1985).

In order to further clarify the phylogenetic position of *Seepiophila jonesi* among other vestimentiferans, we conducted an analysis of the mitochondrial COI gene in specimens of the genera *Seepiophila*, *Escarpia*, *Riftia*, *Tevnia*, *Oasisia*, *Ridgeia*, and *Lamellibrachia* (see Table 2). The average divergence for the COI gene among the four specimens of *S. jonesi* from the Louisiana Slope was low (0.8%), whereas the average divergence among the vestimentiferans in the escarpid cluster was 7.6%. As a comparison, sequence divergence within the described group of *L. barhami* is 0.3%, and the divergence among the lamellibrachids is 4.5%. This difference in divergence is reflected in the deeper branches between species of the escarpid cluster than those of the lamellibrachid group (Fig. 6). The very low sequence divergence among the samples of *S. jonesi* suggests that the four individuals (found within 65 km of each other) are members of a single, freely interbreeding species. The very deep branching pattern between *S. jonesi* and other species in the family Escarpiidae is a reflection of the relatively high degree of sequence divergence between *S. jonesi* and the remaining species of the Escarpiidae. Although no definitive "molecular clock" exists that could generate benchmarks for the naming of genera, families, etc., the deep branching pattern within the Escarpiidae relative to

that within the Lamellibrachiidae supports the placement of the Louisiana Slope vestimentiferans within a new genus but still within the larger cluster of the family Escarpiidae.

#### Acknowledgments

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## Syllidae (Polychaeta) from San Quintín lagoon, Baja California, México, with the description of a new genus

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*Abstract.*—During a recent study of the polychaetes from San Quintín lagoon (Baja California) 514 specimens belonging to the family Syllidae (Polychaeta) were collected, but only a few species were previously reported. In this paper, we report seven species: *Syllis aciculata* (Treadwell, 1945), *Syllis gracilis* (Grube, 1840), *Syllis heterochaeta* (Moore, 1909), *Exogone (Exogone) lourei* (Berkeley & Berkeley, 1938), *Sphaerosyllis californiensis* (Hartman, 1966), *Grubeosyllis mediodentata*, a new combination, and *Cicese sphaerosylliformis*, a new genus, and species. *Grubeosyllis mediodentata* is characterized by having cylindrical, somewhat elongated papilliform dorsal cirri, a long proventriculus and pharynx, pharyngeal tooth located in front of the midline of the pharynx, and compound setae with long bidentate blades provided with long, fine spines on margin. The new genus *Cicese* is similar to the genus *Sphaerosyllis* since it has antennae, tentacular cirri and anal cirri with bulbous bases, as well as papillae on the palps and dorsum, but it has two pairs of tentacular cirri instead of a single pair.

The Syllidae is a very large family of polychaetes with a high number of described species; most species are small and usually overlooked in macrofaunal studies. Syllids of the Pacific coast of Mexico were reported in a few papers: Rioja (1941, 1947a, 1947b, 1959, 1962); the papers of Rioja (1943), Góngora-Garza (1984) and Góngora-Garza & de León González (1993) are the only ones devoted exclusively to this family. The former paper also includes a key for all the syllids known on the Pacific coast of México; a total of 49 species of Syllidae is reported in the key. Other papers treating syllids from close areas are those of Hartman (1968) and Kudenov & Harris (1995) (for California), Hartmann-Schröder (1959) (for El Salvador), Fauchald (1977), Fauchald & Reiner (1975) and López et al. (1997) (for Panamá) and Westheide (1974) (for the Galá-

pagos Islands). Other studies dealing with syllids are Day (1967) and Fauchald & Reiner (1975).

San Quintín lagoon is a highly productive coastal lagoon located between 30°24'–30°30'N and 115°57'–116°01'W on the Pacific coast of Baja California (Fig. 1). This lagoon has an area of 42 km<sup>2</sup> and around 75% of it is covered by the eelgrass *Zostera marina* (Inclán-Rivadeneira & Acosta-Ruiz 1988, Ibarra-Obando 1990). It has been exploited for many years (mariculture), but it can still be considered a relatively non-disturbed area, although intensive oyster mariculture is being considered in the near future.

The lagoon has the shape of an inverted “Y”, the western arm (Falsa Bay) has an average depth of 4 m, whereas the eastern arm (San Quintín Bay) has an average depth of 8 m. Granulometric studies show

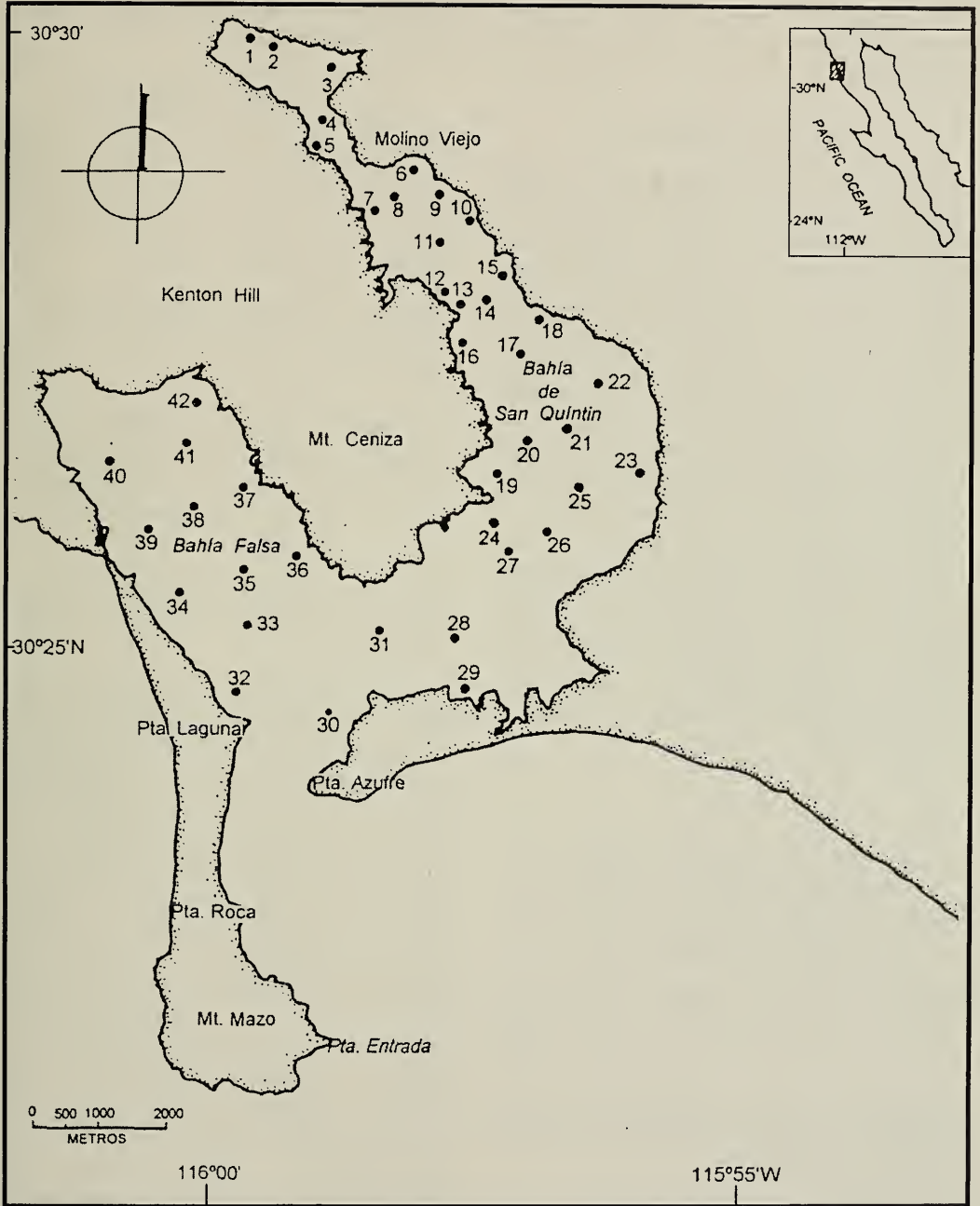


Fig. 1. Study site: sampling stations in San Quintin Bay, Baja California, Mexico.

that in shallow areas, as well as to the north of both arms, clay and silty-sand predominate, whereas near the mouth very fine sands are more abundant. The channel sediments are highly diverse, ranging from me-

dium to fine sand and silt (Barnard 1970, Calderón-Aguilera 1992). The lagoon margins present a typical saltmarsh flora with *Spartina foliosa* and *Salicornia virginica* among other vascular plants. Syllids are

more abundant in areas of fine sand, covered by *Zostera marina* and *Spartina foliosa*.

#### Materials and Methods

Forty-four stations distributed in both arms were sampled in December 1995 and April 1998 (Table 1). Two replicates per station were collected with a geological corer (16 cm internal diameter, 12 cm depth) with a sampling area of 0.02 m<sup>2</sup>. Sediments were sieved in the field using 1 mm mesh size and retained material was preserved in 7% buffered formaldehyde. In the laboratory, samples were washed using a 0.5 mm mesh and transferred to 70% isopropanol. Polychaetes were then sorted and syllids identified to species level.

In the material examined, BSQ represent the initials for Bahía San Quintín, followed by the station number. Samples are represented by M and replicates by R. Specimens are deposited in the Polychaete Collection of Universidad Autónoma de Nuevo León (UANL).

#### Results

Family Syllidae Grube, 1850

Subfamily Syllinae Grube, 1850

Genus *Syllis* Savigny in Lamarck, 1818

*Syllis aciculata* Treadwell, 1945

*Typosyllis aciculata* Treadwell, 1945:1–2, figs. 1–5; Hartman, 1968:475, text-figs. 1–7.

*Material examined*.—BSQ 42R (6).

*Distribution*.—From California to Panamá; South Chinese Sea.

*Syllis gracilis* Grube, 1840

*Syllis gracilis* Grube, 1840:77, pl. 31a–l; San Martín, 1984:376, pls. 97, 98.

*Syllis (Syllis) gracilis*.—Fauvel, 1923:259, fig. 96F–I; Day, 1967:241, fig. 12.1m–p.

*Material examined*.—BSQ 14 (1), BSQ 7M (1), BSQ 7R (1).

*Distribution*.—Cosmopolitan in temperature and tropical seas.

*Syllis heterochaeta* Moore, 1909

*Syllis (Ehlersia) heterochaeta*.—Rioja, 1941:694–695; Hernández-Alcántara, 1992:200.

*Langerhansia heterochaeta*.—Hartman, 1968:434–435, figs. 1–7.

*Material examined*.—BSQ 43M (5).

*Distribution*.—Western Mexico to western Canada.

Subfamily Exogoninae Rioja, 1925

Genus *Grubeosyllis* Verrill, 1900

*Grubeosyllis mediodentata* (Westheide, 1974), new combination  
Figs. 2–4

*Brania mediodentata* Westheide, 1974:93–97, figs. 42A–C, 43; Russell, 1991:52–54, Fig. 2.

*Material examined*.—BSQ 29 (1). BSQ 6R (1). BSQ 19R (2). BSQ 23 (1). BSQ 39 (3). BSQ R15 (1). BSQ R16 (1). BSQ 27R (1). BSQ 17R (1). BSQ 6 (1). BSQ 28R (1). BSQ 25 (1). BSQ 19 (2). BSQ 14 (18) + 2 specimens used for SEM observations.

*Description*.—Body small, slender, 1.9 mm long, 0.2 mm wide, for 31 setigers, without color markings; intersegmental furrows well marked (Fig. 2A). Prostomium ovate, about 2.2 times wider than long; two pairs of lensed eyes in open trapezoidal arrangement and two small anterior eyespots. Antennae elongate, fusiform, with small subdistal enlargement, shorter than prostomium and palps together; median antenna of same length or slightly longer than prostomium, originating in middle of prostomium; lateral antennae somewhat shorter than median antenna, originating in front of anterior eyes, slightly posterior to eyespots (Figs. 2A, B, 3A). Palps small, shorter than prostomium, fused along entire length, with distal notch. Tentacular segment well defined, similar in length to following segments; two ciliated lateral nuchal organs

Table 1.—Station locations and granulometry at San Quintín lagoon, Baja California.

Station	Lat. N.	Long. W.	Eh(mV)	T°C	O.M. (%)	Sand (%)	Silt (%)	Clay (%)
1	30°29'20"	115°59'35"			2.35	39.86	30.68	29.28
2	30°29'34"	115°59'34"	-255	21.4	0.43	96.8	3.2	0
3	30°29'06"	115°59'02"			1.86	63.78	23.64	7.9
4	30°29'23"	115°58'57"	-184	20.8	1.33	60.08	25.81	13.61
5	30°29'06"	115°59'01"	-127	20.1	2.81	44.97	30.12	22.46
6	30°29'02"	115°58'37"	103	20.5	2.78	13.42	65.52	21.26
7	30°28'38"	115°58'26"	-150	20.5	1.91	63.79	23.38	10.21
8	30°28'45"	115°58'10"	-280	20.4	0.58	71.88	27.84	0.77
9	30°28'50"	115°57'51"	-322	20.6	2.66	36.2	36.38	22.78
10	30°28'28"	115°57'29"	168	21.4	2.37	65.82	18.78	14.63
11	30°28'18"	115°57'46"	-294	20.5	0.79	84.38	11.51	4.11
12	30°27'52"	115°57'50"	-145	19.1	0	25.84	66.09	8.1
13	30°27'48"	115°57'46"	-203	20.5	0.58	86.72	13.28	0
14	30°27'49"	115°57'30"	-320	21	1.55	50.59	35.64	12.8
15	30°28'02"	115°57'11"	-126	19.9	3.33	19.77	44.88	27.69
16	30°27'33"	115°57'41"	-360	20	3.1	96.68	3.32	0
17	30°27'21"	115°57'09"	-230	20.4	1.89	54.51	31.55	14.86
18	30°27'46"	115°57'06"	-200	20.4	1.4	69.61	6.59	21.57
19	30°26'32"	115°57'17"	-252	21.4	2.03	60.08	25.81	13.61
20	30°26'46"	115°57'00"	-156	20.1	0.62	74.65	25.04	2.36
21	30°26'52"	115°56'37"	-297	20.3	0.76	78.61	12.34	9.26
22	30°27'07"	115°56'17"	-30	18.9	1.68	37.77	35.52	22.97
23	30°26'33"	115°56'03"	152	19.3	1.27	42.58	40.04	25.89
24	30°25'52"	115°57'11"			2.23	31.95	28.86	24.06
25	30°26'22"	115°56'33"	-257	20.7	0.89	52.38	24.01	20.78
26	30°25'58"	115°56'48"	-166	21.6	0.43	97.06	2.9	0
27	30°25'50"	115°57'09"	-223	21.1	1.38	98.08	1.92	0
28	30°25'12"	115°57'31"	-136	20.5	0.48	89.05	10.95	0
29	30°24'32"	115°57'29"	-242	21.6	0.28	98.13	2.25	0
30	30°24'29"	115°58'38"	-94	20.5	0.05	71.78	17.04	8.86
31	30°25'10"	115°58'12"	-104	21.5	0.37	88.4	11.79	0
32	30°24'39"	115°59'46"	-174	20.5	1.99	66.82	21.8	10.39
33	30°25'12"	115°59'44"	-285	20.6	0.26	93.75	6.25	0
34	30°25'32"	115°00'14"	-84	21.1	2.96	51.3	36.54	12.52
35	30°25'42"	115°59'44"	-326	21.1	2.21	42.27	45.83	6.4
36	30°25'52"	115°59'12"	-104	21.5	0.53	58.99	33.54	7.03
37	30°26'21"	115°59'33"	-205	20.6	0.93	30.03	60	6.05
38	30°26'10"	115°59'58"	-115	21	2.57	39	46.14	15.27
39	30°26'00"	115°00'26"	-148	19.8	1.16	7.26	72.59	8.17
40	30°26'32"	115°00'36"	181	21.9				
41	30°26'42"	115°00'42"	100	21.6				
42	30°26'54"	115°59'55"	-86	21.3				

between prostomium and peristomium (Fig. 3A); two pairs of tentacular cirri, short, smaller than antennae, ovate to conical, somewhat larger at bases (Figs. 2A, B, 3A, B). Dorsal cirri on all setigers; anterior dorsal cirri similar in shape to dorsal tentacular cirri but somewhat longer, shorter than parapodial lobes, but progressively longer and slender with very small difference in

width between bases and tip, cylindrical (Fig. 2A, B, D); dorsal cirri of midbody somewhat longer than parapodial lobes (Fig. 2C); from midbody posteriorly, dorsal cirri progressively smaller. Parapodial lobes conical, with presetal papilla (Fig. 2C). Ventral cirri digitiform, shorter than parapodial lobes. Compound setae heterogomph, with short, fine subdistal spines on

shafts, and blades strongly bidentate, both teeth similar in length and shape or proximal tooth somewhat shorter than distal tooth, well separated from each other, elongate, provided with long, upwardly projecting spines on margin, especially on most anterior and dorsal setae (Figs. 2E, H, 4A–C). Anterior parapodia each with about 10 compound setae, with marked dorsoventral gradation, 28  $\mu\text{m}$  blades on dorsalmost setae, 18  $\mu\text{m}$  blades on ventralmost ones (Fig. 2E); progressively decreasing number of compound setae on each parapodium, posterior parapodia each with about 5 compound setae, blades 32  $\mu\text{m}$  dorsally, 14  $\mu\text{m}$  ventrally (Fig. 2H). Solitary dorsal simple seta from anterior parapodia, thick, strongly bidentate, with large, triangular proximal tooth, forming about a 45° angle with the distal tooth, smooth on anterior parapodia (Fig. 2F), progressively provided with more spines on margin (Fig. 2I), forming several rows of spines (observations by SEM) (Fig. 4D). Solitary ventral simple seta on each posterior parapodium, sigmoid, similar to dorsal simple seta but slender, smooth (Fig. 2J) or provided with few short spines on margin (SEM observations) (Fig. 4E). Anterior parapodia each with two slender aciculae, one straight and other acuminate (Fig. 2G), provided with subdistal enlargement and conical tip; single aciculum on each middle and posterior parapodium, acuminate (Fig. 2K). Pharynx long and wide, through about 5–6 segments (Fig. 2A); mouth opening provided with circle of cilia and about 10 soft, very small papillae (Fig. 3B); pharyngeal tooth very small, inconspicuous, conical, located just in front of middle of pharynx, far from anterior margin of pharynx (Fig. 2A, B). Proventriculus similar in length to pharynx, through about 5 segments, with about 27 rows of muscle cells (Fig. 2A). Females carrying eggs on dorsolateral position of midbody; eggs attached to body by means of thin notosetae (Fig. 3C, D).

*Remarks.*—Most of the species of the genus *Grubeosyllis* have fusiform dorsal cirri,

with bulbous bases and long, pointed tips; however, a few species of this genus have cylindrical, digitiform dorsal cirri, as in *G. mediodentata*. This species has a body very similar to *G. swedmarki* (Gidholm, 1962), from the North Atlantic, but the compound setae are completely different being short and unidentate in *G. swedmarki* (Gidholm 1962, Parapar et al. 1993) and long and bidentate in *G. mediodentata*. *Grubeosyllis celiae* (Parapar & San Martín, 1992), from Ceuta (North West Africa) has longer dorsal cirri, a longer proventriculus, compound setae with shorter blades than those of *G. mediodentata* and the dorsal simple setae are unidentate (Parapar & San Martín 1992).

This species reproduces by external gestation, as many others of the same genus and the subfamily Exogoninae. The eggs are attached to the body by means of epitokous setae (Fig. 3C), as recently reported by Kuper & Westheide (1998) for other similar species.

*Distribution.*—Galápagos Islands, Belize. This species is newly recorded for México.

#### *Cicese*, new genus

*Diagnosis.*—Body small, cylindrical. Prostomium with two pairs of lensed eyes and two eyespots. Palps fused along entire length. Peristomium well defined, not fused to prostomium, with two pairs of tentacular cirri. Dorsal and ventral cirri on all parapodia. Antennae, tentacular cirri, anal cirri and, at least, some dorsal cirri with bulbous bases and slender tips. Palps, pygidium and dorsum provided with papillae. Two anal cirri. Pharynx provided with an anterior middorsal tooth and a crown of papillae. Parapodia each with several compound setae, and dorsal and ventral simple setae on some parapodia. Aciculae acuminate. Females carrying eggs dorsally by means of notosetae and mature males provided with long natatory setae.

*Remarks.*—The new genus is close to a group of species of the genus *Sphaerosyllis*,

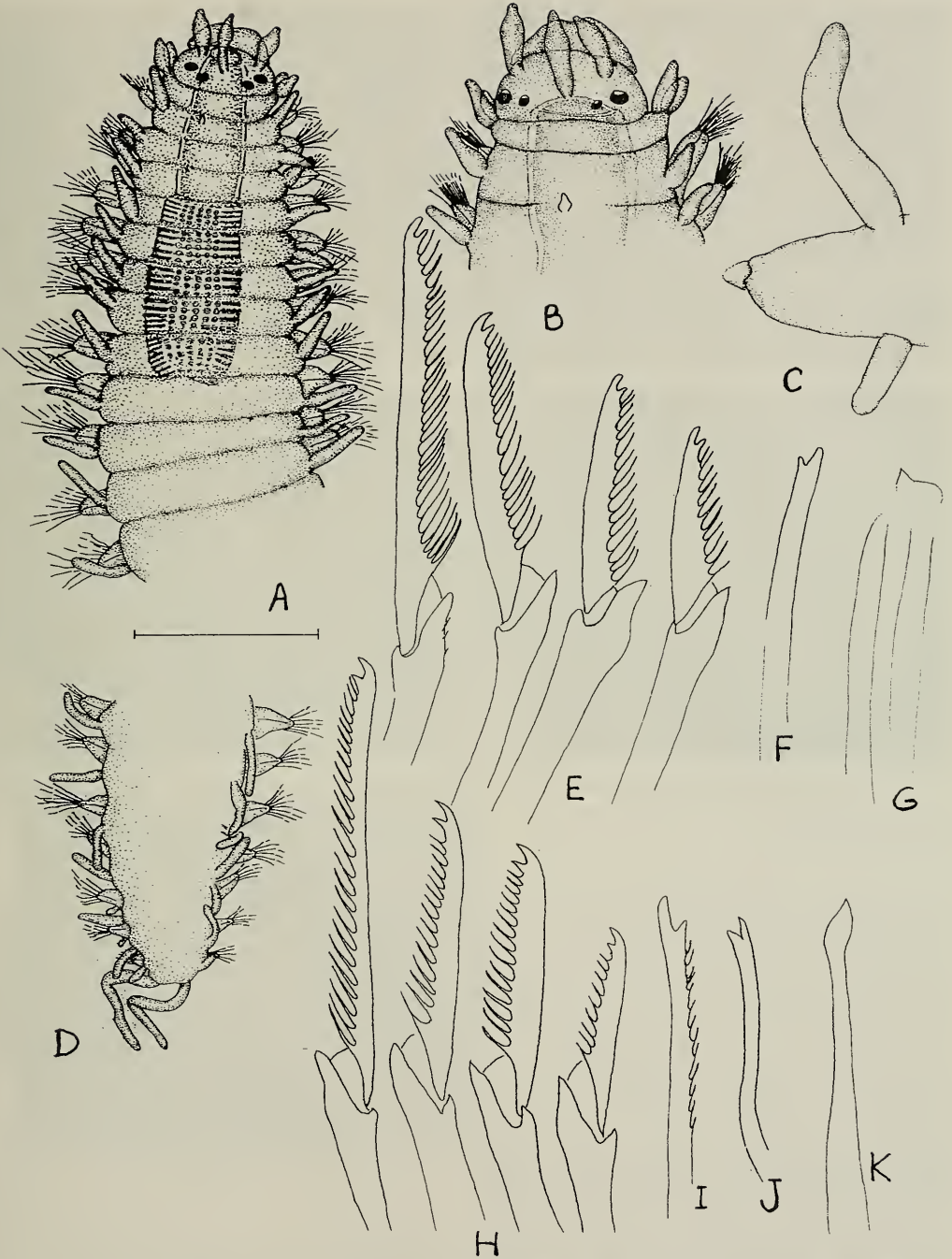


Fig. 2. *Grubeosyllis mediodentata* (Westheide, 1974). A, anterior end, dorsal view. B, detail of prostomium and anterior setigers. C, midbody parapodium. D, posterior end, dorsal view. E, compound setae, anterior parapodium. F, dorsal simple seta, anterior parapodium. G, aciculae, anterior parapodium. H, compound setae, posterior parapodium. I, dorsal simple seta, posterior parapodium. J, ventral simple seta. K, aciculum, posterior parapodium. Scale: A, D—0.14 mm; B—0.6 mm; E—K—15  $\mu$ m.

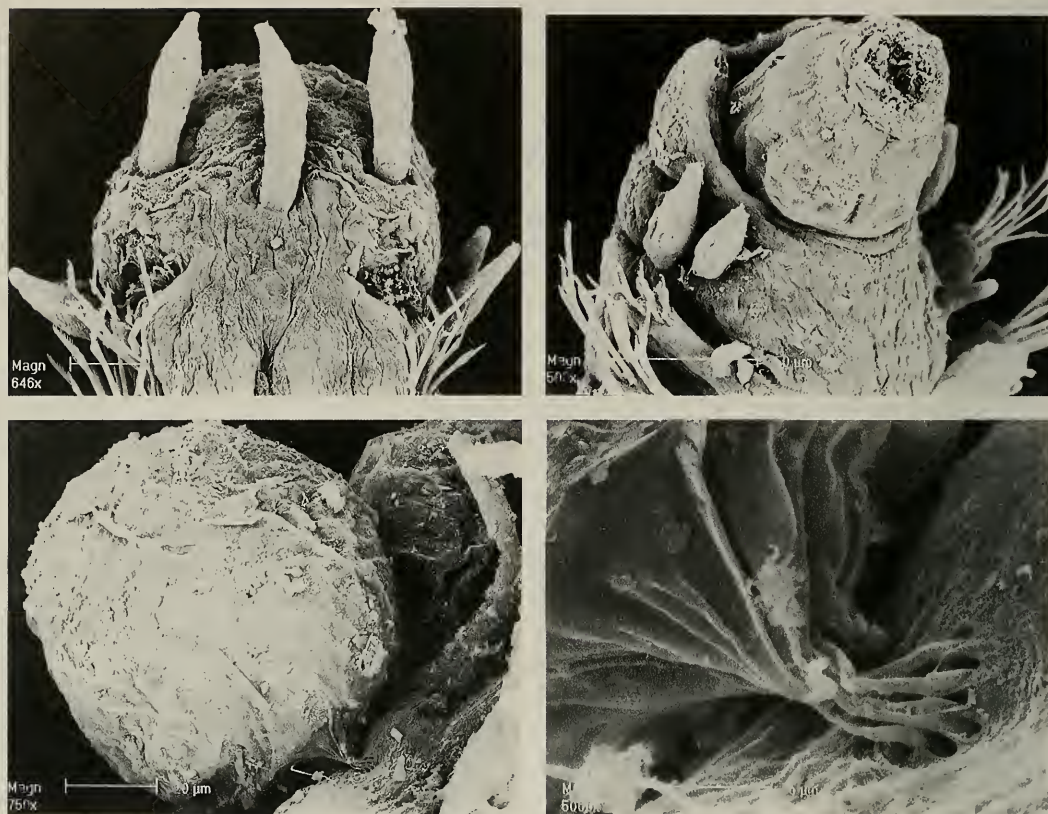


Fig. 3. *Grubeosyllis mediodentata* (Westheide, 1974). SEM. A, detail of prostomium, dorsal view. B, lateroventral view with proboscis everted. C, an egg, attached to body by means of capillary notosetae. D, detail of capillary notosetae.

having more or less elongate dorsal cirri on the midbody, two pairs of eyes and a pair of eyespots on the prostomium, acuminate aciculae, compound setae with bidentate blades and small, inconspicuous papillae on the dorsum, palps and pygidium (e.g., *Sphaerosyllis bilobata* Perkins, 1981, *S. cryptica* Ben-Eliahu, 1977, *S. belizensis* Russell, 1989, and others) (see Perkins 1981, Ben-Eliahu 1977, Russell 1989). However, all these species, as members of the genus *Sphaerosyllis*, are provided with a single pair of tentacular cirri. On the other hand, *Cicese* is also closely related to *Grubeosyllis* (Verrill, 1900), sharing the shape of the aciculae, similar setae, and having two pairs of tentacular cirri. However, *Cicese* has papillae, whereas *Grubeosyllis* has a smooth dorsum, palps and pygidium, a

character considered as exclusive to *Sphaerosyllis*.

*Etymology*.—The name is given in honor of the research center CICESE (Centro de Investigación Científica y Estudios Superiores de Ensenada) located in Baja California, México.

*Cicese sphaerosylliformis*, new species  
Fig. 5

*Material examined*.—BSQ R8; Holotype. BSQ R17; 1 paratype. BSQ 23; 1 paratype.

*Description*.—Body small, short, holotype complete mature female 1.5 mm long, 0.2 mm wide, for 29 setigers, without color markings; dorsum covered with very small papillae, longer on posterior part of body



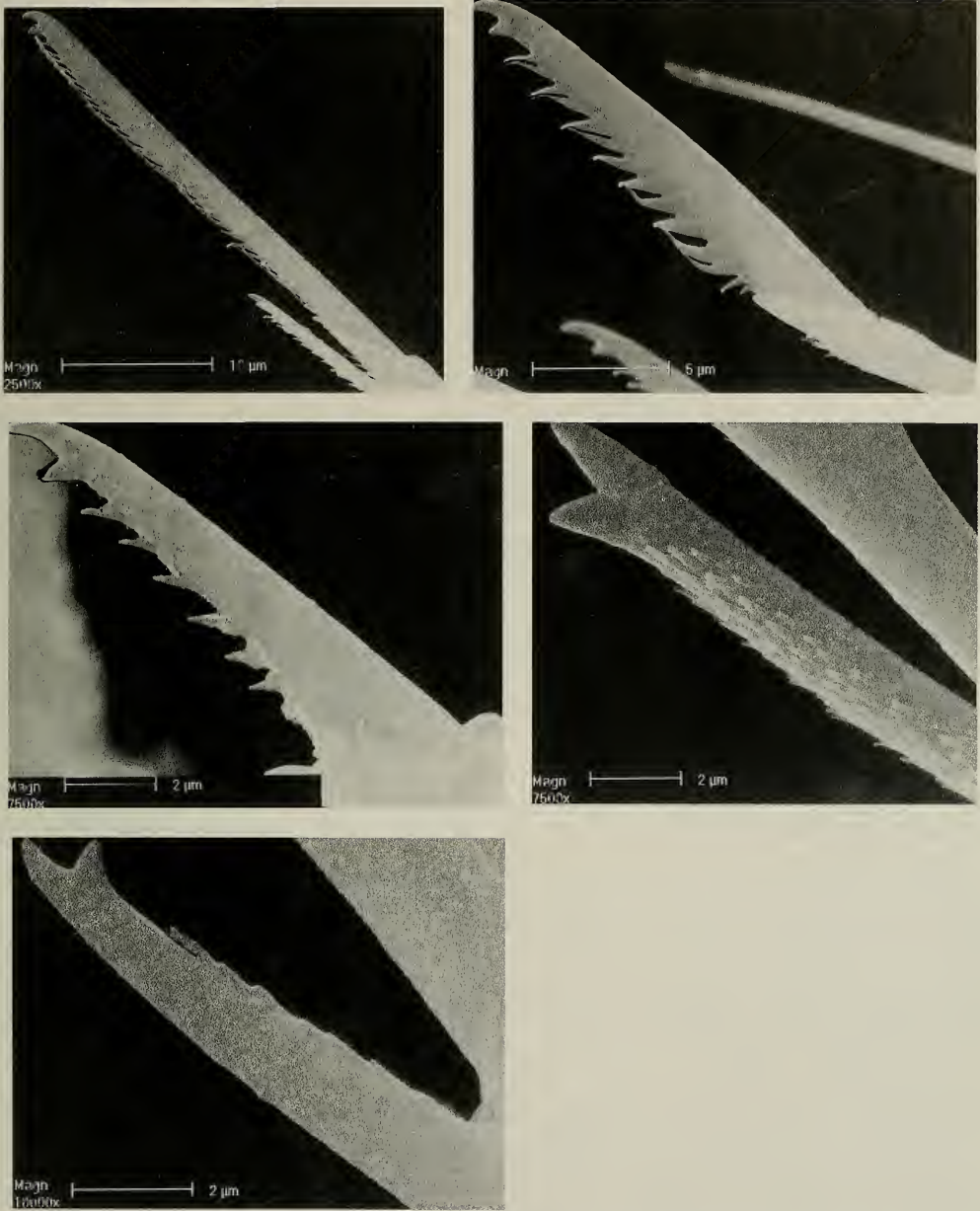


Fig. 4. *Grubeosyllis mediudentata* (Westheide, 1977). SEM. A, dorsal compound seta. B, median compound seta. C, ventral compound seta. D, dorsal simple seta. E, ventral simple seta.

(Fig. 5D, E). Prostomium ovate, more than twice as wide as long (Fig. 5A); two pairs of large, lensed eyes in very open trapezoidal arrangement, nearly on line, anterior pair larger than posterior pair, and two anterior eyespots. Median antenna longer than

prostomium and palps together, large at base, enlarged at midlength and with slender tip, originating between posterior eyes; lateral antennae onion-shaped, with bulbous bases and short, slender tips, shorter than median antenna, originating close to eye-

spots. Palps short, fused along entire length, with indistinct dorsal furrow, provided with few very small, papillae dorsally. Tentacular segment shorter than following segments, well defined, covering dorsal posterior part of prostomium, dorsally bilobed; dorsal tentacular cirri similar in length to median antenna, similar in shape to lateral antennae but somewhat more elongate (Fig. 5A); ventral tentacular cirri similar in shape to lateral antennae, but somewhat smaller (Fig. 5B). Dorsal cirri of setiger one similar in shape to dorsal tentacular cirri, somewhat longer. Dorsal cirri of setigers 2 and 3 small, with strongly bulbous bases and short, slender tips. Dorsal cirri from setiger 3 elongate, with slightly enlarged bases and long, slender tips (Fig. 5C), progressively longer and slender; dorsal cirri on midbody only somewhat shorter than body width (Fig. 5A); dorsal cirri from mid-posterior setigers shorter, less elongate, with wider bases (Fig. 5D). Parapodial lobes short, conical; ventral cirri digitiform, shorter than parapodial lobes (Fig. 5C). Compound setae heterogomph, provided with slender, bidentate blades, proximal tooth smaller than distal tooth, with long, thin, erect basal spines on margin, progressively shorter, smooth distally (Fig. 5H, I). Anterior parapodia each with about 10–13 compound setae, blades 34  $\mu\text{m}$  dorsally, 16  $\mu\text{m}$  ventrally; progressively reduced number of compound setae, on each parapodium to 6–7 on posterior parapodia, similar to anterior compound setae. Solitary dorsal simple seta from anterior parapodia (from setiger 3 in holotype), slender, unidentate, provided with short, thin spines on margin (Fig. 5G). Solitary ventral simple seta on far posterior parapodia, slender, sigmoid, bidentate, smooth. Acicula solitary, slender, acuminate, provided with a subdistal enlargement and a long, filiform tip (Fig. 5F). Pharynx slender, everted in holotype (Fig. 5A), with pharyngeal tooth located anteriorly, surrounded by crown of about 10 small soft papillae; a few, probably 5, subdistal papillae on pharynx (Fig. 5B). Proventriculus

shorter than pharynx, through about 4 segments, with about 17 roes of muscle cells. Pygidium small, provided with small papillae and two long anal cirri, with bulbous bases, longer than posterior dorsal cirri (Fig. 5D). Holotype carrying eggs dorsally from setiger 11; one paratype mature male, provided with natatory setae from setiger 10.

*Remarks.*—Rioja (1943) described *Brania limbata arenacea* from the Pacific coast of México with two pairs of tentacular cirri and the dorsum covered by detritus, a character of the genus *Sphaerosyllis*. Apparently, *Brania limbata arenacea* (Rioja, 1943) is a member of *Cicese*, new genus. However, it differs from *Cicese sphaerosylliformis*, new species, by having antennae, tentacular cirri and dorsal cirri all similar, with small differences in lengths, unidentate blades of compound setae and lacking eyespots.

*Etymology.*—Meaning the form of this species resembles that of *Sphaerosyllis*.

Genus *Sphaerosyllis* Claparède, 1863  
*Sphaerosyllis californiensis* Hartman, 1966  
*Sphaerosyllis californiensis*.—Kudenov & Harris, 1995:28–30, Fig. 1.8.

*Material examined.*—BSQ 6M (1). BSQ 7R (1). BSQ 8R (1). BSQ 11M (1). BSQ 12M (1). BSQ 14M (4). BSQ 14R (1). 21M (2). BSQ 26R (1). BSQ 28M (2). BSQ 31M (1).

*Distribution.*—Southern California to Baja California.

Genus *Exogone* Örsted, 1845  
 Subgenus *Exogone* Örsted, 1845  
*Exogone (Exogone) lourei* Berkeley & Berkeley, 1938

*Exogone (Exogone) lourei* San Martín, 1991:735–737; Kudenov & Harris, 1995:15–17, Fig. 1.3.

*Material examined.*—BSQ 3R (6). BSQ 5M (9). BSQ 5R (5). BSQ 6M (47). BSQ 6R (4). BSQ 8M (2). BSQ 8R (14). BSQ

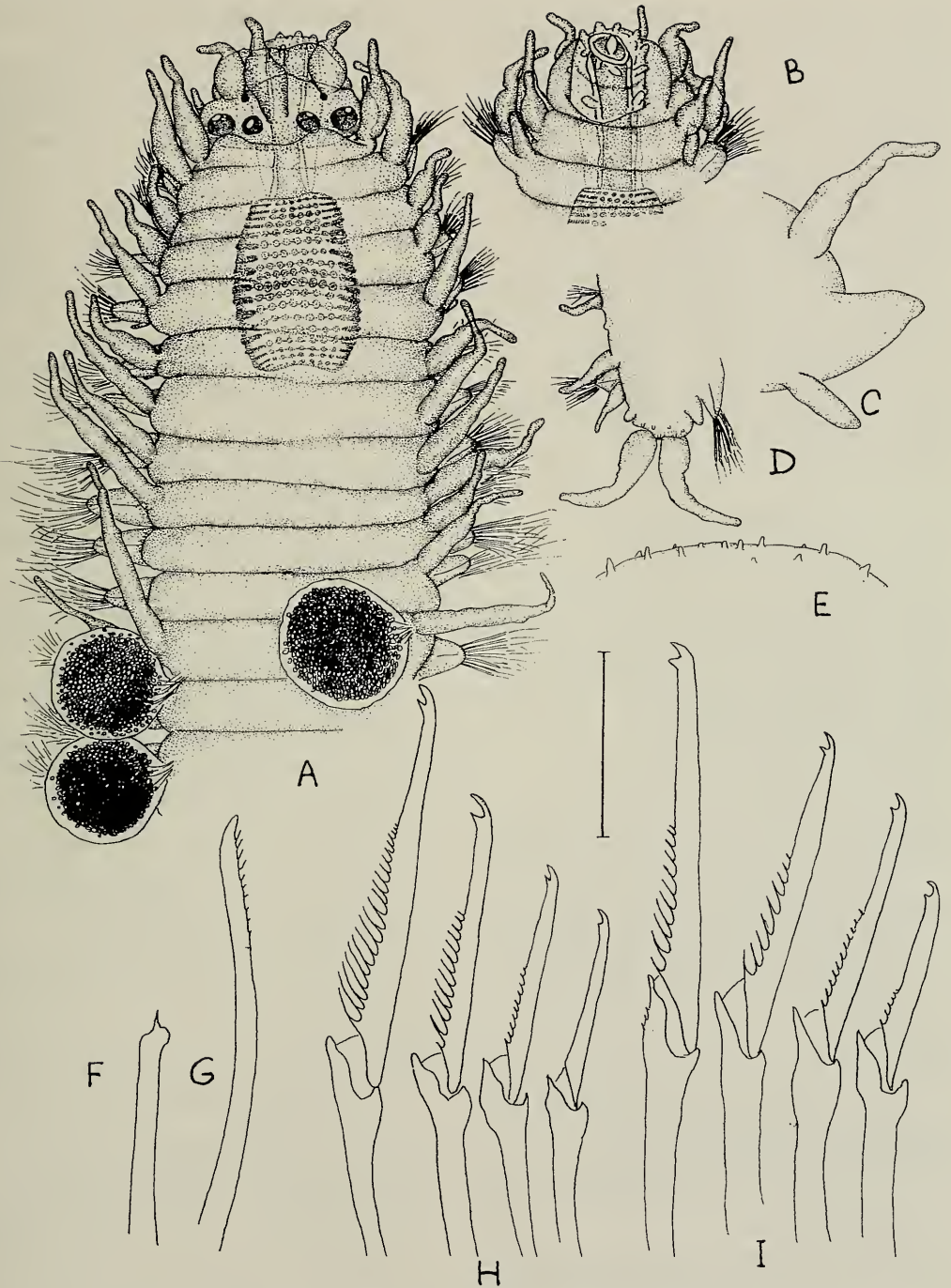


Fig. 5. *Cicese sphaerosylliformis*, new genus, new species. A, anterior end, dorsal view. B, anterior end, ventral view. C, mid-posterior parapodium. D, posterior end, dorsal view. E, detail of surface of dorsum, mid-posterior segments. F, aciculum. G, dorsal simple seta. H, compound setae, anterior parapodium. I, compound setae, posterior parapodium. A, B, F-I, from holotype; C-E, from paratype. Scale: A-E—0.65 mm; F-I—15  $\mu$ m.

9M (2). BSQ 9R (2). BSQ 11R (4). BSQ 12M (1). BSQ 12R (48). BSQ 13R (4). BSQ 14M (16). BSQ 14R (17). BSQ 15R (18). BSQ 16M (8). BSQ 16R (16). BSQ 17M (56). BSQ 17R (104). BSQ 18R (1). BSQ 19R (4). BSQ 20M (1). BSQ 20R (4). BSQ 21M (1). BSQ 21R (2). BSQ 22M (1). BSQ 22R (12). BSQ 23M (1). BSQ 23R (3). BSQ 24R (1). BSQ 25M (1). BSQ 25R (7). BSQ 26M (2). BSQ 26R (5). BSQ 27M (1). BSQ 27R (2). BSQ 34M (4). BSQ 37R (6). BSQ 39M (6). BSQ 39R (6).

*Distribution*.—Northeast Pacific, from British Columbia to México. Gulf of México, Cuba, Florida and Canary and Cape Verde Islands.

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We would like to thank M. Necoechea and G. de la Selva for helping sort the material. Financial and technical support was provided by Centro de Investigación Científica y Estudios Superiores de Ensenada (Baja California, Mexico).

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## Recognition of *Cenogenus* Chamberlin, 1919 (Polychaeta: Lumbrineridae) based on type material

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*Abstract.*—*Cenogenus* Chamberlin with *C. descendens* Chamberlin as its only species has been considered a junior synonym of *Lumbrineris*. It is here redescribed and emended as a distinct genus. Its diagnostic features include a single antenna in the nuchal fold; single digitate branchiae on anterior parapodia; maxillary apparatus of labidognath type, with four plates, maxillae III and IV edentate, maxillae V absent; mandible partially fused and simple multidentate hooded hooks. *Paraninoe* Levenstein (type species *Ninoe fusca* Moore) is a junior synonym of *Cenogenus*; both species, *C. descendens* and *C. fusca* are recognized based on type material.

Previously the external characters in lumbrinerids were considered to be uniform with simplicity and reduction of many morphological parts. Consequently, we have had a simplified generic system for the family, lumping all species described into only three or four genera. Current work on the taxonomy of lumbrinerids is changing this view; however, as a consequence of our earlier conceptions of the group, some genera were regarded as junior synonyms and have been forgotten or not considered during the creation of new taxa.

Chamberlin (1919) erected the genus *Cenogenus* to include specimens collected in abyssal depths provided with “a conical nuchal process present at anterior edge of first segment above, with four pairs of maxillae,” separating it in his key from other genera by the presence of only simple hooded hooks and with maxillae III and IV edentate. Hartman (1944), based upon these features, considered it a valid genus. However, Fauchald (1970) regarded this genus as a junior synonym of *Lumbrineris* de Blainville. Levenstein (1977) erected *Paraninoe* to include species provided with a nuchal organ and simple digitate branchiae;

she noted that most of the included species were confined to abyssal depths.

Here, I redescribe and emend *Cenogenus* and regard *Paraninoe* Levenstein, 1977, as a junior synonym.

### Materials and Methods

Type materials were borrowed from the collections of the National Museum of Natural History (USNM), Smithsonian Institution, Washington, and the Museum of Comparative Zoology (MCZ), Harvard University, Cambridge. The measurements were standardized to setiger 10; they are abridged as L10 for length to setiger 10, and W10 for width at setiger 10. Illustrations were made with a camera lucida.

*Cenogenus* Chamberlin, 1919, emended

*Cenogenus* Chamberlin, 1919:333–334.

*Paraninoe* Levenstein, 1977:189–197, figs. 1–2.

*Type species.*—*Cenogenus descendens* Chamberlin, 1919, by original designation.

*Emended diagnosis.*—Single small antenna in nuchal fold. Setae include limbate capillaries, limbate robust, and simple mul-

tidentate hooded hooks. Anterior segments with a parapodial branchia dorsal and posterior to parapodia. Maxillary apparatus and labidognath type; with four pairs of maxillae, maxillae I forceps-like with smooth edges and bridles poorly developed, maxillae II of similar length to maxillae I, maxillae III and IV edentate plates (maxillae V absent); mandibles partially fused.

### Discussion

Chamberlin (1919) erected *Cenogenus* based on the presence of a nuchal antenna, maxillary apparatus with four well developed plates with maxillae III and IV edentate and setae limbate and simple multidentate hooded hooks.

Chamberlin misinterpreted the parapodial shape of *C. descendens*; he regarded the parapodia as lacking a presetal lobe and having a finger-like postsetal lobe. In fact, the parapodia have both lobes, but they are inconspicuous, and there is a simple digitate branchia posterior to the parapodia on the dorsal side in anterior segments.

Fauchald (1970), following the traditional classification, regarded these characters as present in some species of *Lumbrineris*, and thus considered *Cenogenus* as a junior synonym of *Lumbrineris*. However, *Lumbrineris*, as defined in older systematic works, is a heterogeneous taxon that would include any abranchiate lumbrinerid; *Lumbrineris* s.s. includes only species without nuchal antennae and branchiae, with five pairs of maxillae and both simple and composite multidentate hooded hooks present (Orensanz 1990). Because the maxillary apparatus has four plates, anterior parapodia have a single branchia, nuchal antenna is present and only simple multidentate hooded hooks occur, Fauchald's synonym is here considered erroneous and *Cenogenus* is a distinct valid genus.

Levenstein (1977) erected *Paraninoe* to include species with a nuchal antenna, maxillary apparatus with four plates and postsetal lobe with a simple digitate branchia;

most were formerly included in *Ninoe* Kinberg. She stated that *Paraninoe* differs from *Ninoe* in the number of branchial filaments and in the shape of maxillae III and IV and listed five species included in her new genus. Later, Orensanz (1990) increased this list to 10 species.

Examination of type material of *Cenogenus descendens* Chamberlin, 1919 and *Ninoe fusca* Moore, 1911 (type species of *Paraninoe*) revealed that *Cenogenus* is a valid genus and *Paraninoe* Levenstein, 1977 is a junior synonym of it.

Following the list of species provided by Levenstein (1977) and Orensanz (1990), the species of *Cenogenus* includes *C. abyssalis* (Imajima & Higuchi, 1975), *C. antarctica* (Monro, 1930), *C. brevipes* (McIntosh, 1903), *C. descendens* Chamberlin, 1919, *C. fusca* (Moore 1911), *C. fuscooides* (Fauchald, 1970), *C. hartmanae* (Levenstein, 1977), *C. monotentaculata* (Averincev, 1972), *C. nagae* (Gallardo, 1968), and *C. simpla* (Moore, 1905).

*Lumbrineris minuta* Théel, 1879 was placed as a member of *Paraninoe* by Miura (1980); in the original description, its maxillary apparatus was described without maxillae V and only simple hooded hooks. However, Oug (1998) reviewed the type material and stated that it has a maxillary apparatus with five pairs of maxillae, with maxillae V free. Oug also indicated the presence of more than one species in the type material of Théel's species. A study of better material is needed to assess its generic status.

Consequently, *Lumbrineris minuta* Théel, 1879 cannot belong to *Cenogenus*; however, *P. minuta* sensu Miura (1980) is a species of *Cenogenus*.

*Cenogenus descendens* Chamberlin, 1919  
Fig. 1A–G

*Cenogenus descendens* Chamberlin, 1919:  
333–334.

*Material examined.*—Syntypes of *Cenogenus descendens* Chamberlin (USNM

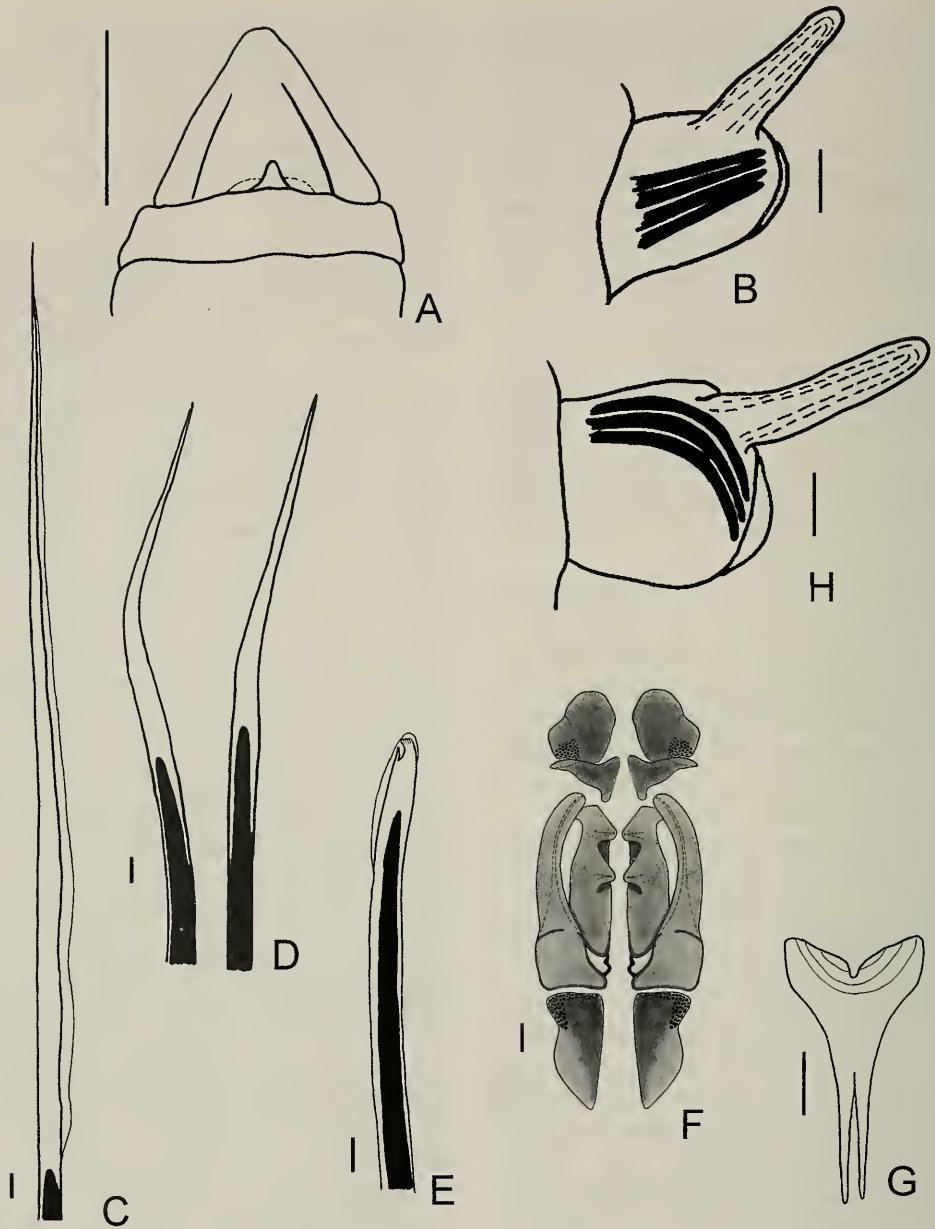


Fig. 1. *Cenogenus descendens* Chamberlin, 1919. A, prostomium, dorsal view (USNM 19344); B, second parapodium, frontal view (USNM 19344); C, long limbate seta (MCZ 2302); D, stout limbate setae (MCZ 2302); E, simple multidentate hooded hook (MCZ 2302); F, maxillary apparatus (USNM 19344); G, mandibles (USNM 19344); *Cenogenus fusca* (Moore, 1911); H, second parapodium in frontal view (USNM 17338). Scales: A = 15 mm; B, C, G, H = 0.2 mm; D-E = 13  $\mu$ m; F = 26  $\mu$ m.

19344, one specimen and MCZ 2302, one specimen and one slide). Peru, 111 miles NW off Aguja Point (5°42'S, 83°0'W), 11 Nov 1904, *Albatross* sta. 4651, 4066 m.

*Description*.—Syntypes of *C. descendens* are all incomplete. USNM specimen broken in four fragments, anterior end with 29 setigers (L10 = 5.2 mm, W10 = 2.5



mm); MCZ specimen broken in two parts with ca. 70 setigers (L10 = 5.1 mm and W10 = 2 mm).

Prostomium conical, short, about as long as wide, with a pair of divergent dorsal longitudinal black bands; with a pair of nuchal organs and an antenna in the nuchal fold (Fig. 1A). Peristomium shorter than prostomium; separation between rings distinct dorsally and laterally, ventrally with a shallow lip; both rings of similar length.

All parapodia well developed, but first four smaller. Parapodia with inconspicuous pre- and postsetal lobes. First parapodia with an unilobulated digitate branchia attached dorsal and posterior to the parapodia (Fig. 1B), diminishing in length on middle segments and absent on the posterior segments.

Anterior parapodia with very long limbate setae (Fig. 1C), middle and posterior parapodia with stout limbate setae, shorter than setae of anterior parapodia (Fig. 1D), and simple multidentate hooded hooks (Fig. 1E). All setae with black core from the base to near tip where they become translucent. Parapodia with three to five black aciculae with mucro; aciculae located in the middle of parapodia in all setigers; straight.

Short and stout maxillary apparatus, with four pairs of maxillae (Fig. 1F). Mandibles well calcified, with shaft separated along half of length (Fig. 1G). Maxillary carriers distinctly shorter than maxillae I, anterior end slightly constricted. Maxillae I forceps-like with smooth edges, bridles poorly developed; maxillae II stout, of similar length to maxillae I, with two broad teeth in the anterior end; maxillae III and IV edentate plates.

*Distribution*.—Off Aguja Point, Peru, in abyssal depth.

*Cenogenus fusca* (Moore, 1911)

Fig. 1H

*Ninoe fusca* Moore, 1911:285–288, Pl. 19, Figs. 110–118.

*Paraninoe fusca* Levenstein 1977:190–191.

*Material examined*.—Holotype of *Ninoe fusca*, Moore (USNM 17338), off Santa Catalina Islands, California, U.S.A. (33°10'15"N, 121°42'15"W) 1 Apr 1904, Albatross Sta. 4397, 3953 m.

*Description*.—Specimen broken in two fragments, anterior end with 45 setigers (L10 = 6.3 mm and W10 = 3.2 mm).

The holotype of *Ninoe fusca* lacks maxillary apparatus, but it was well described and illustrated by Moore (1911) with four pairs of maxillary plates, maxillae II bidentate and maxillae III and IV edentate.

The shape of prostomium, peristomium, parapodia, setae and the distribution of the branchiae and setae resemble those of *C. descendens*. However, in parapodia two to five the aciculae are located in dorsal position and are curved (Fig. 1H).

*Distribution*.—Off Santa Catalina Islands, California, U.S.A. in abyssal depth.

#### Acknowledgments

I wish to thank Ardis B. Johnston (Museum of Comparative Zoology, Harvard University) and Kristian Fauchald (National Museum of Natural History, Washington, D.C.) for making available the type materials that made this study possible, and for making laboratory facilities available. I am grateful to Leonard P. Hirsch and K. Fauchald for housing me during my visit to the NMNH. I also wish to thank Sergio I. Salazar-Vallejo, Kristian Fauchald and José M. Orensanz for discussions and help in preparation of the final version of the manuscript. This study was partially financed by a research fellowship from El Colegio de la Frontera Sur and by CONACyT (32529-T).

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**On the rotifer fauna of Bermuda, including notes on the associated  
meiofauna and the description of a new species of *Encentrum*  
(Rotifera: Ploima: Dicranophoridae)**

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*Abstract.*—The rotifer fauna of Bermuda was investigated by examining samples from 12 localities, including marine, brackish, and freshwater localities. The majority of the 14 species that were identified are common cosmopolites, but some also have a more limited distribution. No endemics were recorded. The dominant genus present in the samples, *Lecane*, was represented by 5 species. The relatively small total number of species is probably due to one or both of two factors: the lack of stable freshwater bodies, and Bermuda's isolated geographic position. All but one of the recorded species are new to Bermuda. One species, *Encentrum astridae*, is new to science. The species has previously been found in Danish waters. Finding the new species in both Danish and Bermudan waters suggests that it is distributed in at least the boreal and tropical West Atlantic regions.

Few studies concerning rotifers from isolated oceanic islands have been accomplished. However, to understand the zoogeographic dynamics and dispersal potential of rotifers it is important to know the distribution of these island-dwelling species. These include Galapagos (De Smet 1989a, 1989b; Segers & Dumont 1993a), the Easter Island (Segers & Dumont 1993a), the South Pacific islands (Russell 1957), and the Azores (Green 1992). This study presents the first faunistic study on the rotifer fauna of the Bermuda archipelago. The localities studied include marine, brackish, and freshwater bodies.

Bermuda is located in the Atlantic Ocean at about 32°N, 64°W, almost 1000 km SE of North Carolina, USA, which represents the nearest continental coast. The Bermuda seamount was first formed by volcanic eruptions about 100 mya, and re-erupted 35 mya, covering an area much larger than the present area of Bermuda. Subsequent erosion, formation of coral reefs, a covering of limestone accreted by the wind-blown skel-

etons of reef organisms, and the postglacial rise of the sea level formed the islands' present appearance (Watson et al. 1965).

On land, dune hills and limestone dominate Bermuda. There are no streams or rivers and only a few canals. A few lakes and ponds are present, but all are to some extent connected with the sea and therefore permanently or temporarily brackish.

Bermuda's location in the Gulf Stream provides the islands a climate with hot summers and mild winters. This enables the corals to form large reefs, and provide the calcareous coral sand that dominates the sea floor around Bermuda. This coral sand has proved to host a rich marine interstitial fauna (Higgins 1982; Eibye-Jacobsen & Kristensen 1994; Sterrer 1998a, 1998b). For a more comprehensive review of the Bermudan fauna see Sterrer (1986).

#### Materials and methods

During a three-weeks stay at the Bermuda Aquarium Museum and Zoo (BAMZ), six-

teen localities were sampled for the purpose of collecting rotifers and gnathostomulids (Fig. 1). Seven marine, four brackish, and one freshwater station yielded rotifers (Tables 1, 2).

Intertidal samples were dug up with a shovel, while subtidal samples were taken by snorkeling. In both cases the upper 10 cm of the sediment was collected, placed in buckets, and returned to the laboratory for processing. Meiofaunal organisms were extracted from the sediment by using an isotonic solution of magnesium sulfate to anaesthetize the animals. Approximately 1 liter sediment was transferred to a conical plastic bottle and a corresponding amount of magnesium sulfate solution was added. After a ten minutes incubation period the containers were agitated vigorously, and after a brief period settling the supernatant was decanted through a 30  $\mu\text{m}$  mesh sieve. This procedure was repeated once. Samples taken from detritus, algae and plants were squeezed and concentrated in a 30  $\mu\text{m}$  mesh sieve.

All samples were sorted using a Wild M420 dissection microscope and a Wild M20 microscope. Rotifers were identified and drawn using a Wild M20 compound microscope with camera lucida. Trophi were isolated by dissolving the animals using dilute sodium hypochlorite and then prepared for SEM and light microscopy (De Smet 1998). Trophi for light microscopy were mounted in a modified Faure's solution. Trophi for SEM were examined and photographed with a JEOL JSM-840 microscope. All material is deposited in the Zoological Museum, University of Copenhagen (ZMUC).

## Results

Sixteen localities investigated yielded a total of 14 identified rotifer species, two forms of the same species, a number of unidentified bdelloid species from the genera *Philodina* and *Rotaria*, and one dead specimen of *Monommata* which could not be

identified. All recorded species are listed in Table 3.

Five species, of the genera *Colurella*, *Encentrum*, and *Proales*, were recorded from the marine localities. One of these, *Encentrum astridae* new species, is new to science. The brackish water localities yielded eight species, distributed among six genera. Furthermore, some unidentified *Rotaria* were recorded. Two species, *Colurella uncinata uncinata* and *Proales similis*, occurred both at marine and brackish localities. The single freshwater locality produced three identified species, one unidentified *Monommata* and some *Philodina* spp. *Colurella uncinata* was recorded from the freshwater locality as well as from a brackish and a marine locality. In the freshwater locality the species was represented by the form *C. uncinata bicuspitata*.

The remaining interstitial fauna at the marine localities was only investigated superficially. However, it was noted that the samples contained a rich meiofauna. Most samples contained several species of macrodasyid gastrotrichs, including the easily recognized genus *Urodasys*. Nematodes were numerous, including different desmoscolicids. Also several interstitial polychaetes, including the families Dorvilleidae and Syllidae were represented. Five species of Gnathostomulida, *Haplognathia rosea* (Sterrer, 1969), *Tenuignathia rikeri* Sterrer, 1976, *Problognathia minima* Sterrer & Farris, 1975, *Gnathostomula peregrina* Kirsteuer, 1964, and *Austrognathia christianae* Farris, 1977, were recorded. *Gnathostomula peregrina* was the most abundant and was present at stations 3–7. Two species of Kinorhyncha, *Antygomonas* cf. *oreas* Bauer-Nebelsick, 1996 and *Echinoderes bermudensis* Higgins, 1982, were recorded from station 7 and 4, respectively. Except for the arrangement of the lateral spines on segment 11 the *Antygomonas* species fits perfectly the description given by Bauer-Nebelsick (1996). In the specimens described by Bauer-Nebelsick (1996) the cuspidate spines are located laterally to the acicular

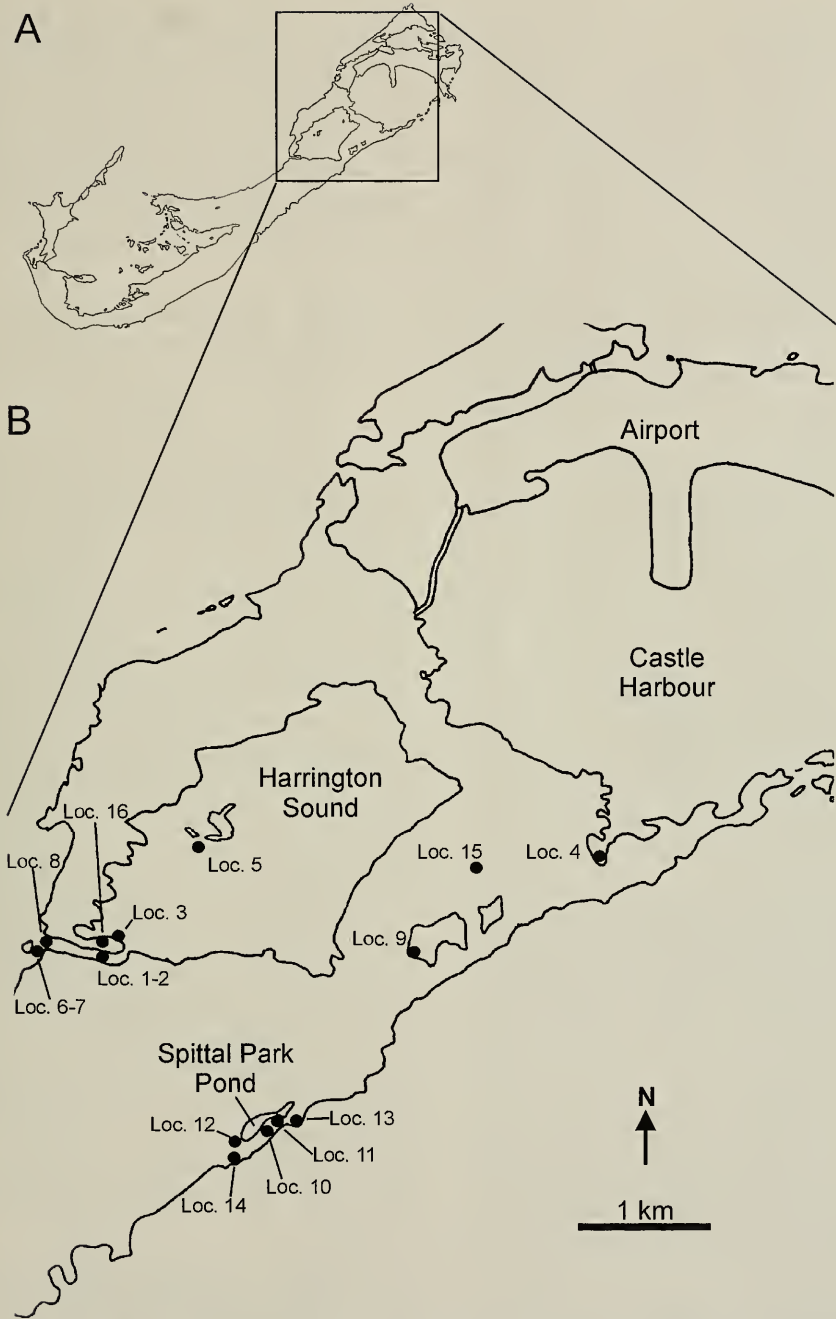


Fig. 1. Map showing location of sampling sites on Bermuda. Localities 2, 13, 14, and 15 yielded no rolifers and are omitted in the following tables, thus Loc. 1 = st. 1, Loc. 2 = st. 2, Loc. 4 = st. 3, Loc. 5 = st. 4, etc., and Loc. 16 = st. 12.

Table 1.—Data on marine localities. Salinity on all stations ca. 33‰.

St. No.	1	2	3	4	5	6	7
Name	Flatts Inlet	BAMZ docks	Tuckers Cove	At Trunk Island	Gibbon Bay	Gibbon Bay	Mouth of Flatts Inlet
Position	32°19'19"N 64°44'17"W	32°19'21"N 64°44'10"W	32°19'49"N 64°41'30"W	32°19'51"N 64°43'39"W	32°19'16"N 64°44'31"W	32°19'16"N 64°44'31"W	32°19'18"N 64°43'32"W
Coll. Date	6 Sep 2000	6 Sep 2000	7 Sep 2000	7 Sep 2000	15 Sep 2000	17 Sep 2000	15 Sep 2000
Depth	1 m	2 m	—	3 m	0.5 m	—	3 m
Temp.	28.4°C	28°C	28.3°C	27°C	28.2°C	29.2°C	28.2°C
Remarks	Subtidal, from fire sponges, <i>Tedania ignis</i>	Subtidal, from red algae on reef docks	Intertidal, from red dium coral sand w. detritus	Subtidal, from me-dium coral sand w. detritus	Subtidal, from fine coral sand w. detritus	Intertidal from fine clean coral sand	Subtidal, from me-dium, clean coral sand

spines, while the position of these have shifted in the Bermuda specimen, so the acicular spines on segment 11 are most lateral. *Antygomonas oreas* was described from coral sand at relatively deep water (500–600 m) in the Pacific Ocean (Bauer-Nebelsick, 1996). This is the first reported record of the species since then.

Family Dicranophoridae Haring, 1913

Genus *Encentrum* Ehrenberg, 1838

*Encentrum astridae*, new species

Figs. 2–3

*Type material*.—All type material was obtained from samples taken on 15 September 2000 at station 5, Gibbon Bay close to Flatts Inlet, Bermuda (Table 1). Position: 32°19'16"N, 064°44'31"W. Holotype: Adult female, mounted in glycerol (ZMUC ROT-223). Paratypes: 9 adult females, mounted in glycerol (ZMUC ROT-224 to ROT-232); 2 isolated trophi mounted for LM (ZMUC ROT-233 and ROT-234); 3 isolated trophi from adults mounted for SEM (ZMUC ROT-235 to ROT-237); 1 isolated trophus from a juvenile mounted for SEM (ZMUC ROT-238). All types are stored at ZMUC.

*Other material*.—Further material was obtained 7 July 1999, at Præstebugten, Hirscholmene, Denmark, a small group of islands in the northern Kattegat off Frederikshavn, Denmark. Samples were taken in the tidal zone from well-sorted medium sized quartz sand covered with sulfur bacteria. Position: 57°29'17"N, 010°37'29"E. 2 isolated trophi mounted for SEM (ZMUC ROT-244 and ROT-245) and stored at ZMUC.

*Diagnosis*.—Large animals (ca. 350 µm long), trunk with longitudinal folds (Fig. 2A–B). Foot ventrally displaced (Fig. 2B). Posterior part of stomach covered by yellowish to brownish glandular syncytium with brown nuclei (Fig. 2A–B). Trophi large, forcipate. Rami large with sharp apical rami teeth, and a pair of smaller, hook-shaped preuncinal teeth. Unci very long, almost as long as rami length, with sharp in-

Table 2.—Data on brackish and fresh water localities. All samples taken just below the water surface.

St. No.	8	9	10	11	12
Name	Mangrove Lake	Bird Sanctuary Pond	Spittal Pond, east	Spittal Pond, west	Pond in Zoo, BAMZ
Position	32°19'26"N 64°42'38"W	32°18'34"N 64°43'33"W	32°18'39"N 64°43'29"W	32°18'32"N 64°43'39"W	32°19'20"N 64°44'18"W
Coll. Date	7 Sep 2000	12 Sep 2000	12 Sep 2000	14 Sep 2000	15 Sep 2000
Salinity	10–15‰	3–8‰	12–18‰	7–12‰	0‰
Temp.	27°C	26.4°C	25.6°C	29.6°C	25.1°C
Remarks	From algae on man-grove roots	From red bacteria mats and degraded plants	From detritus and degraded plants	From detritus and degraded plants	From plankton, algae and plants

ward-curved teeth. Supramanubria with long curved extensions, meeting each other in center of trophi (Figs. 2C, 3).

*Description.*—Body elongate, fusiform. Head medium size; rostrum short; corona slightly oblique, ventrally. Brain large, saccate, extending into neck; subcerebral glands elongate; no light-refracting elements; retrocerebral sac absent; eyespots absent (Fig. 2A–B). Neck short. Trunk with three distinct transverse folds; posterior pseudosegment with broad tail. Dorsal and lateral sides of trunk with irregularly distributed longitudinal folds. Mastax large, with pair of salivary glands. Proventriculus present. Stomach surrounded by yellowish to brownish glandular syncytium with brown nuclei; number of nuclei ranging between 12 and 19 (Fig. 2A–B). Gastric glands elongate, close to stomach. Vitellarium large, elongate. Foot long, conical, retractable, ventrally displaced (Fig. 2A–B). Toes close-set, almost parallel sided, tapering distally to tips. Pedal glands elongate, narrow (Fig. 2A–B).

Trophi forcipate, large, elongate, slender (Figs. 2C, 3). Rami expanded ¼ from proximal ends; outer margins slightly concave medially, slightly diverging distally (Figs. 2C, 3A–C). Median opening wedge-shaped. Each ramus tip terminating dorsally in a sharp, slightly curved, inwardly projecting apical ramus tooth (Figs. 2C, 3A, C); ventrally, at bases of apical rami teeth, a small, stout, slightly hook-shaped, inwardly projecting preuncinal tooth (Figs. 2C, 3B, D). Scapus long, narrow, extending into anterior part of ramus (Fig. 2C); fenestra of scapus small, opening basally on dorsal side of each ramus (Fig. 3C). Bulla small, almost rectangular (Fig. 2C); fenestra of bulla small, opening caudally on ramus (Fig. 3D, F). Fulcrum rod-shaped in dorsal view (Figs. 2C, 3A–C), gradually tapering towards truncate tip in lateral view (Fig. 3D). Unci very long, almost 9/10 of rami length; shaft long, rod-shaped; teeth long, sharp, inwardly curved, with small dorsal apophysis at bases (Figs. 2C, 3). Manubria gradually

Table 3.—Occurrence of rotifer species at stations 1 to 12.

	1	2	3	4	5	6	7	8	9	10	11	12
<i>Brachionus urceolaris</i> (Müller, 1773)					X				X			
<i>Cephalodella forficata</i> (Ehrenberg, 1832)				X							X	
<i>Colurella colurus</i> (Ehrenberg, 1830)	X				X		X					X
<i>C. obtusa</i> (Gosse, 1886)								X				
<i>C. uncinata uncinata</i> (Müller, 1773)		X										X
<i>C. uncinata bicuspidata</i> (Ehrenberg, 1832)		X		X	X	X	X					
<i>Encentrum astridae</i> new species		X	X	X	X	X						
<i>Encentrum tectipes</i> Remane, 1949		X							X			
<i>Rotaria</i> spp.												
<i>Lecane bulla</i> (Gosse, 1851)								X				X
<i>L. closteroerca</i> (Schmarda, 1859)									X	X		
<i>L. grandis</i> (Murray, 1913)									X	X		
<i>L. hastata</i> (Murray, 1913)									X	X		
<i>L. punctata</i> (Murray, 1913)										X		X
<i>Mononimata</i> sp. indet.												X
<i>Philodina</i> spp.												X
<i>Procladius similis</i> De Beauchamp, 1907							X			X		

curved inwardly towards distal ends (Figs. 2C, 3); proximal ends with anterior and median chamber retained. Anterior chamber present in dorsally pointed extension; median chamber with small fenestra ventroapically on manubrium. Intramallei small, triangular, attached to ventral side of supramanubria (Figs. 2C, 3B). Supramanubria very large, with stout bases tapering into long extensions with curved terminals; terminals meet each other in center of trophi (Figs. 2C, 3A–C).

Juveniles about 2/3 of adult size; very hyaline, no coloration of any organs yet; trophi as in adults (Fig. 3B). No males were found.

Measurements of adult females: Body length 308–388  $\mu\text{m}$ ; toes 26–31  $\mu\text{m}$ ; trophi 38  $\mu\text{m}$ ; rami 22  $\mu\text{m}$ ; fulcrum 10  $\mu\text{m}$ ; unci 19  $\mu\text{m}$ ; manubria 24–26  $\mu\text{m}$ ; intramallei 3  $\mu\text{m}$ ; supramanubria 10  $\mu\text{m}$ .

*Etymology*.—The species is named after my daughter Astrid.

*Remarks*.—The presence of relatively simple forcipate trophi with intramallei and supramanubria, and a long fulcrum, combined with the absence of teeth on inner margins of rami and single-toothed unci clearly place *Encentrum astridae* new species in the genus *Encentrum* (see De Smet 1997). The presence of elongate rami with very long scapus, dorsal incurved apical ramus teeth and ventral preuncinal teeth set at right angles to rami place the species in subgenus *Encentrum* s. str. Ehrenberg, 1838 (see De Smet 1997).

The species can hardly be confused with other known species due to the presence of large trophi with very long unci with inwardly pointed teeth, and long supramanubrial extensions reaching each other (Figs. 2C, 3A–C).

The species was found at five of the investigated marine localities (see Table 3), and is probably common in the psammon around Bermuda. It was found in intertidal as well as subtidal psammon, but was most abundant in the subtidal. It occurred on depths ranging from 0 to 3 meter. In June



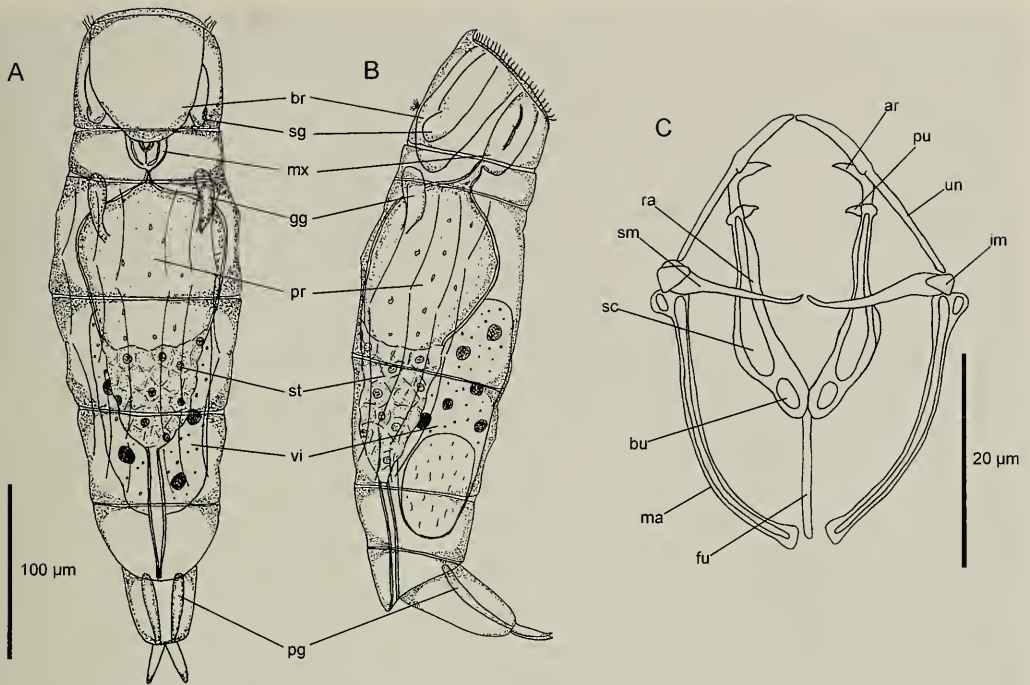


Fig. 2. *Encentrum astridae* new species. A. Female habitus, dorsal view. B. Female habitus, lateral view. C. Trophi, ventral view. Abbreviations: ar, apical ramus tooth; br, brain; bu, bulla; fu, fulcrum; ga, gastric glands; gl, glandular syncytium; im, intramalleus; ma, manubrium; mx, mastax; pg, pedal gland; pr, proventriculus; pu, preuncinal tooth; ra, ramus; sc, scapus; sg, subcerebral glands; sm, supramanubrium; st, stomach; un, uncus; vi, vitellarium.

1999 it was found in psammon samples from Danish waters. The species was found during meiofauna collections on Hirsholmene, a small group of islands in the northern part of Kattegat, off Frederikshavn, Denmark, but was not described then due to insufficient material. This distribution suggests that the species may be found in well-sorted sandy sediments at shallow waters in most of the Northern Atlantic.

### Discussion

No systematic study has been made of the Bermudan rotifer fauna before. Only four species were previously recorded, and none of these were identified to more than genus level (von Bodungen et al. 1982; Sterrer 1986, 1998a). von Bodungen et al. (1982) recorded *Trichocerca* sp. from Hamilton Harbour and Sterrer (1986) reports *Encentrum* sp., *Lindia* sp., and *Synchaeta*

sp. from different localities, and illustrates the recorded species (Sterrer 1986: plate 69). *Encentrum* sp. is probably identical to *Encentrum tectipes* (Fig. 4A–B). *Lindia* sp. is identical to *L. tecusa* Haring & Myers, 1922, due its presence in sublittoral psammon. This identity was confirmed during my stay at BAMZ, where I had the opportunity to investigate unpublished LM pictures of the species. The species was not recorded during this study, and Sterrer (1986) refers to it as “rare”. Neither *Synchaeta* sp. nor *Trichocerca* sp. were recorded in this study. Both species were found in planktonic samples (von Bodungen et al. 1982; Sterrer 1986), and since the marine samples in this study only were taken from psammon or phyton, it explains why these were not recorded. Based solely on the illustrations, the *Synchaeta* species reported by Sterrer (1986) cannot be identified. von

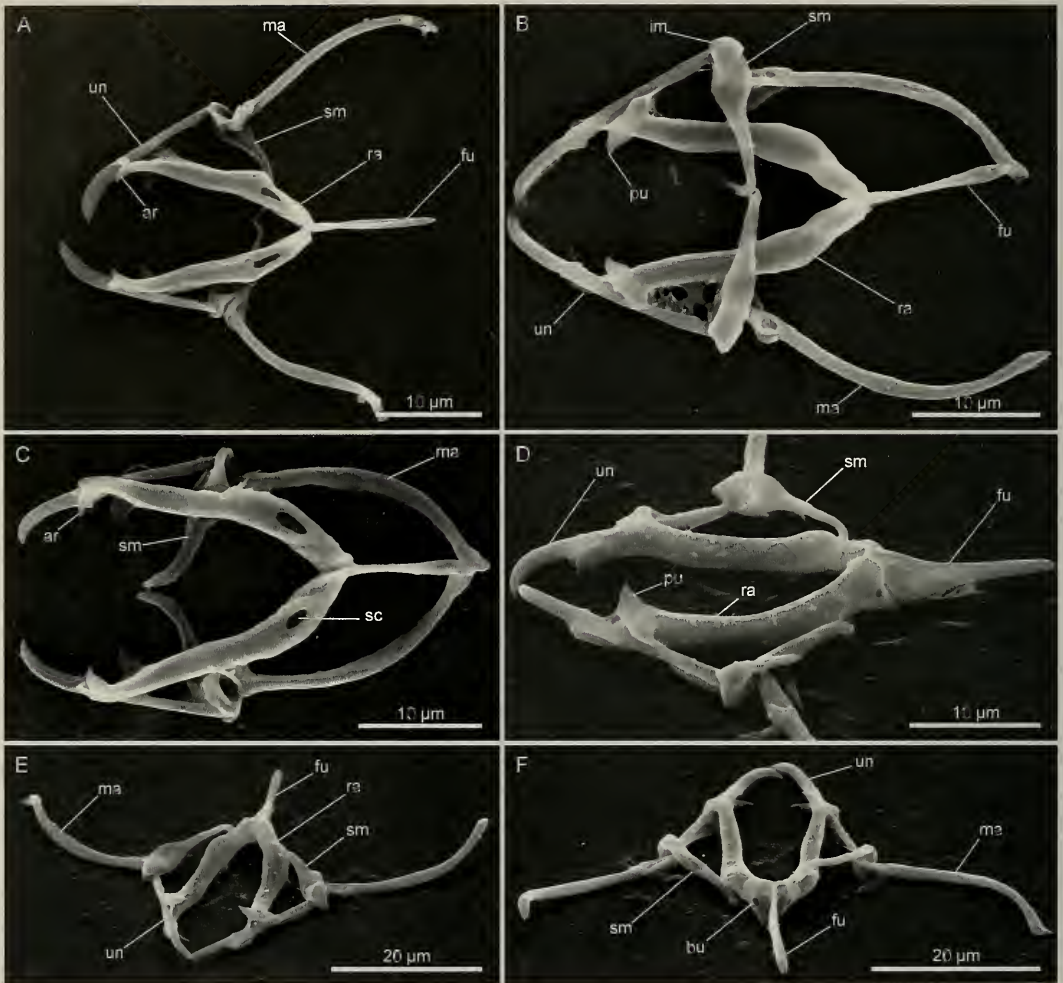


Fig. 3. *Encentrum astridae* new species. SEM photos of trophi. A is a Danish specimen, B–F is Bermudan specimens. A. Dorsal view. B. Ventral view, from juvenile specimen. C. Dorsal view, rami opened. D. Lateral view. E. Frontal view. F. Caudal view. Abbreviations: ar, apical ramus tooth; bu, bulla; fu, fulcrum; im, intra-malleus; ma, manubrium; pu, preuncinal tooth; ra, ramus; sc, scapus; sm, supramanubrium; un, uncus.

Bodungen et al. (1982) do not illustrate the recorded *Trichocerca* sp, but it might be identical to *T. marina* (Daday, 1890), which is the only known marine planktonic *Trichocerca*.

*Lecane* was the dominating species and accounted for 31% of the total amount of identified species. Though the material in this study is rather small, it confirms the pattern that *Lecane* displays high species diversity in tropical and subtropical regions (see Harring 1914; De Smet 1988; Segers & Dumont 1993a, 1993b, 1995; Segers &

De Meester 1994; Segers & Sanoamuang 1994; Janetzky et al. 1995; Sanoamuang 1998; Samraoui et al. 1998).

A few specimens of *Cephalodella forficata* (Fig. 4E–F) were recorded from one of the brackish water localities (Table 3). All specimens were juveniles, and the gastric glands were only light red. The species is considered cosmopolitan, but is mainly found in freshwater (Koste 1978; Nogrady & Pourriot 1995).

*Proales similis* (Fig. 4C–D) was found at brackish as well as marine localities (Table

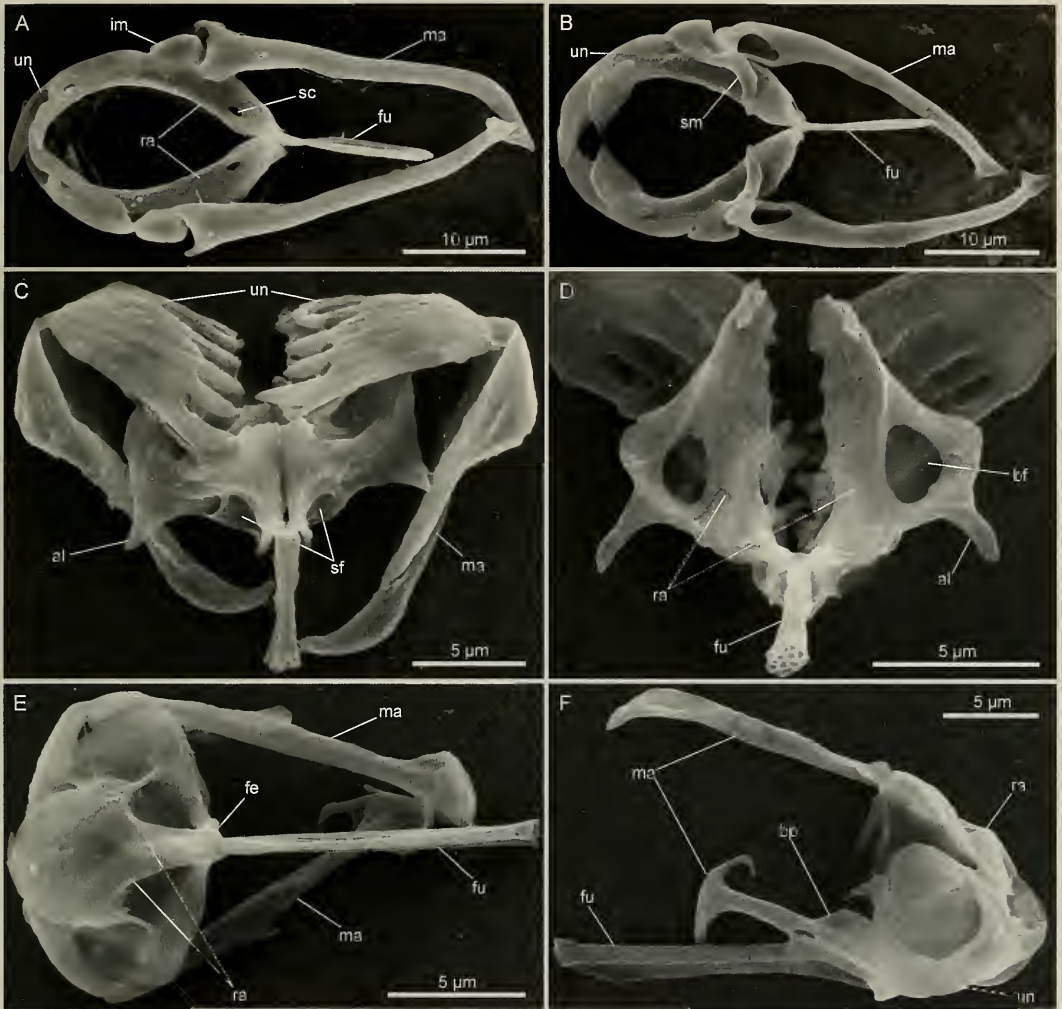


Fig. 4. SEM photos of trophi. A. *Encentrum tectipes*, dorsal view. B. *E. tectipes*, ventral view. C. *Proales similis*, ventral view. D. *P. similis*, rami, dorsal view. E. *Cephalodella forcicata*, ventral view. F. *C. forcicata*, lateral view. Abbreviations: al, alula; bf, basifenestra; bl, basal lamella; fe, fulcral extension; fu, fulcrum; im, intramalleus; ma, manubrium; ra, ramus; sc, scapus; sf, subbasifenestra; sm, supramanubrium; un, uncus.

3). The species is recognized by its fusi-form trunk and offset foot with one pseudosegment and distinct wrinkles. The apical rami tips were rather short (Fig. 4D) in the recorded specimens, and not extended as in the specimens pictured by De Smet (1996). The species has been recorded from most parts of the world and is found in marine waters as well as inland saline or brackish ponds (De Smet 1996).

Beside *Encentrum astridae* new species, another dicranophorid, *E. tectipes*, was re-

corded from the marine localities. The species is easily recognized by its robust and compact trophi (Fig. 4A–B), and the presence of yellowish glandular tissue around the posterior part of the stomach, also described by Remane (1949). Like many other marine, interstitial dicranophorids, the species has formerly only been recorded from the northwestern Europe (De Smet 1997), but finding the species on Bermuda suggests that it is much more widely distributed. As a matter of fact, the known distri-

butional patterns of many marine, interstitial rotifers with an apparently limited distribution are probably mostly a reflection of our insufficient knowledge of species from such habitats, rather than a picture of their actual distribution. Recently, *E. tenuidigitatum* De Smet, 2000, described from tidal psammon in Belgium, was recorded from Greenland (Funch & Sørensen 2001), and *E. porsildi* Sørensen, 1998 described from Disko Island, Greenland, was recorded from Denmark (Sørensen, in press). I find it very likely that the interstitial habitat in clean, well-sorted sand offers a stable environment, and since marine environments generally are more climatologically stable than terrestrial, it enables the psammobiontic species to be widely distributed and makes factors as climate less important. This is also suggested by the distribution of *E. astridae* new species. The study of the marine psammobiontic rotifers has often been neglected compared to the more species-diverse freshwater habitats, but if more attention were paid to this special habitat, our knowledge would certainly be increased greatly.

The fauna on isolated oceanic islands can theoretically be expected to have low species diversity and a relatively high proportion of endemism (Segers & Dumont 1993a). A total of 14 identifiable species, as recorded in this study, must be considered a low number of species compared to the number of investigated localities. However, it is most likely that this is caused by the lack of stable freshwater bodies rather than isolation by distance. This does not overrule that isolation also plays a role. Of the total number of species, 65% are cosmopolites while three, *L. grandis*, *L. hastata*, and *L. punctata*, have a tropical/subtropical distribution. Two species, *E. astridae* new species and *E. tectipes*, have at least a boreal and tropical West Atlantic distribution. No endemics were recorded. The dominance of cosmopolites can probably be explained by the fact that migrations of such species are more likely to occur than

migration of species with a more limited distribution.

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## New Unguiphora (Platyhelminthes: Proseriata) from India

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*Abstract.*—Three new species of Unguiphora are described from Goa (India). Two species belong to the genus *Nematoplana* (*N. indica* and *N. calamus*). They are distinguished from the known species of the genus on the basis of the morphology of sclerotized structures. The new genus *Alloeostylyphora* is established for the third species (*A. mirabilis*), based on the unique features of its copulatory apparatus, with two symmetrical copulatory organs, and a few, non-glandular accessory stylets.

The Unguiphora is the smallest surborder of the Proseriata (Platyhelminthes). At present, the taxon is comprised of 5 genera and 34 species. In general, very few species are known from any given biogeographical area (Curini-Galletti & Martens 1991, 1992). However, the recent finding of an exceedingly rich unguiphorid fauna in eastern Australia raises the question of our actual understanding of the diversity of the taxon in extra-boreal areas (Curini-Galletti 1998, Curini-Galletti et al. 2001). The present contribution deals with three unguiphorid species found in a small sediment sample from Goa, India.

### Materials and Methods

The sample (about one-half liter of sediment) was collected in intertidal pockets of clean medium-fine sand among rocks, in front of Fort Aguada Beach Hotel, Aguada, Goa (India) (May 1993). The animals were extracted from the sediment in the laboratory with the MgCl<sub>2</sub> decantation technique (Martens 1984). Preservation and histological techniques routinely adopted for Proseriata were used (see Martens et al. 1989); whole mounts were made with polyvinyl-lactophenol or Faure. Karyological techniques are described in Curini-Galletti et al. (1989). Idiograms (Figs. 2E, 3G) are based

on karyometrical data presented in the karyotype formula: haploid genome absolute length in  $\mu\text{m}$ , relative length and centromere index of each chromosome; chromosome nomenclature between parentheses (m = metacentric; sm = submetacentric). Type material is deposited in the collections of the Queensland Museum, S. Brisbane, Australia (QM).

Family Nematoplanidae Meixner, 1938  
Genus *Nematoplana* Meixner, 1938  
*Nematoplana indica*, new species  
Figs. 1, 4A

*Material examined.*—Holotype, India, Goa, Aguada: whole mount (lactophenol) (QM-G211833).

*Etymology.*—Named after the geographical area, from which the species is recorded.

*Description.*—The holotype is an adult worm, about 4.2 mm long in fixed condition, without pigment or pigmented eye-spots. Anterior end elongate, provided laterally and terminally with sensory bristles. The pharynx, short and collar shaped, is located in the posterior fifth of the body.

Male genital organs: with numerous testes irregularly arranged between vitellaria in front of the pharynx. The copulatory organ consists of an elongate, muscular bulb

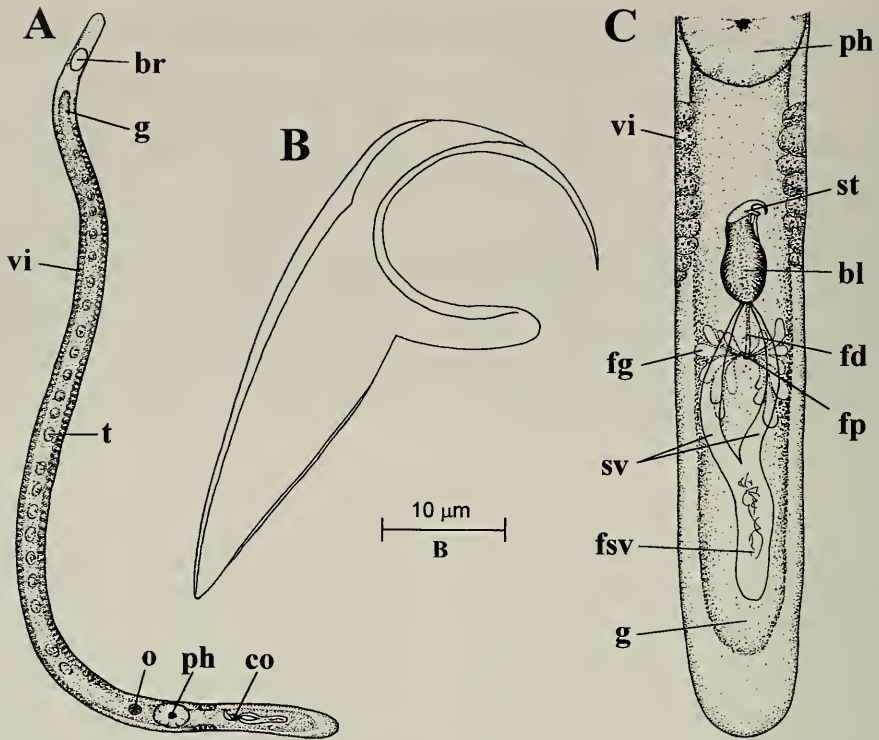


Fig. 1. *Nematoplana indica*, new species. (A) general organization of live animal; (B) stylet (from holotype); (C) detail of the post-pharyngeal area. Abbreviations in figures: ast—accessory stylet; br—brain; bl—bulb; co—copulatory organ; e—eye-spot; fd—female duct; fg—female glands; fp—female pore; fsv—fused seminal vesicles; g—gut; ma—male antrum; o—oocyte; ph—pharynx; phg—pharyngeal glands; sv—seminal vesicle; st—stylet; t—testis; vi—vitellaria.

(about 110  $\mu\text{m}$  long), provided with a copulatory stylet, and two seminal vesicles, which enter the bulb proximally. The seminal vesicles, which have a very thin lining, are fused caudally. The stylet is funnel shaped, 48  $\mu\text{m}$  long, with a broad, markedly oblique, proximal opening and a narrow distal opening (Fig. 1B). Its slender base is about 30  $\mu\text{m}$  long; its maximum diameter (about 11  $\mu\text{m}$ ) is attained just below the apophysis, which is about 14  $\mu\text{m}$  long and 4  $\mu\text{m}$  wide. The apophysis is nearly perpendicular to the main axis of the stylet. Numerous, thick longitudinal muscles, most of which are connected basally with the musculature surrounding the bulb, are attached to the apophysis. The distal end of the stylet narrows above the apophysis into a nearly straight tube, about 0.33 of the to-

tal length of the stylet. It is provided with a long, slightly recurve, distal tip (about 20  $\mu\text{m}$  long), perpendicular to the main axis of the stylet.

Female genital organs: the specimen examined possessed one mature oocyte, medially in front of the pharynx. Vitellaria extend from posterior to the brain to in front of the ovaries, and from posterior to the pharynx to the level of the copulatory bulb. The oviducts fuse posterior to the bulb into a short common female duct, which opens to the outside through a female pore, medially between the seminal vesicles.

*Remarks.*—The distinctly claw-shaped stylet, with an elongate base, a slightly recurve distal tip, and a long apophysis, is comparable to that of the *N. coelogyne* species group (which includes *N.*



*coelognoporoides* Meixner, 1938, *N. ciliovesiculae* Tajika, 1979, *N. riegeri* Curini-Galletti & Martens, 1992 and *N. cannoni* Curini-Galletti, Oggiano & Casu, 2001) (cf. Curini-Galletti & Martens 1992, Curini-Galletti et al. 2001). The insertion of the apophysis with the axis of the stylet differs; it is perpendicular in *N. indica* and oblique (at an angle of about 45°) in the species listed above. Furthermore, the stylet of *N. indica* is straighter above the apophysis, with a much longer distal tip, that is more clearly orthogonal to the main axis, than any of the species listed above. Among the Indo-Pacific members of the *N. coelognoporoides* group, the Japanese *N. ciliovesiculae* has a more recurve, markedly larger (about 130 µm long) stylet, with a very short distal tip and a relatively very short, obtuse apophysis. *Nematoplana cannoni* from eastern Australia is similar to *N. indica* for the size of the stylet. Furthermore, both species share the presence of unpaired oocytes, and of an elongate muscular bulb. However, in *N. cannoni* the portion of the stylet above the apophysis is recurved and comparatively longer and broader than in *N. indica*. Furthermore, its stylet is provided with a much shorter distal tip; the apophysis is oblique, narrow, and angled distally; the basis is broader proximally. *Nematoplana cannoni* has pigmented eye-spots, enclosed within the brain capsule.

*Nematoplana calamus*, new species  
Figs. 2, 4C, D

*Material examined*.—Holotype: India, Goa, Aguada: whole mount (lactophenol): QM-G211834. Paratype: one karyological slide made permanent with Faure (QM-G211835), same data as holotype.

*Etymology*.—The name refers to the shape of the stylet, which resembles an old-fashioned pen-nib (lat. *calamus*, a noun used as an apposition).

*Description*.—Animals small: the holotype is an adult worm, about 1.2 mm long

in fixed condition. Without pigment or pigmented eye-spots. Anterior end elongate, provided laterally and terminally with sensory bristles. The short, collar-shaped pharynx is located in the posterior sixth of the body.

Male genital organs: with a few testes irregularly arranged among vitellaria, in front of the pharynx. The copulatory organ consists of a single seminal vesicle, and a bulb provided distally with a stylet. The seminal vesicle is broadly elongate, and provided with a coating of circular musculature. The seminal vesicle enters the bulb at its proximal base. The ovoid bulb is about 20 µm long, and is provided with numerous prostatic glands, some of which have their cell bodies outside the bulb itself. The stylet (Figs. 2B, C, 4C, D), about 18 µm long, is thin and diaphanous. Its base (about 11 µm wide) is gutter-shaped, widely open proximally and ventrally, with a marked notch at its dorsal side. The ventral sides are nearly straight, and are distinctly angled distally. The stylet is provided distally with a recurve, convex distal spike, about 10 µm long. In living specimens, the stylet appeared distinctly claw-shaped. Presumably, it acts functionally as a funnel, with the distal opening located beneath the dorsal spike, and the proximal opening formed by the adjoining of the ventral flaps.

Female genital organs: mature oocytes were not present. Vitellaria extend from behind the brain to in front of the pharynx. Female pore, surrounded by female glands, posterior to the male pore.

*Karyotype*: most chromosomes are metacentric ( $n = 6$ ). Karyotype formula: 10 µm; I: 22.49, 46.36 (m); II: 18.7, 40.92 (m); III: 15.98, 44.16 (m); IV: 15.23, 29.54 (sm); V: 15.1, 43.15 (m); VI: 12.47, 43.56 (m).

*Remarks*.—The stylet of *Nematoplana calamus* is peculiar. In no other unguiphorid species is it gutter-shaped, gaping ventrally, and with a distal opening located beneath a dorsal spike. The presence of a single seminal vesicle is shared with *N. martensi* Curini-Galletti, Oggiano & Casu, 2001, *N. ha-*

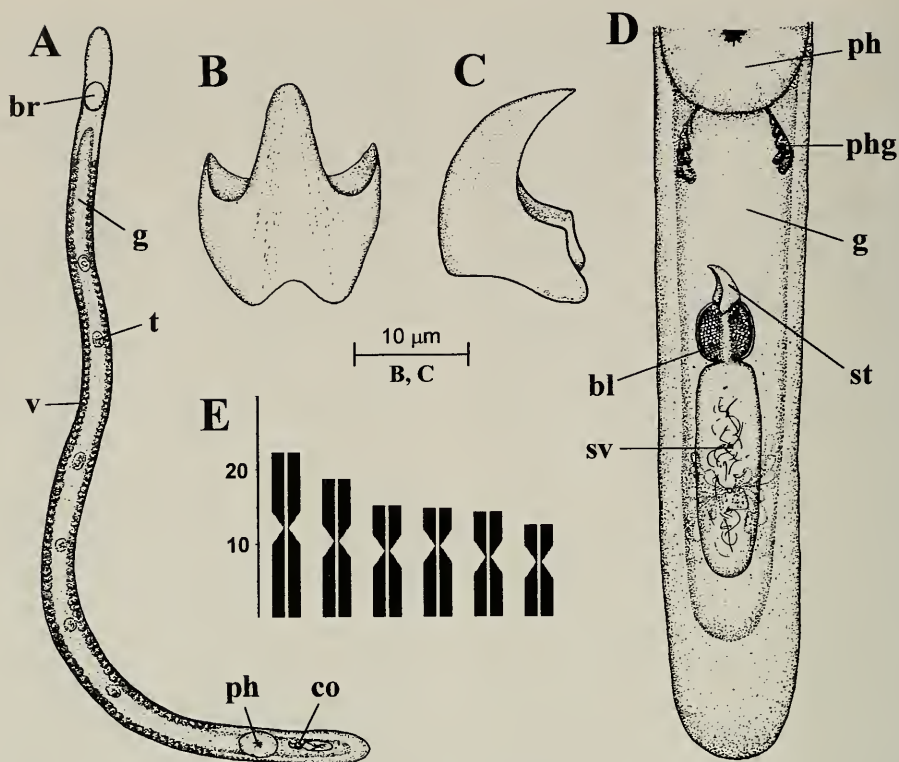


Fig. 2. *Nematoplana calamus*, new species. (A) general organization of living animal; (B, C) stylet: (B) dorsal view (from holotype); (C) lateral view (from paratype); (D) detail of post-pharyngeal area; (E) idiogram. See Fig. 1 for explanation of abbreviations.

*mata* Curini-Galletti, Oggiano & Casu, 2001, *N. cyclops* Curini-Galletti, Oggiano & Casu, 2001, and *N. pullolineata* Tajika, 1979 (Curini-Galletti et al. 2001, also for discussion of the problematical *N. naia* Marcus, 1949). The single-vesicle condition has been considered as a secondarily derived character status for the genus *Nematoplana*, resulting from the total fusion of the two partially fused vesicles found in the other species (Curini-Galletti & Martens 1992). This condition is not reported for any other Unguiphora. The *Nematoplana* species cited above share a further derived condition, i.e., the presence of a cylindrical stylet, not provided with an apophysis, and have been considered as constituting a monophyletic group within the genus *Nematoplana* (Curini-Galletti et al. 2001). *Nematoplana calamus* lacks any obvious

apophysis; the structure of its stylet is, however, so apomorphic that, at the moment, it precludes the inclusion of *N. calamus* in any evolutionary line known within the Unguiphora. The inclusion of *N. calamus* (as well as of the species listed immediately above, see Curini-Galletti et al., 2001) within the genus *Nematoplana* should be considered as conservative, until more data on polarization and distribution of characters are available, and a more significant fraction of the world species is described.

#### *Alloeostylyphora*, new genus

**Diagnosis.**—A new genus of Unguiphora with two symmetrical copulatory organs, provided with reduced bulbs. With accessory (replacement?) stylets, not connected to glandular structures. With a large male antrum anterior to the copulatory organs.

*Type species.*—*Alloeostylyphora mirabilis*, new species (by monotypy).

*Etymology.*—The generic name is coined from *alloeos*, latinized from Greek *alloios* = different + *stylyphora* from the generic name *Polystylyphora* Ax, 1958. The generic name is feminine.

*Alloeostylyphora mirabilis* new species  
Figs. 3, 4B

*Material examined.*—Holotype: India, Goa, Aguada: whole mount (lactophenol): QM-G211836. Paratype: one specimen sagittally sectioned (QM-G211837), same data as holotype. One immature studied karyologically.

*Etymology.*—*mirabilis* ('admirable') refers to the striking features of the new species.

*Description.*—Animals very small for the group: the holotype is about 0.8 mm long. With two pigmented eye-spots located within the brain capsule. Anterior end elongate, provided laterally and terminally with sensory bristles. Subepidermal longitudinal musculature well developed on the ventral side. Epithelium entirely ciliated (cilia length about 1  $\mu\text{m}$ ), with non-insunk nuclei. The short, collar-shaped pharynx is located in the posterior fifth of the body. Its epithelium has insunk nuclei, and is ciliated except for a small area at the distal tip, where a few pharyngeal glands discharge. The cell bodies of these glands are located outside the pharynx itself. Pharyngeal cilia about 1.5  $\mu\text{m}$  long. No esophageal area could be seen.

Male genital organs: with very few (one to two), large testes among vitellaria well in front of the pharynx. With two symmetrically paired copulatory organs, posterior to the pharynx. Each consists of an elongate seminal vesicle connected to a copulatory stylet. One of the copulatory organs of the holotype had a proximally bifurcated seminal vesicle; each end was connected to a copulatory stylet. A variable number of accessory stylets (1–3) were observed, lying

very close to the copulatory stylets. In living animals, they were arranged in a row, just caudal to the copulatory stylets. These accessory stylets are not connected to the seminal vesicle, nor, apparently, to any glandular structure. The copulatory and accessory stylets are tubular structures, identical in morphology. The proximal opening is about 10  $\mu\text{m}$  wide. The dorsal side of the stylet is markedly oblique, while the ventral side is straighter, about 7  $\mu\text{m}$  long. The distal opening is about 4  $\mu\text{m}$  in diameter. The stylet is provided with a straight or slightly recurved tip, about 7  $\mu\text{m}$  long. In sections, a very small glandular area is seen, at the connection of the seminal vesicle with the copulatory stylet; this may be considered as homologous to the bulb of other species of *Unguiphora*. Each copulatory stylet protrudes into a small antrum, which opens into a broad male antrum.

Female genital organs: with only one oocyte, medially in front of the pharynx. Vitellaria extend from behind the brain to in front of the pharynx. Female pore behind the male pore.

Karyotype: chromosome 1 is appreciably larger than the other pairs ( $n = 5$ ). Chromosomes are meta- or submetacentric. Karyotype formula: 6.5  $\mu\text{m}$ ; I: 29.33, 44.92 (m); II: 19.58, 46.73 (m); III: 19.16, 46.19 (m); IV: 17.44, 36.94 (sm); V: 14.48, 36.62 (sm).

*Remarks.*—*Alloeostylyphora mirabilis* presents a remarkable set of features, which justifies the establishment of a new genus. Among the most striking is the fact that no other Proseriata *Unguiphora* has two functional copulatory organs. Among Proseriata *Lithophora*, *Monotoplana diorchis* Meixner, 1938 has a continuous production of copulatory organs, which are arranged into an irregular row (Meixner 1938). In *M. diorchis*, however, only the distalmost copulatory organ is functional at any time and appears to be progressively replaced by a new one. In *A. mirabilis*, the two organs are symmetrical, and both appear to be functional at the same time. The presence of two

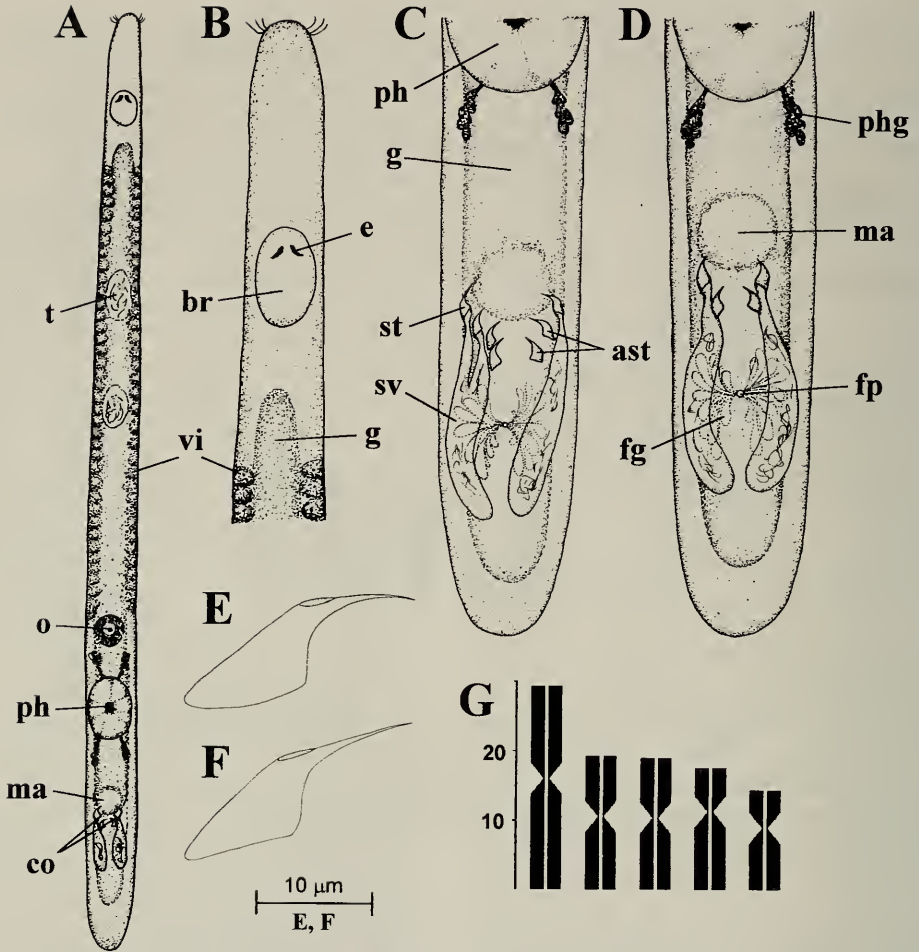


Fig. 3. *Alloestyliophora mirabilis*, new genus, new species. (A) general organization of live animal; (B) detail of the cephalic area; (C, D) detail of post-pharyngeal area: based on holotype (C), and paratype (D); (E) copulatory stylet; (F) accessory stylet (both from holotype); (G) idiogram. See Fig. 1 for explanation of abbreviations.

seminal vesicles, connected to a copulatory bulb, is the plesiomorphic condition for the Unguiphora (Curini-Galletti & Martens 1992). The condition seen in *A. mirabilis* may thus have involved a separation of the seminal vesicles and their connection to a copulatory stylet. The presence of two copulatory organs plausibly justifies the existence of the large male antrum, similarly unknown in other Unguiphora. The extreme reduction of the copulatory bulb is a further character peculiar to *A. mirabilis*.

In addition, among Unguiphora, acces-

sory stylets are only known in the genus *Polystyliophora*, where, however, they are serially arranged, up to 55 in number, morphologically distinct from the copulatory stylet, and connected to a glandular ("prostatoid") organ (Curini-Galletti 1998, Curini-Galletti & Martens 1991). In *A. mirabilis*, copulatory and accessory stylets are morphologically identical, and the few accessory stylets present do not appear to be connected to any glandular structure. Their function is puzzling. They may act as a reservoir of functional stylets and replace the

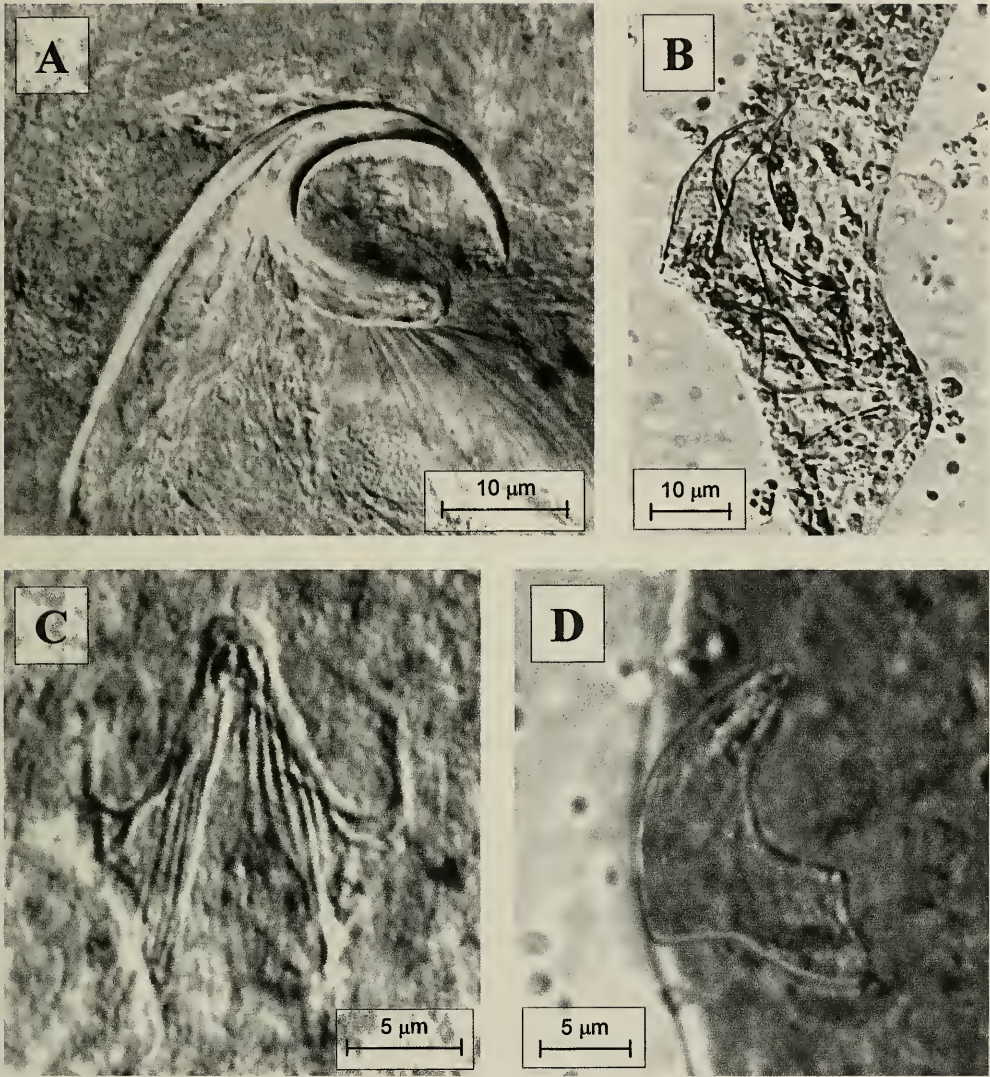


Fig. 4. (A) *Nematoplana indica*, new species, stylet (holotype). (B) *Alloeostryliphora mirabilis*, new genus, new species, post-pharyngeal area (holotype: lactophenol whole mount, contracted after fixation). (C, D) *Nematoplana calamus*, new species, stylet: (C) from holotype; (D) from paratype.

copulatory stylet once it is damaged or discharged. Should this be the case, the holotype, which possesses one of the copulatory organs with two copulatory stylets connected to the same seminal vesicle, may thus show the transitory stage of the connection of the first accessory stylet to the seminal vesicle, before the former copulatory stylet is discharged.

The eye-spots of *Alloeostryliphora mira-*

*bilis* appear identical to those found in a few species of *Nematoplana* (Curini-Galletti & Martens 1992). Their occurrence supports the hypothesis of the plesiomorphic nature of the character in the Unguiphora, proposed by Ehlers & Sopott-Ehlers 1990.

The phylogenetic relationships of *Alloeostryliphora mirabilis* are unclear. Proposal of a sister-group relationship with the

genus *Polystyliphora* would imply the homology of the 'prostatoid stylets' with the 'accessory stylets' of *A. mirabilis*, which, at the moment, does not appear to be supported. In fact, the morphology of the 'accessory stylets' (claw-shaped, without apophysis) appears uniquely derived for the Unguiphora and is not phylogenetically informative. However, it is parsimonious to assume that the additional stylets (with a shifting of function from 'replacement' (?) to 'prostatoid', or vice versa) may have evolved only once in the Unguiphora. Findings of additional species of the group may shed light on the question.

### General Considerations

Although accuracy of the morphological descriptions was in some cases hampered by the small number of specimens available for study, the sample was, nonetheless, worthy of interest due to the paucity of data from extra-European areas and for its specific and phylogenetic diversity. The presence of three unguiphorid species in a very small sample of sediment is surprising and points to a remarkable local diversity of proseriate fauna. For comparisons, the whole of northern Europe harbors only two unguiphorid species, while three species are known for the Mediterranean basin, where, however, each species occupies a distinct habitat and never co-occurs in the same sediment (Curini-Galletti & Martens 1991, 1992).

The finding of species showing unsuspected features, and whose phylogenetic relationships can not be assessed at present, clearly reflects the inadequate state of our knowledge of proseriate diversity, especially from tropical areas. A peculiar derived feature, which is apparently widespread in indo-pacific unguiphorids, but not elsewhere, is the presence of unpaired (in cases only one) oocytes in front of the pharynx (Curini-Galletti et al. 2001, present paper). There is no evidence of any further shared synapomorphies among these species, and

the character does not appear to have a phylogenetic base. A common adaptive strategy may, however, be involved. In contrast to the prevalently stocky and torpid, boreal unguiphorids, most tropical unguiphorids appear markedly smaller and more slender. Differential timing of maturity of oocytes on the two sides of the body might be due to morphological constraints of the egg size in tiny, exceedingly filiform, organisms.

### Acknowledgments

We are grateful to Donatella Ciaccava Curini-Galletti, who collected and transported the sediment sample.

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## Studies on western Atlantic Octocorallia (Coelenterata: Anthozoa). Part 1: The genus *Chrysogorgia* Duchassaing & Michelotti, 1864

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*Abstract.*—The nine species of *Chrysogorgia* known from the western Atlantic are described and illustrated. One species is described as new (*C. herdendorfi*), three species are synonymized (*C. orientalis*, *C. affinis*, *C. elisabethae*), and two species are elevated in rank from variety to species (*C. multiflora* and *C. thyriformis*). Lectotypes are chosen for six of the species and a neotype for one, *C. desbonni*, the type species of the genus. A type species is also designated for the genus *Dasygorgia*, a junior synonym of *Chrysogorgia*. An identification key to the nine species is given, as well as a list of the 59 currently recognized species in the genus, along with their type locality, depth of capture, and branching sequence. The study was based on newly reported specimens from over 150 deep-water stations as well as re-examination of all historical material; additional records of *C. squamata* and *C. spiculosa* represent the first reports of these species since their original description in 1883.

Species of the genus *Chrysogorgia* are reputed to be among the most interesting and beautiful of the gorgonians (Agassiz 1888; Verrill 1883), their golden, iridescent branches and mathematically precise branching pattern making them truly elegant organisms. They occur exclusively in deep water (100–3375 m) and are found worldwide except off Antarctica. Members of this genus are extremely diverse in colony form and sclerite complement, the 59 recognized species (Table 1) representing the most speciose of the calcaxonian genera. The western Atlantic *Chrysogorgia* were reviewed by Verrill (1883) and Deichmann (1936); however, significant collections made after 1936 and improved methods of study have made a faunistic revision of this genus desirable. Indeed, the discovery of one such undescribed “golden corals” from the gold-carrying wreck of the S.S. *Central America* was the original motivation for this paper.

### Materials and Methods

This study was based on an examination of previously unreported specimens collected from 157 stations within the western Atlantic (Table 2), most collected after Deichmann’s (1936) classic revision of the western Atlantic Octocorallia. These specimens are deposited primarily at the USNM and MCZ, the USNM material originating primarily from the prodigious collecting of the Rosenstiel School of Marine and Atmospheric Science, University of Miami in the 1970’s. Historically important specimens, including the types for all species discussed, were also examined; these specimens are deposited at the MCZ, USNM, and BM.

The terminology used for the descriptions follows Bayer, Grasshoff & Verseveldt (1983), whereas general methodology of specimen examination can be found in Bayer (1961) and Alderslade (1998). Synonymies for all species are purported to be



Table 1.—The 59 valid species of the genus *Chrysogorgia*, arranged by group, and within group by branching sequence and then date of description. Species from Western Atlantic in bold face. Type localities and depths also included.

Group A: "Spiculosae" (rods and/or spindles in body wall and tentacles)		
<i>C. cupressa</i> (Wright and Studer, 1889)	(Banda Sea, 256 m)	1/4L
<i>C. lata</i> Versluys, 1902	(Celebes Sea, 1901 m)	1/4L
<i>C. terasticha</i> Versluys, 1902	(Banda Sea, 204 m)	1/4L
<i>C. pusilla</i> Versluys, 1902	(Timor Sea, 520 m)	1/4L
<i>C. dispersa</i> Kükenthal, 1908	(Japan, depth?)	1/4L
<i>C. pyramidalis</i> Kükenthal, 1908	(Japan, "upper abyssal")	1/4L
= <i>C. aurea</i> Kinoshita, 1913		
<i>C. rotunda</i> Kinoshita, 1913	(Japan, 732 m)	1/4L
<i>C. papillosa</i> Kinoshita, 1913	(Japan, 730 m)	1/4L
<i>C. minuta</i> Kinoshita, 1913	(Japan, 146 m)	1/4L
<i>C. okinosensis</i> Kinoshita, 1913	(Japan, 366 m)	1/4L
<i>C. comans</i> Kinoshita, 1913	(Japan, 146 m)	1/4L
<i>C. sphaerica</i> Aurivillius, 1931	(Japan, 183–732 m)	1/4L
<i>C. desbonni</i> Duch. & Mich., 1864	(Lesser Antilles, 161 m)	2/5R (biflabellate)
= <i>C. occidentalis</i> Versluys, 1902		
<i>C. spiculosa</i> (Verrill, 1883)	(Lesser Antilles, 991 m)	2/5R
<i>C. elegans</i> (Verrill, 1883)	(Barbados, 433 m)	2/5R
= <i>C. affinis</i> Versluys, 1902		
<i>C. fewkesii</i> Verrill, 1883	(Lesser Antilles, 1048 m)	2/5R
<i>C. flexilis typica</i>	(Southern Chile, 220 m)	2/5R
(Wright & Studer, 1889)		
<i>C. flexilis</i> var. <i>africana</i> Kükenthal, 1908	(East Africa, "upper abyssal")	2/5R
<i>C. flexilis</i> var. <i>maldivensis</i>	(Maldive Ids., 229–914 m)	2/5R
Hickson, 1940		
<i>C. pentasticha</i> Versluys, 1902	(Timor Sea, 520 m)	2/5R
<i>C. anastomosans</i> Versluys, 1902	(Indonesia, 520–827 m)	2/5R
<i>C. arborescens</i> Nutting, 1908	(Hawaii, 722–914 m)	2/5R
<i>C. debilis</i> Kükenthal, 1908	(Japan, depth?)	2/5R
<i>C. quadruplex</i> Thomson, 1927	(Azores, 1022 m)	2/5R
<i>C. multiflora</i> Deichmann, 1936	(Lesser Antilles, 991 m)	2/5R
<i>C. thyriformis</i> Deichmann, 1936	(Barbados, 183 m)	2/5R
= <i>C. elisabethae</i> Bayer, 1951		
<i>C. herdendorfi</i> , n. sp	(off S. Carolina, 2178 m)	2/5R–3/8R
<i>C. pellucida</i> Kükenthal, 1908	(Japan, 100 m)	dichotomous
<i>C. squarrosa</i> (Wright & Studer, 1889)	(Philippines, 914 m)	irreg.
<i>C. orientalis</i> Versluys, 1902	(Indonesia, 918–924 m)	irreg.
<i>C. mixta</i> Versluys, 1902	(Celebes, 1165–1264 m)	irreg.
<i>C. indica</i> Thomson & Henderson, 1906	(Sri Lanka, 1038 m)	irreg.
<i>C. irregularis</i>	(Sri Lanka, 1271 m)	irreg. (1/3)
Thomson & Henderson, 1906		
<i>C. dichotoma</i>	(Bay of Bengal, 165 m)	irreg. (L)
Thomson & Henderson, 1906		
Group B: "Squamosae aberrantes" (rods and/or spindles in tentacles but not in body wall)		
<i>C. flavescens</i> Nutting, 1908	(Hawaii, 1688–1977 m)	1/3L
<i>C. expansa</i> (Wright & Studer, 1889)	(Kermadec Ids., 951 m)	1/4R
<i>C. octogonos</i> Versluys, 1902	(Timor Sea, 520 m)	1/4R
<i>C. versluysi</i> Kinoshita, 1913	(Japan, 732 m)	1/4R
<i>C. calypso</i> Bayer & Stefani, 1988	(Celebes, 732 m)	1/4R
<i>C. intermedia</i> Versluys, 1902	(Timor Sea, 250 m)	1/4R–1/7R
<i>C. squamata</i> (Verrill, 1883)	(Lesser Antilles, 431 m)	1/5R–1/7R
<i>C. bracteata</i> Bayer & Stefani, 1988	(Philippines, 329 m)	1/6R
<i>C. admete</i> Bayer & Stefani, 1988	(New Caledonia, 390 m)	1/7R

Table 1.—Continued.

<i>C. agassizii</i> (Verrill, 1883)	(Georges Bank., 2271 m)	2/5R
<i>C. curvata</i> Versluys, 1902	(Indonesia, 1089 m)	biflabellate
<i>C. chryseis</i> Bayer & Stefani, 1988	(Ceram Sea, 732 m)	biflabellate
<i>C. stellata</i> Nutting, 1908	(Hawaii, 649–678 m)	multiflabellate
Group C: "Squamosae typicae" (rods and/or spindles not present; only scales)		
<i>C. axillaris</i> (Wright & Studer, 1889)	(Phil./Kerm., 150, 1097 m)	1/3L
<i>C. geniculata</i> (Wright & Studer, 1889)	(Philippines, 150–187 m)	1/3L
<i>C. fruticosa</i> (Studer, 1894)	(Gulf of Panama, 837 m)	1/3L
<i>C. rigida</i> Versluys, 1902	(Philippines, 522 m)	1/3L
<i>C. sibogae</i> Versluys, 1902	(Banda Sea, 204 m)	1/3L
<i>C. excavata</i> Kükenthal, 1908	(Japan, "abyssal")	1/3L
<i>C. delicata</i> Nutting, 1908	(Hawaii, 536–1463 m)	1/3L
<i>C. cavea</i> Kinoshita, 1913	(Japan, 640–752 m)	1/3L
<i>C. ramosa</i> Versluys, 1902	(Philippines, 522 m)	1/4L
<i>C. acanthella</i> (Wright & Studer, 1889)	(Kermadec, 1097 m)	2/5L
<i>C. pendula</i> Versluys, 1902	(Banda Sea, 1595 m)	2/5L
<i>C. campanula</i> Madsen, 1944	(Iceland, 2448 m)	2/5L
<i>C. electra</i> Bayer & Stefani, 1988	(Paumotu Ids., 1485 m)	flabellate
<i>C. scintillans</i> Bayer & Stefani, 1988	(Hawaii, 1758–1937 m)	flabellate
<i>C. japonica</i> (Wright & Studer, 1889)	(Japan, 3375 m)	unknown

complete, including every reference to the species discussed. In the material examined sections for each species, the station number is followed by the number of specimens in that lot and then the catalog number. The SEM photomicrographs were taken by the author using an AMRAY 1810 scanning electron microscope.

The following abbreviations are used: Vessels: *Alb*—U. S. Fish Commission Steamer *Albatross*; *Atl*—*Atlantis* and *R/V Atlantis II*; *BL*—U. S. Coast Survey Steamer *Blake*; *CI*—*R/V Columbus Iselin*; *G*—*R/V Gerda*; *Gos*—*R/V Gosnold*; *GS*—*R/V Gilliss*; *O*—*M/V, R/V Oregon* and *R/V Oregon II*; *P*—*R/V Pillsbury*; *SB*—*M/V, R/V Silver Bay*.

Museums: *BM*—The Natural History Museum (London); *MBD BR*—Blake Ridge Expedition of the Museum of Biological Diversity (The Ohio State University, Columbus); *MCZ*—Museum of Comparative Zoology, Harvard (Cambridge); *USNM*—United States National Museum (now known as the National Museum of Natural History), Washington D. C.

### Subclass Octocorallia

#### Order Alcyonacea

Suborder Calcaxonia Grasshoff, 1999

Family Chrysogorgiidae Verrill, 1883

Chrysogorgiidae Verrill, 1883: 21.—Nutting, 1908: 587.

Chrysogorgiidae Versluys, 1902: 2–4.—Kükenthal, 1919: 486–496 (key to genera); 1924: 38 (key to genera).—Deichmann, 1936: 220–222 (key to genera).—Hickson, 1940: 306–307.—Madsen, 1944: 44.—Bayer, 1949: 237–238; 1956: F216; 1961: 297–299 (key to genera); 1973: 84–86; 1974: 262–263.—Bayer & Muzik, 1976: 67–69 (key to genera).—Bayer, 1979: 876–878 (key to genera).—Bayer & Stefani, 1988: 257–259 (key to genera).—Williams, 1992a: 379; 1992b: 251.

Dasygorgiidae Studer, 1887: 39.—Wright & Studer, 1889: xxxix, 1.

Dasygorgiidae Hickson, 1904: 221.—Thomson & Henderson, 1906: 26.

Malacogorgiidae Hickson, 1904: 226.

*Diagnosis*.—Calcaxonians having an unjointed, solid (non-spicular), concentrically

Table 2.—Station list.

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
<i>U.S.F.C.S. Albatross (Alb)</i>				
2034	39 27 10	69 56 20	2462	17 VII 1883
2035	39 26 16	70 02 37	2491	17 VII 1883
2129	19 56 04	75 48 55	501	27 II 1884
2220	39 43 30	69 23 00	1928	23 VIII 1884
2342	23 10 39	82 20 21	368	19 I 1885
2347	23 10 39	82 20 21	395	20 I 1885
2397	28 42 00	86 36 00	512	14 III 1885
2415	30 44 00	79 26 00	805	1 IV 1885
2573	40 34 18	66 09 00	3186	2 IX 1885
2655	27 22 00	78 07 30	618	2 V 1886
2751	16 54 00	63 12 00	1257	28 XI 1887
4151	Vicinity of Bird Id., Hawaii		572-1593	5 VIII 1902
5080	34 10 30	138 40 E	923	19 X 1906
<i>Atlantis and R/V Atlantis II (Atl)</i>				
266-40	30 53	78 47		
2980 B	22 48	78 48	402-412	10 III 1938
2999	23 10	81 29	265-421	17 III 1938
3306	23 04 30	82 37	604	23 III 1938
3326	22 09	81 09	485	4 IV 1939
3436	22 12	81 11 30	365-439	6 IV 1939
3437	23 05	79 32	476	2 V 1939
3438	23 05 30	79 37	485	2 V 1939
3479	23 10	81 26 30	384	11 V 1939
3480	23 10	81 28	366	11 V 1939
<i>U.S.C.S.S. Bibb</i>				
22	24 14 00	80 59 40	79	6 V 1868
<i>U.S.C.S.S. Blake (BL)</i>				
44	25 33	84 35	986	1877
55	22 09	82 21	443	1877
101	off Morro Light, Cuba		320-457	1878
190	15 18 12	61 26 32W	199	29 I 1879
195	14 42 35	61 13 15	917	5 II 1879
	14 31 55	61 07 28	863	7 II 1879

Table 2.—Continued.

Station	Latitude ( $^{\circ}$ N)	Longitude ( $^{\circ}$ W)	Depth (m)	Date
200				
205	14 25 15	60 56 35	607	10 II 1879
222	13 50 15	61 04 45	772	16 II 1879
227	13 10 10	61 18 15	1048	19 II 1879
232	13 06 45	61 06 55	161	21 II 1879
241	12 28 22	61 32 18	298	24 II 1879
260	12 03 30	61 47 10	532	28 II 1879
281	12 54 48	59 36 30	527	6 III 1879
283	13 05 05	59 40 50	432	7 III 1879
284	13 07 10	59 43 50	635	7 III 1879
297	13 02 36	59 37 45	42	10 III 1879
308	41 24 45	65 35 30	2272	29 VI 1880
43	18 02 00	67 51 15	439-549	11 II 1933
102	18 50 30	64 43 00	165-915	4 III 1933
4502	28 35 01	86 45 44	625	13 V 1985
4504	28 28 47	86 02 32	351-357	14 V 1985
4507	28 01 04	85 39 38	629	16 V 1985
4508	28 07 38	85 51 36	624-631	16 V 1985
4509	28 13 33	86 06 39	616-620	17 V 1985
4510	28 16 42	86 12 05	613-618	17 V 1985
4511	28 18 58	86 18 56	600-625	17 V 1985
4512	28 07 08	86 17 10	823-845	17 V 1985
4513	28 09 35	86 23 56	871	18 V 1985
4514	28 16 00	86 36 16	838-847	20 V 1985
5505	27 43 10	92 09 14	516-527	10 VI 1985
15	23 29	77 09	1116	5 VII 1972
37	25 08	77 12	512	9 VII 1972
46	23 29	77 05	1234	24 II 1973
447	25 07	79 15	549	23 VII 1957

R/V *Columbus Iselin (CI)*M/V *Combat*

Table 2.—Continued.

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
26549	27 17 30	79 12 30	370	30 II 1975
31281	26 53 54	79 07 18	320	III 1977
<i>R/V Eastward</i>				
128	23 49	81 37	1390-1463	20 VI 1963
129	23 46	81 15	1280	20 VI 1963
130	23 59	81 10	1021	21 VI 1963
168	27 00	79 15 30	229-274	29 VI 1963
190	25 57	78 07	732-896	4 VIII 1963
232	25 36	79 20 30	421-439	29 I 1964
233	25 40	79 21	402-421	30 I 1964
235	25 44	79 22	530	30 I 1964
246	26 57	79 12 30	512	5 II 1964
368	24 03	81 10	960-1015	15 IX 1964
369	24 03	81 10	960-1015	15 IX 1964
370	23 54	81 19	1280	16 IX 1964
371	23 53	81 22	1262	16 IX 1964
372	23 51	81 02	1107	16 IX 1964
387	27 17	79 15	412	19 IX 1964
391	27 20	79 12	46-91	19 IX 1964
403	27 49	78 50	823	20 IX 1964
503	26 31	78 51	366	4 II 1965
678	25 57	78 13	540-576	20 VII 1965
679	25 56	78 09	594-710	20 VII 1965
692	26 35	78 25	329-421	21 VII 1965
705	26 29	78 41	362-393	22 VII 1965
798	25 56	79 22	402	12 IX 1966
859	23 54	81 57	1161-1200	29 VIII 1967
889	20 55	86 28	177-220	10 IX 1967
893	21 10	86 21	241-320	10 IX 1967
897	20 59	86 24	210-293	10 IX 1967
898	21 04	86 19		10 IX 1967
899	20 57	86 34	40-165	10 IX 1967
925	25 58	78 29	439-457	29 IX 1967
927	26 15	78 48	476	29 IX 1967
<i>R/V Gerda (G)</i>				

Table 2.—Continued.

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
936	26 35	79 20	603	1 X 1967
965	23 45	81 49	1394-1399	1 II 1968
1010	23 34	79 35	296-329	14 VI 1968
1111	23 51 54	80 42 42	1080-1089	30 IV 1969
1112	23 44	81 14	1245-1291	30 IV 1969
1125	26 45	79 05	494-531	13 VI 1969
1312	26 38 24	79 02 30	505-527	31 III 1971
1314	26 52 24	79 11 48	531-540	31 III 1971
134	N. Atlantic Ocean			5 V 1976
2385	30 57 12	78 54 36	779	27 VIII 1965
2387	28 17 36	86 14 48	603-640	16 IV 1984
2429	28 06 00	86 35 18	1170	18 IV 1984
S36	28 57 53	87 33 40	716-1852	V1 2000
MA2:04	38 45 48	72 39 06	2110-2180	2 VIII 1984
58-I-827	Between Rhode Id. and Bermuda			
489	27 44	85 09	565	29 IX 1951
548	27 01 24	96 16 48	366-512	18 IV 1952
549	26 58 30	96 06 42	229	18 IV 1952
2081	01 52	46 54	320	17 XI 1957
2636	17 36	63 32	439-476	30 IX 1959
2655	18 26	67 10 30	229	06 X 1959
4413	11 53	69 25	640	03 X 1963
4701	27 42	90 32 30	915	22 II 1964
4729	27 46	92 13	549	26 II 1964
4811	24 01	96 33	1829	11 IV 1964
4812	24 03	96 24	1646	11 IV 1964
4940	20 30	86 14	311-329	12 VI 1964
5021	11 21 12	60 38 42	165-183	21 IX 1964

R/V Gilliss (GS)

R/V Gosmold (Gos)

Gyre

R/V Knorr

M/V, R/V Oregon and Oregon II (O)

Table 2.—Continued.

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
5419	20 50	73 29	311–329	25 V 1965
10849	20 50	73 23	311	13 XII 1969
10878	28 54	87 29	1829	16 I 1970
<i>R/V Pillsbury (P)</i>				
200	27 30	79 10	329–348	11 VIII 1964
208	27 12	79 17	512	12 VIII 1964
209	26 59	79 16	330–450	12 VIII 1964
391	10 03	76 29	1235–1768	16 VII 1966
394	9 28 42	76 26 18	421–641	16 VII 1966
478	11 34 24	62 10 42	586–608	2 VIII 1966
594	21 00 30	86 23	307–329	15 III 1968
607	18 30	87 37	715–787	15 III 1968
610	17 02 00	87 38 16	296–329	18 III 1968
611	16 50	87 37	750–990	18 III 1968
689	08 14 00	57 38	1372–1445	15 VII 1968
739	10 54 42	66 17 48	234–280	22 VII 1968
776	12 13 18	72 50 00	408–576	29 VII 1968
781	11 30 06	73 26 30	530–567	30 VII 1968
784	11 26 30	74 10	567–713	31 VII 1968
847	11 37 18	60 59 24	733–1281	2 VII 1969
848	11 22 00	61 26 24	146	2 VII 1969
850	11 45 30	61 29 30	798–985	3 VII 1969
857	12 23 30	61 21 36	9–348	3 VII 1969
877	13 16 42	61 05 36	389–467	6 VII 1969
881	13 20 48	61 02 30	576–842	6 VII 1969
890	14 05 36	60 51 24	198–430	7 VII 1969
892	14 17	60 45 12	1116–1354	7 VII 1969
904	13 45 30	61 05 42	201–589	9 VII 1969
907	14 26 48	60 58 18	115–214	9 VII 1969
919	16 05 18	61 19 18	689–733	12 VII 1969
931	15 31 12	61 12 18	146–494	15 VII 1969
984	18 26 24	63 12 36	393–451	22 VII 1969
988	18 29 18	63 24 36	686–724	23 VII 1969
991	18 47	64 46 48	205–380	23 VII 1969
1141	20 52	73 14	403–488	13 I 1970

Table 2.—Continued.

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Date
1262	17 21 24	77 34 48	805–1089	15 VII 1970
1410	20 11 00	68 52 54	180	17 VII 1971
440	27 21 N	79 15	439–503	8 VI 1958
3497	20 53	73 44	265	4 XI 1961

MV, R/V *Silver Bay* (SB)

layered scleroproteinous axis. The axis of stem and branches may be branched or unbranched, arising from a root-like or discoidal, strongly calcified holdfast. The axial layers are not undulated and the axial surface is smooth (not longitudinally grooved); the axis usually displays metallic or iridescent reflections. Polyps contractile but not retractile, arranged in rows, never in whorls or on opposite sides of branch. Sclerites predominantly flat, smooth scales and plates, in some species accompanied by warty rods or spindles. Scales show concentric bands of interference colors in polarized light.

*Remarks.*—The Chrysogorgiidae is one of five families placed in the newly created suborder Calcaxonina (Grasshoff 1999). Previously placed in the suborder Holaxonia, these families differ in having an axis that does not have a cross-chambered, hollow central core, but rather a solid axis containing abundant calcareous material that is embedded in gorgonin or as purely calcareous segments. The taxonomic history of the family is integrated into the generic account.

#### Subfamily Chrysogorgiinae Verrill, 1883

Chrysogorgiinae Studer, 1887: 41.—Wright & Studer, 1889: xl, 4.

Chrysogorgiinae Versluys, 1902: 4, 17.—Nutting, 1908: 588.—Madsen, 1944: 49.—Bayer, 1956: F216.

*Diagnosis.*—Chrysogorgiids having branching colonies.

*Remarks.*—Two other subfamilies are currently recognized: the Lepidogorgiidae, for species having unbranched colonies and uniserially arranged polyps, and the Chalcogorgiinae, for species having unbranched colonies and polyps arranged bi- or multiserially. However, over the last several decades, subfamilial classification has rarely been used.

#### Genus *Chrysogorgia* Duchassaing & Michelotti, 1864

*Chrysogorgia* Duchassaing & Michelotti, 1864: 13 (107).—Verrill, 1883: 21.—Stu-



der, 1887: 41.—Wright & Studer, 1889: xli, 23.—Versluys, 1902: 17–33.—Nutting, 1908: 588.—Kükenthal, 1919: 505–511 (key to species); 1924: 388–390 (key to species).—Deichmann, 1936: 227–228 (key to w. Atlantic species).—Hickson, 1940: 307.—Madsen, 1944: 49.—Bayer, 1956: F216.—Bayer & Stefani, 1988: 259 (key to species of “Squamosae aberrantes”).—Williams, 1992b: 252.

*Dasygorgia* Verrill, 1883: 21.—Studer, 1887: 41.—Wright & Studer, 1889: xli, 6–9, 278.

*Diagnosis.*—Sympodially branched chrysogorgiids, the branches subdividing dichotomously, either arising from a regular single, ascending spiral around the main stem or forming two parallel fans above a short main stem. Polyps large relative to branches on which they sit, few in number, and well separated from one another. Sclerites consist of spindles, rods and scales. Axis with a brilliant metallic luster, usually amber, yellow or golden in color.

*Discussion.*—Verrill (1883) established the family Chrysogorgiidae for three genera: *Chrysogorgia*, *Dasygorgia*, and *Iridogorgia*. He distinguished *Dasygorgia* from *Chrysogorgia* mainly by its longitudinal arrangement of sclerites in the body wall, *Chrysogorgia* having transversely and often curved sclerites. He included five newly described species in *Dasygorgia* but did not designate a types species. Thus, the first species described by Verrill, *D. agassizii*, is herein designated the type of that genus. In that paper Verrill (1883) described a majority of the chrysogorgiid species now known from the western Atlantic. Shortly thereafter, Studer (1887) unnecessarily rechristened the family Dasygorgiidae, arguing that the type species of *Chrysogorgia*, *C. desbonni*, could not be correctly identified. He also divided the family into two subfamilies, the Chrysogorginae containing all genera having branched colonies and thus including *Chrysogorgia*. Two years later, Wright & Studer (1889) informally suggested two groupings among the species of

*Dasygorgia*: the “Spiculosae” (species having spindles and/or rods) and the “Squamosae” (species having predominantly scale-like sclerites).

Based on the chrysogorgiids collected on the *Siboga* expedition, Versluys (1902) essentially monographed the genus *Chrysogorgia*, describing or redescribing the 36 species known at that time and presenting a lengthy and thorough discussion of the morphology of the species in this genus. He convincingly demonstrated that *Dasygorgia* was a junior synonym of *Chrysogorgia*, making Dasygorgiidae subordinate to Chrysogorgiidae. He adopted the species groupings suggested by Wright & Studer (1889), added a third group with intermediate characteristics, and formalized the diagnoses on these groupings. Thus, the “Spiculosae” (also called Group A) contained species having rods and/or spindles in both the body wall and tentacles, the “Squamosae typicae” (also called Group C) contained species having sclerites in the form of scales in both body wall and tentacles, and Versluys’ new grouping, the “Squamosae aberrantes” (also called Group B), contained species having scales in the body wall, but rods and/or spindles in the tentacles. Versluys further subdivided each of these groupings into two to four subgroups based on the branching sequence of each species. Although Kükenthal (1919, 1924) used the characteristics of these subgroupings in his species key, no author has ever suggested that the three major groupings or nine subgroupings be used as the basis for subgeneric taxa. Other significant works concerning the taxonomy of the species of *Chrysogorgia* include: Kinoshita (1913), a review of the Japanese species; Deichmann (1936), a review of the western Atlantic species; Madsen (1944), the *Ingolf* specimens from off Iceland; Bayer (1973), ecological remarks; and Bayer & Stefani (1988), new species from the western Pacific.

*Type species.*—*Chrysogorgia desbonni* Duchassaing & Michelotti, 1864, by monotypy.



Fig. 1. *Chrysogorgia herdendorfi*, holotype, USNM 91934, height 20 cm.

Type species of *Dasygorgia*: *D. agassizii* Verrill, 1883, here designated.

*Chrysogorgia herdendorfi*, new species  
Figs. 1–2

*Description*.—The holotype is 20 cm in height and about 3 cm in width, the colony being of a bottlebrush shape. Colonies are attached to the substrate by a roughly circular, thin, encrusting (not rhizoidal) holdfast 5–10 mm in diameter, the holdfast being milky white in color. The main stem just above the holdfast is circular in cross section, 0.9–1.1 mm in diameter, and of a metallic golden-brown luster. The main stem ascends in a tight, counterclockwise spiral (producing a zig-zag pattern), giving off branches in a regular manner in a predominantly 2/5R sequence; however, in parts of the colony a 3/8R sequence appears to hold. The lowest branch of the holotype occurs 16 mm above the holdfast, whereas the lowest branch of the paratype is at 60

mm height, but bears scars of broken branches as low as 30 mm. Branches occur approximately every 2.5–3.0 mm along the main stem, the distance between aligned branches (defined as the “orthostiche interval” by Versluys 1902) in the 2/5R sequence being 14–17 mm. The lowermost branches are often unbranched, up to 32 mm in length, and bear up to 6 polyps. The branches of the mid-portion of the colony usually have only one node, the first internode 6–7 mm in length, the terminal twigs up to 35 mm, producing a total branch length of about 42 mm. One polyp occurs on the first internode at or within 0.5 mm of the node, and 4–6 polyps occur on the terminal twigs. Branches toward the top of the colony usually have two nodes, the first internode about 4 mm in length, the second 6–7 mm, and the terminal twigs up to 30 mm, also producing a total branch length of about 42 mm. There is usually one polyp on the first and second internodes adjacent to the nodes, and 4–5 polyps on the terminal twigs. Branches near the growing tip of the colony also usually have two nodes, but the terminal twigs are shorter (about 10 mm), thus result in shorter branches. Hence, most branches of the colony are of the same total length, i.e., 40–45 mm, regardless of the number of internodes present or the location of the branch, except for those near the developing tip, which are shorter. No branches containing three internodes were noted. The branches arise at gradually increasing angles from the base upward, the lowest branches about 45° from the vertical, those toward the top of the colony 60–70° from the vertical. Branch internodes adjacent to the main stem are quite slender, about 0.08 mm in diameter; distal twig branch diameters are even smaller, about 0.04 mm. These slender branches produce a very flexible limp structure to the colony, such that when a colony is removed from fluid the branches will coalesce with one another. Corresponding internodes and terminal twigs of the same branch are of the same lengths. There is no anastomosis.

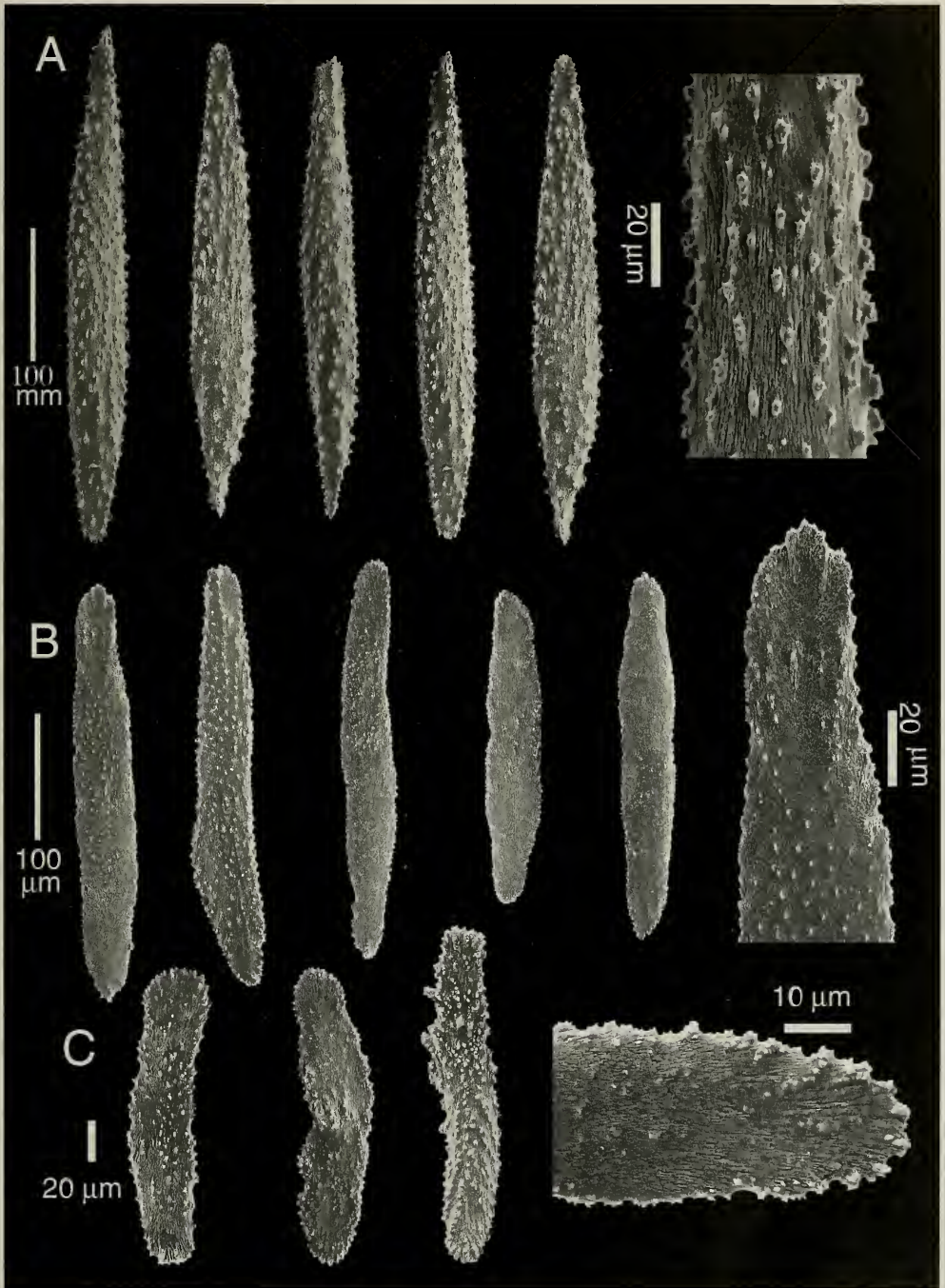


Fig. 2. *Chrysogorgia herdendorfi*, sclerites from holotype, USNM 91934. A, six spindles from body wall and tentacles; B, six coenenchymal scales; C, four pinnular scales.

The polyps are elongate, up to 2.3 mm in height and 0.6 mm in width, slightly constricted at mid-level, and diverge at an oblique angle to the branch. The thin coenenchyme covering both the main stem and branches contains straight, elongate scales that are usually blunt at each end, up to 0.43 mm in length and 0.06–0.07 mm in width. These scales have finely serrated edges and bear very small granules (1.8–2.5  $\mu\text{m}$  diameter) on their faces. Toward the base of the polyps and continuing up the body wall the scales gradually change into longitudinally oriented, straight spindles of virtually the same size; the spindles are pointed at both ends and bear small compound warts, the warts 4–8  $\mu\text{m}$  in diameter. Thus the body wall consists of both elongate scales and spindles of similar size and shape. The lower, backs of the tentacles also contain robust, finely-warted spindles, usually arranged three across a tentacle, up to 0.43 mm in length and 0.11 mm in width. The pinnules contain small, irregularly-rectangular scales, most about 0.15–0.20 mm in length. They have finely-serrated edges and virtually flat faces that bear very small granules, the largest only 1  $\mu\text{m}$  in diameter.

*Discussion.*—At first glance, the branching sequence of *C. herdendorfi* appears to be a typical 2/5R, like the morphologically similar *C. elegans*. This branching formula, a shorthand notation developed by Versluys (1902), implies that five branches originate from the main stem in two counterclockwise revolutions up the main stem (i.e., counterclockwise, as viewed from the apex of the colony; and as moving to the “right”, as viewed for the side of the colony), such that every sixth branch will lie directly above the first, forming five rows of branches along the main stem. However, the branch correspondence was often found to be slightly off after two revolutions up the stem. But when branch origins were traced for three revolutions around the main stem, an exact correspondence was discovered, such that the branch sequence would appear to be 3/8R. This implies that there

are eight longitudinal rows of branches from the main stem, but that three revolutions of branch origins must occur before a branch (the 9th) lies directly above the first. The angular separation between adjacent branches is thus  $135^\circ$ , instead of  $144^\circ$ , the latter being typical of the 2/5 sequence. This is believed to be the first example of a chrysogorgiid branching sequence that requires three revolutions to achieve alignment.

Although two specimens are unquestionably assigned to this species, both from the wreck of the *Central America*, five *Chrysogorgia* colonies were collected from that site. Two of the other three specimens (USNM 91935 and BR127) are identical to *C. herdendorfi* in all characters described above, except that their body wall sclerites are longitudinally arranged, elongate scales, much like those in the lower body wall of *C. herdendorfi*, but never graduating to the spindle shape characteristic of the upper body wall of *C. herdendorfi*. This may represent variation in sclerite form, or a closely-related undescribed species, but, because of the paucity of specimens available and the uncertainty in interpreting this character, they are presented here as a non-type variety of *C. herdendorfi*. The fifth specimen (BR234) is even more perplexing in that it has sclerites similar to *C. herdendorfi* but it is a larger colony (36 cm height) with more nodes (0-2-5) and longer, flabellate branches. It may well represent an undescribed species and is probably the species most often figured *in situ* by Herdendorf, et al. (1995: 93–94, 111, 189, figs. 62–64, 66–67, 71–72, 83, 85, 89, 93–95, 99, 105, 109, 113 (also back cover), 128–129, 147), figure 89 being the actual specimen collected (BR234). But, until additional specimens are collected and examined, this species will remain undescribed.

Within the western Atlantic, *C. herdendorfi* is most similar to two species: *C. elegans* and *C. agassizii* (see Table 3). But, although similar in colony shape and spiculation, *C. elegans* differs in having a more

Table 3.—Distinguishing characteristics of the nine western Atlantic species of *Chrysoyorgia*.

	Colony shape; maximum height	Branching sequence	Distance between branches; orthostiche interval	Number of inter- nodes; length of 1st internode	Flexibility	Number of polyps on first inter- node	Group	Orientation of bw sclerites	Sclerite complement (coen. = coenenchymal; bw = body wall; tent. = tentacular); measurements are maximum	Distribution and depth range in Western Atlantic
<i>C. herdendorfii</i>	bottlebrush; 22 cm	2/5R or 3/8R	2.5–3.0 mm; 14–17 mm	0-1-2; 4-7 mm	limp	1	A	long.	coen.: elongate scales, 0.43 mm bw: straight spindles, 0.43 mm tent.: straight spindles, 0.43 mm	off S. Carolina, 2178 m
<i>C. elegans</i>	bottlebrush; 16 cm	2/5R	1.0–1.5 mm; 7.0–7.5 mm	1-2-3; 6–8 mm	wiry	1	A	long.	coen.: elongate scales, 0.65 mm bw: rotund rods, 0.65 mm tent.: rods, 0.65 mm	Gulf of Mexico, se Caribbean, Brazil, 128–1716 m
<i>C. spiculosa</i>	bottlebrush; 25 cm	2/5R	3.5–4.5 mm; 20–25 mm	3-4-6; 15– 20 mm	wiry	3	A	long.	coen.: elongate scales, 0.60 mm bw: rotund rods, 0.96 mm tent.: rods, 0.54 mm	Gulf of Mexico, Lesser Antilles, 914–2265 m
<i>C. multiflora</i>	bottlebrush; 25 cm	2/5R	1–4 mm; 6– 22 mm	4-5-9; 10– 14 mm	wiry	2–4	A	trans.	coen.: elongate plates, 0.77 mm bw: curved spindles, 1.08/ 0.13	Antilles, Bahamas, 320–1280 m
<i>C. fewkesii</i>	bottlebrush; 23 cm	2/5R	3–6 mm; 17– 20 mm	5-6-10; 10– 12 mm	wiry	2–4	A	trans.	tent.: spindles, 0.86 mm coen.: elongate plates, 0.95 mm bw: curved spindles, 0.71/ 0.06 mm	Antilles, Caribbean, 403–1200 m
<i>C. desbonni</i>	biflabellate; 16 cm	2/5R	0.6–1.0 mm; 5 mm	up to 40; 3–4 mm	wiry	1	A	trans.	tent.: rods, 0.35 mm coen.: elongate scales, 0.71 mm bw: curved spindles, 0.75 mm	Greater and Lesser Antilles, Bahamas, 155–595 m
<i>C. thyrsoformis</i>	bushy; 8 cm	2/5R	0.5–0.7 mm; 2.7–5.0 mm	up to 12; 5–8 mm	wiry	2–3	A	trans.	tent.: rods, 0.24 mm coen.: elongate scales, 0.54 mm bw: curved spindles, 0.71 mm tent.: rods, 0.42 mm	Greater and Lesser Antilles, Bahamas, 146–526 m

Table 3.—Continued.

Colony shape; maximum height	Branching sequence	Distance between branches; orthostichic interval	Number of inter- nodes; length of 1st internode	Flexibility	Number of polyps on first inter- node	Group	Orientation of bw sclerites	Sclerite complement (coen. = coenochymal; bw = body wall; tent. = tentacular), measurements are maximum	Distribution and depth range in Western Atlantic
<i>C. agassizii</i> bottlebrush; 41 cm	2/5R	1.5–2.0 mm; 10–12 mm	2–3–5; 2–4 mm	limp	0	B	long.	coen.: elongate scales, 0.36 mm bw: elongate scales, 0.48 mm tent.: straight rods, 0.60 mm	off Georges Bank 1928–3700 m
<i>C. squamata</i> bottlebrush; 20 cm	1/5R to 1/7R	2.1–3.0 mm; 8.5–12 mm	2–3; 4–8 mm	wiry	0	B	trans.	coen.: scales, 0.45 mm bw: scales, 0.54 mm tent.: rods, 0.42 mm	Antilles, Yucatan, 431–1046 m

petite colony with much more closely spaced branches, a rhizoidal holdfast, a 2/5R branching sequence, branches with predominantly two nodes, relatively short terminal twigs, thicker terminal twigs that produce a wiry (not limp) colony, and larger and more rotund body wall sclerites (rods instead of spindles). Also, *C. elegans* is known only to the south of *C. herdendorfii* and at lesser depths. *C. agassizii* is similar in colony shape and branch flexibility, but differs in having more closely-spaced branches, longer branches with predominantly three nodes, slightly larger tentacular spindles, and the absence of “true spicules” (i.e., spindles or rods) in the body wall. The exclusive presence of flattened scales in the body wall of *C. agassizii*, in fact, places it in the a different subgroup of the genus, the “Squamosae aberrantes”.

*Etymology.*—This species is named in honor of Charles E. Herdendorf, biological coordinator aboard the R/V *Arctic Discoverer* during its recovery operations of the S.S. *Central America*.

*Material examined* (Types).—Holotype: USNM 91934, 1 colony, 31°35' N, 77°10'W, (270 km off Charleston, South Carolina), 2178 m, August 1990; Paratype: MBD BR-128, 1 colony, locality as above. Type Locality: wreck of the S.S. *Central America* (collected by the research submersible “Nemo” operated by the R/V *Arctic Discoverer*): 31°35'N, 77°10'W (approx. 270 km off coast of South Carolina), 2178 m.

*Distribution.*—Known only from the type locality.

*Chrysogorgia elegans* (Verrill, 1883)  
Figs. 3–4

- Dasygorgia elegans* Verrill, 1883: 23.  
*Dasygorgia spiculosa* Verrill, 1883: 23–24  
(in part: BL-44, 1 of 2 specimens; BL-195, 1 of 2 specimens; BL-205, 1 specimen).  
*Dasygorgia spiculosa*: Wright & Studer, 1889: 9–10, pl. 4, fig. 1, pl. 5, fig. 1.

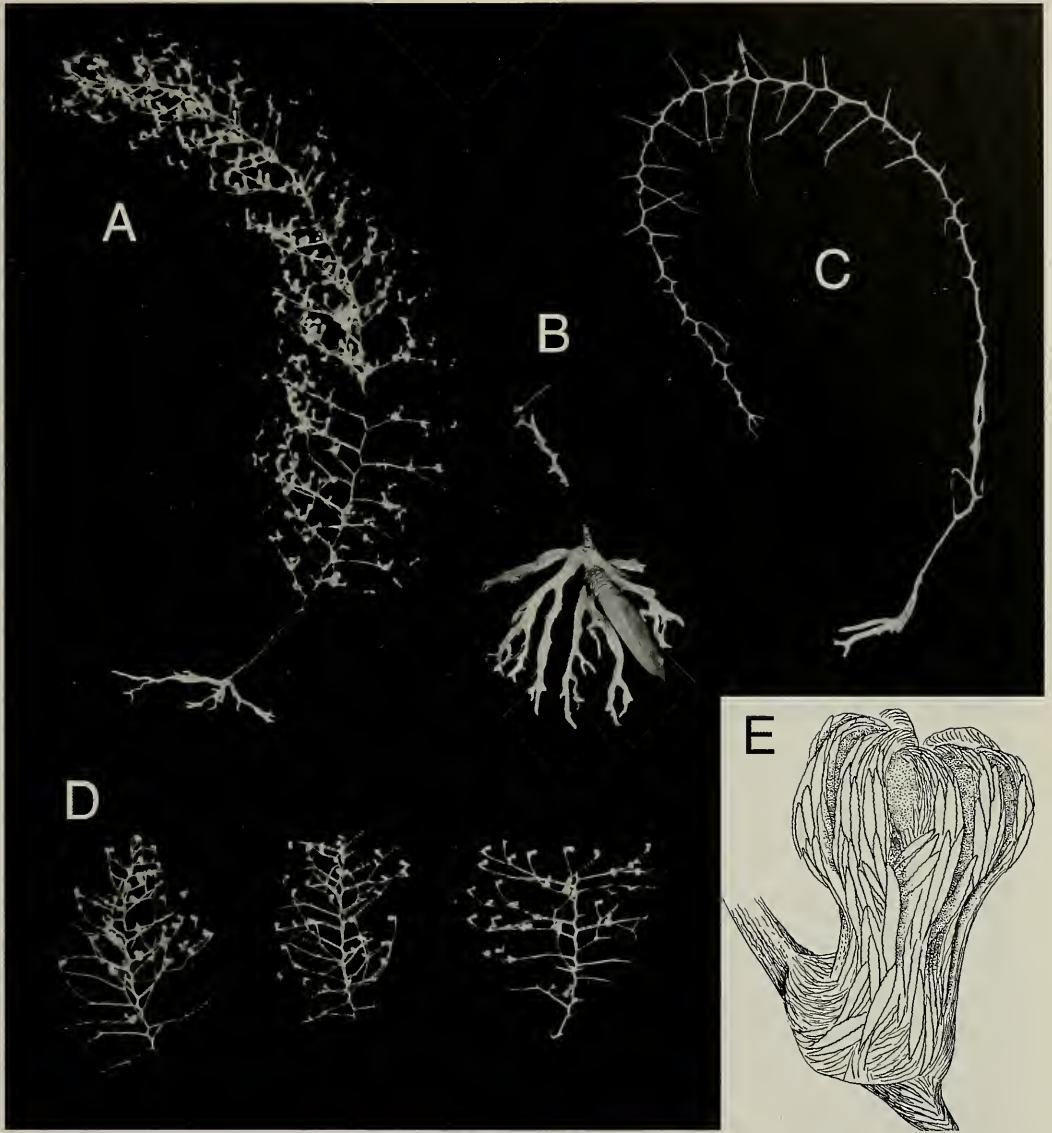


Fig. 3. *Chrysogorgia elegans*. A, colony from O-4812, USNM 52859, 14 cm in height; B, rhizoidal holdfast with attached cirripede, Citation-5505, USNM 89100, height 19 mm; C, lectotype, MCZ 4860, BL-283, 12 cm in height; D, three fragments of holotype of *C. affinis*, BM 89.5.27.5, tallest fragment 33 mm in height; E, line drawing of polyp from lectotype (courtesy of F. M. Bayer), polyp 1 mm in width.

*Chrysogorgia affinis* Versluys, 1902: 47–48, figs. 64–65.—Kükenthal, 1919: 521; 1924: 396.—Deichmann, 1936: 221–222.—Bayer, 1959: 29. [new synonym]  
*Chrysogorgia elegans*: Versluys, 1902: 61.—not Nutting, 1908: 590.0—Kükenthal, 1919: 533, fig. 234; 1924: 405.—Deichmann, 1936: 231–232, in part: pl. 23, figs. 53–59:

BL-44 (in part), BL-195 (in part), BL-205, BL-283); not pl. 33, fig. 1 (= *C. spiculosa*).—Bayer, 1952: 189; 1954: 280 (listed); 1956: F216, fig. 155, 3a–c, 158,6; 1958: 389, 390 (listed).—?Tixier-Durivault & d'Hondt, 1974: 1409.—Grygier, 1984: 143 (*Oregon-548*).—?Grasshoff, 1986: 25.—Grygier, 1990: 667.

?*Chrysogorgia flexilis*: Thomson, 1927: 22.

*Chrysogorgia agassizii*: Deichmann, 1936: in part (pl. 34, figs. 1–2: labeled correctly as *D. elegans* in Verrill's unpublished plates).

*Chrysogorgia* sp. Grygier, 1984: 143 (*P*-781).

*Description*.—Colony bottlebrush-shaped, up to 16 cm in height, and possessing a rhizoidal holdfast. Main stem up to 1.1 mm in diameter, golden-brown in luster. Branching sequence consistently 2/5R: branches closely spaced, one every 1.0–1.5 mm; orthostiche interval 0–7.5 mm apart. Distal branch diameter 0.2 mm; branches wiry. Number of nodes per branch ranges from 1–3, but usually 2, producing 4 relatively short (4–6 mm) terminal twigs; some branches have 1 or even 3 nodes, but they are never without at least 1 node. First internode 6–8 mm in length; second, 2–5 mm, and terminal twigs 4–6 mm, producing a total branch length that rarely exceeds 25 mm. Usually one polyp occurs per internode, and 1–3 on the terminal twigs. Polyps up to 2.3 mm in height and 0.8 mm in diameter, the base of the polyps sometimes swollen. Coenenchymal sclerites sparsely warted, slender scales up to 0.65 mm in length and 0.09 mm in width, serrate on the edges. Body wall and tentacular sclerites longitudinally arranged, rotund rods 0.44–0.65 mm in length and up to 0.12 mm in width, usually straight but sometimes slightly curved. Body wall rods evenly warted, each compound wart about 7  $\mu$ m in diameter and composed of several smaller elements, each about 1.8  $\mu$ m in diameter. Pinnular and distal tentacle sclerites rectangular to medially-constricted scales 0.12–0.20 mm in greater length and 0.0–0.05 mm in width. Their faces are sparsely ornamented and their edges are finely serrate, an apex occurring about every 4.2  $\mu$ m.

*Discussion*.—Nutting (1908) reported *C. elegans* from three *Albatross* stations in the Hawaiian Islands; however, Kükenthal (1919) and most other authors have doubted

this identification based on the circumstantial evidence of its disparate location. These three specimens, all deposited at the USNM, were examined and confirmed to differ from *C. elegans* in branching pattern and spiculation, the Hawaiian specimens having only irregularly-shaped scales in their body walls, and thus pertaining to a different subgroup of *Chrysogorgia*, the "Squamosae aberrantes".

The holotype of *C. affinis* Versluys, originally described as *D. spiculosa* by Wright & Studer (1889), was based on a specimen 10 cm in length but apparently broken into three fragments by the time Versluys described it, the largest fragment 6 cm in length. The holotype is now in six fragments, the longest segment 44 mm in length. The holotype was examined and found to perfectly match the characteristics of *C. elegans*, and thus it considered to be a junior synonym, as implied by Bayer (1959). *C. affinis* has been reported only from its type locality.

Deichmann (1936) considered *C. affinis* (= *C. elegans*) and *C. spiculosa* to be synonymous; however, these species can be distinguished (see Discussion of *C. spiculosa* and Table 3). Versluys (1902) reaffirmed that distinction by renaming Wright & Studer's (1889) *D. spiculosa* as a new species, *C. affinis* (which is *C. elegans*), distinct from *C. spiculosa*.

*Chrysogorgia elegans* is reputed to occur in the eastern Atlantic off the Azores, Cape Verde, Bay of Biscay, and off Morocco (Thomson 1927 as *C. flexilis*, Tixier-Durivault & d'Hondt 1974, Grasshoff 1986) at depths of 946–3088 m. None of the specimens on which these reports were based was illustrated or described, nor have I examined them. Given the great depths of capture for some of the specimens and the gross similarity of various Atlantic species, these eastern Atlantic records remain to be confirmed.

*Material examined*.—*Alb*-2397, 3, USNM 49741; *Atl*-3306, 2, MCZ; *G*-403, 1, USNM 100885; *G*-1010, 1, USNM



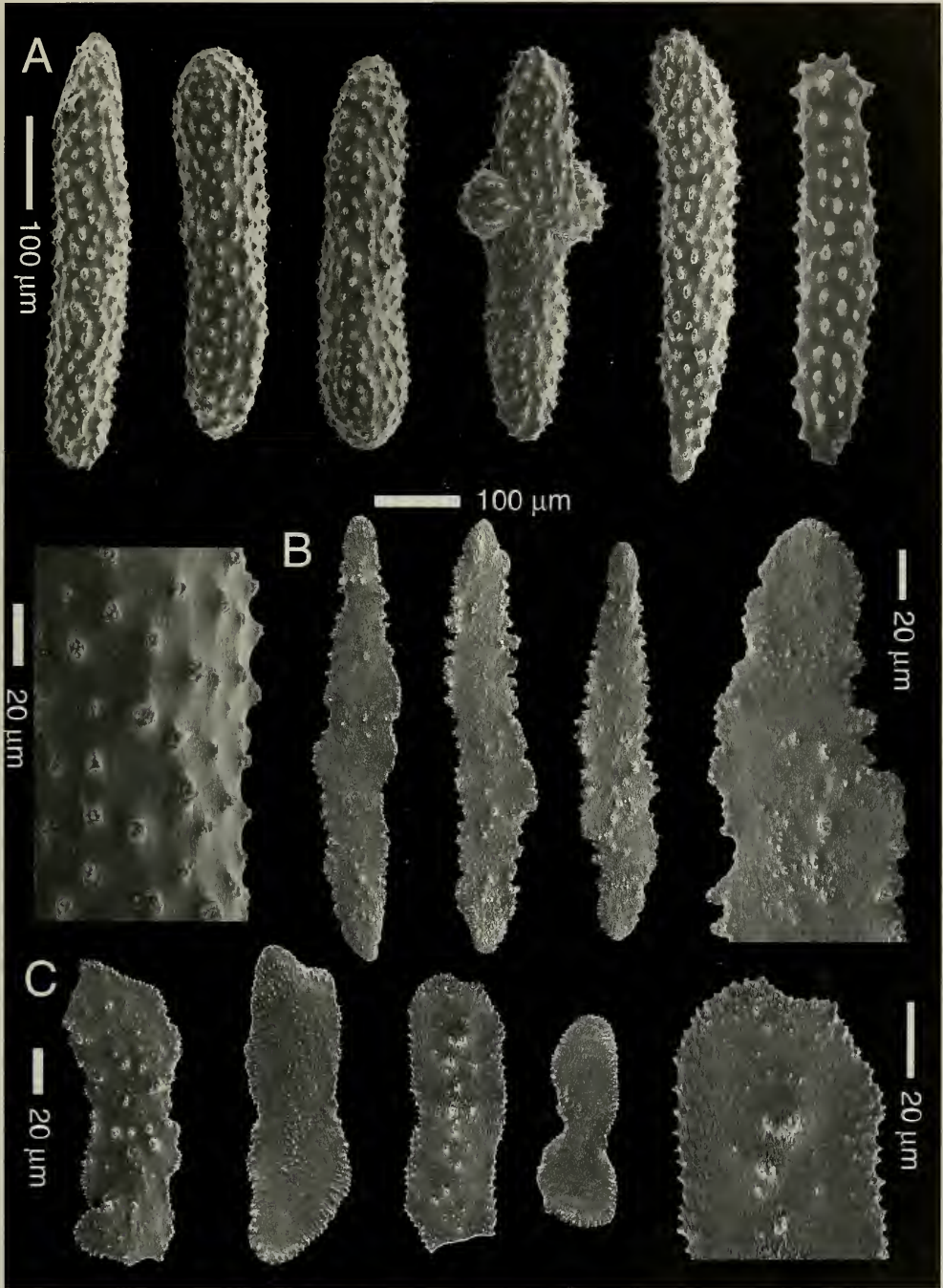


Fig. 4. *Chrysogorgia elegans*, sclerites from P-904, USNM 52865. A, seven rods from body wall; B, four coenenchymal scales; C, five pinnular scales.

100883; *Citation*-4502, over 30, USNM 89090; *Citation*-4504, 1, USNM 89091; *Citation*-4507, 18, USNM 89092; *Citation*-4508, over 100, USNM 89093; *Citation*-4509, over 50, USNM 89094; *Citation*-4510, over 50, USNM 89095; *Citation*-4511, over 50, USNM 89096; *Citation*-4512, 10, USNM 89097; *Citation*-4513, 3, USNM 89098; *Citation*-4514, 1, USNM 89099; *Citation*-5505, 44, USNM 89100; *Gyre*-2387, over 50, USNM 89089; *Gyre*-2429, 3 dry, USNM 89101; *Gyre*-S36, 3, USNM 100729; *O*-489, 5, USNM 49944; *O*-548, 3, USNM 50027, 52866; *O*-549, 8, USNM 50024; *O*-4413, 1, USNM 52860; *O*-4729, 2, USNM 52866; *O*-4812, 1, USNM 52859; *P*-394, 1, USNM 52864; *P*-478, 4, USNM 52863; *P*-776, 10, USNM 100884; *P*-781, 4, USNM 52908 (reported by Grygier, 1984 as *Chrysogorgia* sp.); *P*-784, 1, USNM 55919; *P*-847, 1, USNM 52849; *P*-850, 1, USNM 52861; *P*-881, over 70, USNM 52858; *P*-904, 3, USNM 52865; *P*-919, 1, USNM 52909; *P*-988, 2, USNM 52862; specimens reported by Deichmann (1936); types of *D. elegans* and *C. affinis* (see below).

*Types*.—Verrill based the species on six specimens (syntypes) collected at three *Blake* stations: one from *BL*-260 (unknown MCZ catalog number), two from *BL*-283 (MCZ 4860), and three from *BL*-284 (MCZ 4859), made off Grenada and Barbados at depths of 433–636 m. Deichmann (1936) restricted the type locality to *BL*-283, but did not choose a lectotype from among the five (not two) specimens from that station. A lectotype is therefore designated as one of the five syntypes collected at *BL*-283 (MCZ 4860), making the type locality consistent with Deichmann's statement, which is: 13°05'05"N, 59°40'50"W (west coast of Barbados), 433 m. The remaining four specimens from *BL*-283 (MCZ 4860a) and the specimens from *BL*-284 (MCZ 4859) and *BL*-260 are considered to be paralectotypes; however, the specimen from *BL*-260 appears to be lost, and only one of the

three specimens from *BL*-284 could be found.

The holotype of *C. affinis*, now in six pieces (see Discussion), is deposited at The Natural History Museum, London (89.5.27.5) Type locality: *Challenger*-122: 9°05'S, 34°50'W (off Pernambuco, Brazil), 640 m.

*Distribution*.—Disjunct distribution: northern Gulf of Mexico from Tamaulipas Province, Mexico to off Florida Panhandle; Little Bahama Bank; southeastern Caribbean throughout Lesser Antilles to border of Colombia and Panama; Pernambuco, Brazil; 128–1716 m, although most records between 500–800 m.? Eastern Atlantic; 946–3088 m (see text).

*Chrysogorgia spiculosa* (Verrill, 1883)  
Figs. 5–6

*Dasygorgia spiculosa* Verrill, 1883 (in part: 1 of 2 specimens from *BL*-44, both specimens from *BL*-190, 1 of 2 specimens from *BL*-195, not *BL*-205, ?*BL*-222, ?*BL*-227), 23–24, pl. 2, fig. 5.—not Wright & Studer, 1889: 9–10 (= *C. affinis/elegans*).

*Chrysogorgia* sp. Agassiz, 1888: 144, fig. 456.—Bayer, 1973: fig. 18.

*Chrysogorgia spiculosa*: Versluys, 1902: 53, 60, 61.—not Nutting, 1908: 591.—Kükenthal, 1919: 537, fig. 235; 1924: 407–406.—Bayer & Macintyre, 2001: 342 (minerology).

*Chrysogorgia elegans*: Deichmann, 1936: 231–232 (in part: pl. 22, fig. 7, pl. 33, fig. 1: *BL*-44 (in part), *BL*-190, *BL*-195 (in part), *BL*-200, and MCZ 4861).

*Description*.—Colony bottlebrush-shaped (but with rather elongate branches), up to 25 cm in height; rhizoidal holdfast. Main stem up to 1.5 mm in diameter; golden-brown in luster. Branching sequence consistently 2/5R; branches well spaced, one every 3.5–4.5 mm; orthostiche interval 20–25 mm; branches diverge from main stem at 80–90° from the vertical. Terminal twig diameter 0.2 mm, producing a rigid to

wiry colony. Number of nodes per branch 3–6, but usually 4 on a well-developed branch. First internode long (15–20 mm); second through fourth internodes, 10–15 mm; terminal twigs can be much longer, resulting in a total branch length of 70–110 mm. Internodes and terminal twigs of a branch usually oriented in a horizontal plane, sometimes bent slightly downward distally. Three polyps usually present on first internode; 2 or 3 on successive internodes; 2–8 on terminal twigs. Polyps large, up to 3.0 mm in height, oriented perpendicular to branch, and often having a swollen basal region that encircles the stem. Coenenchymal sclerites elongate, slender, pointed scales up to 0.60 mm in length and 0.06 mm in width. Their edges are slightly serrate and their faces sparsely warted. Body wall sclerites primarily rotund rods and sometimes spindles (or rods with one blunt end and the other pointed), the rods straight to slightly bent, and up to 0.96 mm in length and 0.18 mm in diameter. Body wall sclerites bear small compound warts about 18  $\mu\text{m}$  in diameter, each wart consisting of 10–15 smaller elements 3.6–4.2  $\mu\text{m}$  in diameter. Tentacular sclerites also rods and spindles, but usually smaller, only up to 0.54 mm in length. Pinnular sclerites elongate scales about 0.20 mm in length, having serrate edges.

*Discussion.*—Deichmann (1936) synonymized *C. spiculosa* with *C. elegans*, implying that even Verrill was uncertain about their distinction. In her material examined for *C. elegans*, she listed most (but not all) of the type series of both *C. spiculosa* and *C. elegans*, as well as material from two other stations (see synonymy). Deichmann's confusion was justified, in that Verrill did include two species (*C. elegans* and *C. spiculosa*) in his type series of *C. spiculosa*, both species sometimes even occurring at the same station (see synonymies of respective species). Although *C. spiculosa* is similar to *C. elegans* in branching sequence, flexibility, and geographic distribution, it differs in several significant char-

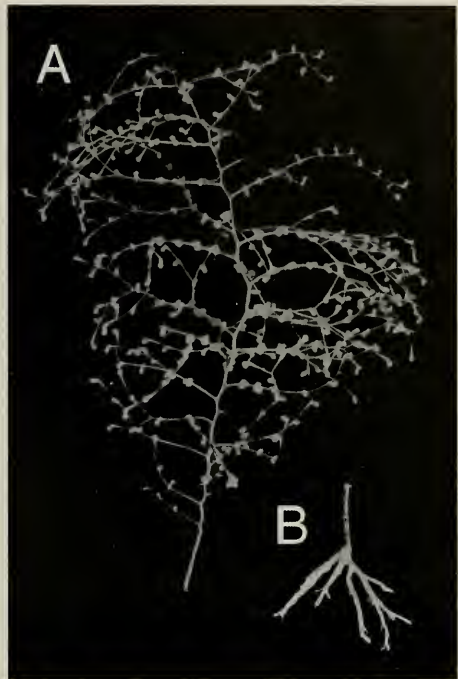


Fig. 5. *Chrysogorgia spiculosa*. A, colony from G-1112, USNM 52854, height 15 cm; B, holdfast from G-130, USNM 52856, height 18 mm.

acters as summarized in Table 3. Specimens of *C. spiculosa* are much more robust, having more widely spaced and longer branches; more nodes per branch; and more polyps per node. Furthermore, the body wall of *C. spiculosa* has much larger rods. Versluys (1902) also noted the difference between these two species by distinguishing his *D. affinis* (= *C. elegans*) from *D. spiculosa*. These are the first additional records of *C. spiculosa* since its original description.

*Material examined.*—*Alb*-2751, 1, USNM 44109; *G*-128, 3, USNM 52850; *G*-129, 2, USNM 52851; *G*-130, 14, USNM 52856; *G*-368, 4 dry, USNM 100875; *G*-370, 1, USNM 100876; *G*-371, 1, USNM 52855; *G*-372, 1 dry, USNM 100873; *G*-965, 3, USNM 52907; *G*-1112, 3, USNM 52854; *GS*-134, 1, USNM 100877; *O*-4701, 1, USNM 100878; *O*-4811, 1, USNM 52852; *O*-10878, 2, USNM 100879; *P*-391, 1, USNM 52853; misidentified specimen of Nutting (1908), *Alb*-4151, USNM 25356;

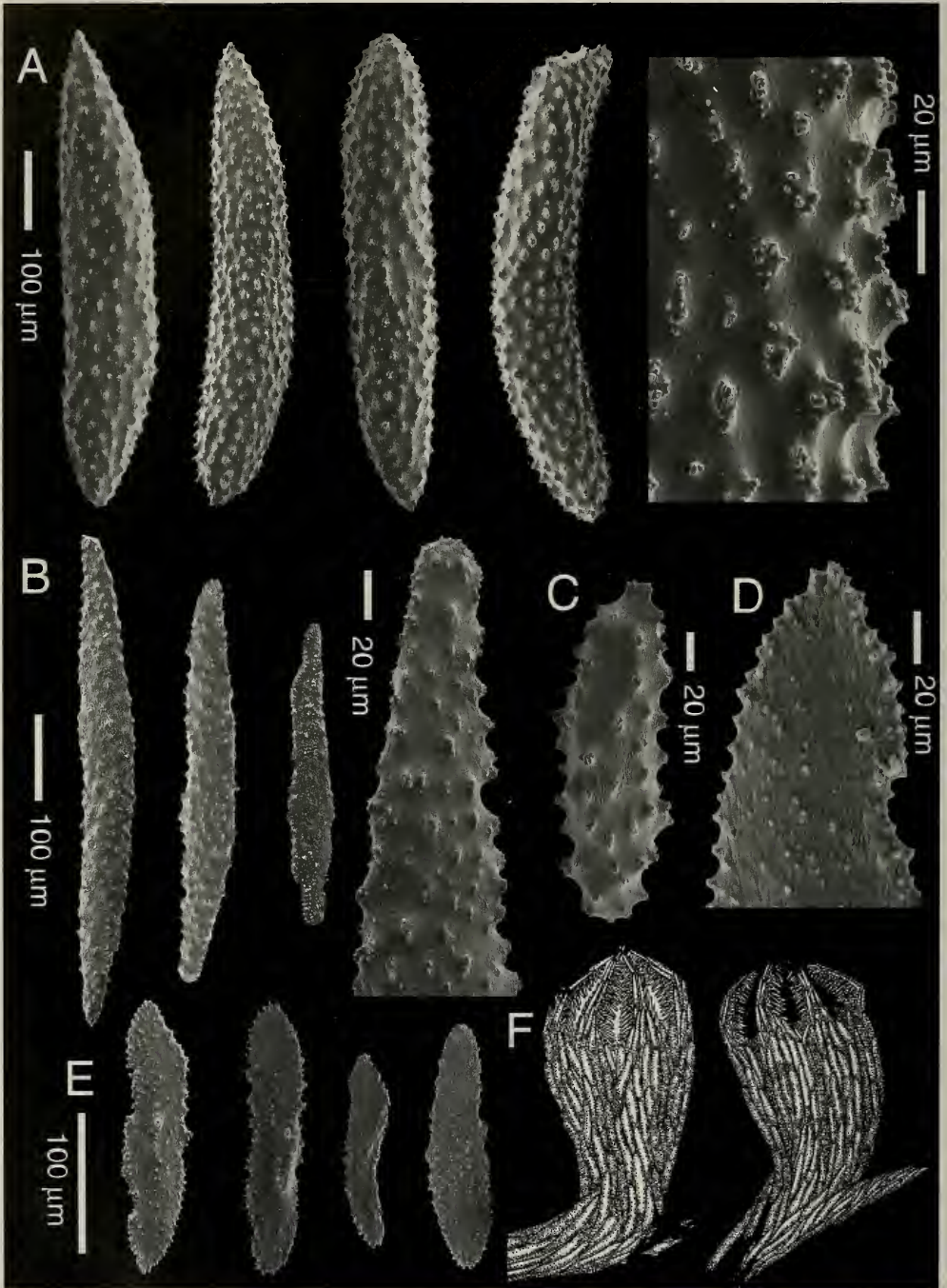


Fig. 6. *Chrysogorgia spiculosa*, sclerites from G-130, USNM 52856. A, five rods from body wall; B, four coenenchymal scales; C, a tentacular rod; D-E, pinnular scales; F, two polyps, width of polyps 1.2-1.3 mm (from Verrill, unpublished plates).

specimens listed by Deichmann (1936); types of *D. spiculosa* (see below).

*Types.*—Verrill (1883) reported nine specimens plus some fragments from six Blake stations in his original description, all of which must be considered to be syntypes: *BL-44*, 2, MCZ 4855; *BL-190*, 2, MCZ 4856 and 4856a; *BL-195*, 2, MCZ 4857; *BL-205*, 1, MCZ 4859; *BL-222*, 1; and *BL-227*, 1. However, because Verrill included both *C. elegans* and *C. spiculosa* in his syntype series (see synonymies of these two species), a lectotype is chosen from *BL-190* (MCZ 4856), a specimen 5.5 cm tall that is consistent with the more robust species originally envisioned and described by Verrill. The other syntypes thus become paralectotypes; however, the specimens from *BL-222* and *BL-227* could not be found at the MCZ in 2001. Type Locality (as restricted by lectotype): 15°18'12"N, 61°26'32"W (off western Dominica, Lesser Antilles), 991 m.

*Distribution.*—Disjunct distribution: northern Gulf of Mexico from Tamaulipas Province, Mexico to Havana, Cuba; Lesser Antilles from Dominica to St. Vincent; off Colombia; 914–2265 m.

*Chrysogorgia multiflora* Deichmann, 1936  
new rank  
Figs. 7-8

*Chrysogorgia fewkesi* var. *multiflora* Deichmann, 1936: 231, pl. 22, fig. 6, pl. 23, figs. 51–52.—Bayer, 1959: 27–29, fig. 13a–i.

*Description.*—Colonies bottlebrush-shaped, but somewhat bushy; colonies up to 25 cm in height. Colony attached by an encrusting holdfast; main stem up to 2.1 mm in diameter, golden-brown in luster. Branching sequence consistently 2/5R: branches well spaced, one every 3.5–4.0 mm; orthostiche interval 20–22 mm; however, some colonies are diminutive (indicated with an asterisk in the Material examined section), having branches separated from one another by only about 1 mm and

an orthostiche interval of 6 mm. Branches usually diverge from main stem at 90–110° from the vertical, thus projecting perpendicular to slightly downward from the direction of growth, and often giving a false impression of the top and bottom of the colony, especially if the holdfast is missing. Branches gently curve upward after the first several internodes; fusion of branches occasionally occurs. First internode robust (up to 1.3 mm in diameter), whereas terminal twigs are quite delicate (0.1 mm in diameter), but altogether producing a robust, wiry colony. Number of nodes per branch up to nine, although usually only 5 or 6, the first internode being 10–14 mm in length, subsequent internodes 5–6 mm in length, and terminal twigs of variable lengths, resulting in branches up to 90 mm in length. Internodes and terminal twigs not arranged in a plane but as a bush. Two to 4 polyps usually present on first internode; 1 or 2 on all successive internodes; and a variable number on the terminal twig, depending on length. Polyps small, up to 1.5 mm in height. Coenenchymal sclerites of main stem elongate, flattened plates, up to 0.65 mm in length and 0.06 mm in width, bearing prominent, compound warts up to 24 mm in diameter. Coenenchymal sclerites of branches also flattened plates, but usually more elongate (up to 0.77 mm), with pointed ends and less prominent warts. Lower body wall sclerites obliquely arranged; upper body wall sclerites transversely arranged. Most body wall sclerites curved spindles, the curvature corresponding to the circumference of the polyp wall, the largest spindles up to 1.08 mm in length and 0.07–0.13 mm in width, although smaller spindles are interspersed. Body wall spindles sparsely covered with compound warts up to 9 µm in diameter. Tentacular sclerites longitudinally arranged, curved spindles, but usually shorter (up to 0.86 mm). Pinnular sclerites finely granular, often medially-constricted, rectangular scales up to 0.20 mm in length.

*Discussion.*—Grasshoff (1981) legiti-



Fig. 7. *Chrysogorgia multiflora*, colony from G-859, USNM 52846, height 20 cm.

mized and elevated the distinction of variety *multiflora* by synonymizing it with *C. quadruplex* Thompson, 1927, a species heretofore known only from the eastern Atlantic (Azores, Bay of Biscay, Atlantis Seamount, Celtic Sea; 507–2682 m) Examination of the types of *C. fewkesii* and variety *multiflora* show small but consistent differences (see Discussion of *C. fewkesii*). The synonymy of *C. multiflora* with *C. quadruplex* may be correct but I have not verified it. Until this is proven, I choose to recognize Deichmann's western Atlantic variety *multiflora* as a distinct species, but only marginally different from *C. fewkesii* (see "Discussion" of *C. fewkesii* and Table 3 for their distinctions). The records reported herein are the first from the western Atlantic since its original description.

*Material examined.*—\*Alb-2415, 3, USNM 44128 and 52841; \*Atl-266-40, 1, USNM 100880; CI-15, 1, USNM 100881; CI-46, 1, USNM 100882; G-130, 4, USNM 52847; \*G-403, 1, USNM 52839; G-859, 2, USNM 52846; G-1111, 3, USNM 52842;

\*Gos-2385, 1, USNM 56896; O-2081, 4, USNM 50907 (reported by Bayer, 1959); \*O-2636, 1, USNM 51579; P-892, 2, USNM 52844; Waldo Schmitt station 65-32, off Dry Tortugas, 1064 m, USNM 50094; specimens reported by Bayer (1959); types of *C. fewkesii multiflora* (see below).

*Types.*—Deichmann alluded to "some" specimens of *C. fewkesii* var. *multiflora* from Blake-190, which are considered as syntypes (MCZ 4854). These specimens consist of several small, poorly-preserved branches, not including any complete colonies. Type locality: 15°18'12"N, 61°26'32"W (off southwestern Dominica, Lesser Antilles), 991 m.

*Distribution.*—Disjunct distribution: off mouth of Amazon River, Brazil; Lesser Antilles (St. Christopher to St. Lucia), Straits of Florida, and Tongue of the Ocean, Bahamas; 320–1280 m.

#### *Chrysogorgia fewkesii* Verrill, 1883

Figs. 9–10

*Chrysogorgia Desbonni*: Pourtalès, 1868: 131–132.

*Chrysogorgia Fewkesii* Verrill, 1883: 26.

*Chrysogorgia fewkesii*: Wright & Studer, 1889: 24.

*Chrysogorgia fewkesii*: Versluys, 1902: 55–56.—Kükenthal, 1919: 533–534; 1924: 405.—?Thomson, 1927: 21–22, pl. 1, figs. 6–7.—Deichmann, 1936: 222, 230–231, pl. 23, figs. 41–50.—Tixier-Durivault & d'Hondt, 1974: 1409.

*Description.*—Colonies bottlebrush-shaped, but bushy; colonies up to 22.5 cm in height. Nature of holdfast unknown; basal branch diameter up to 2.9 mm. Branching sequence consistently 2/5R; branches well spaced, one every 3–6 mm; orthostiche interval 17–20 mm. Branches diverge from main stem at 100–110° from the vertical, thus projecting slightly downward at first. First internode robust; terminal twigs quite narrow, altogether producing a wiry colony. Number of nodes per branch usually 5–7,

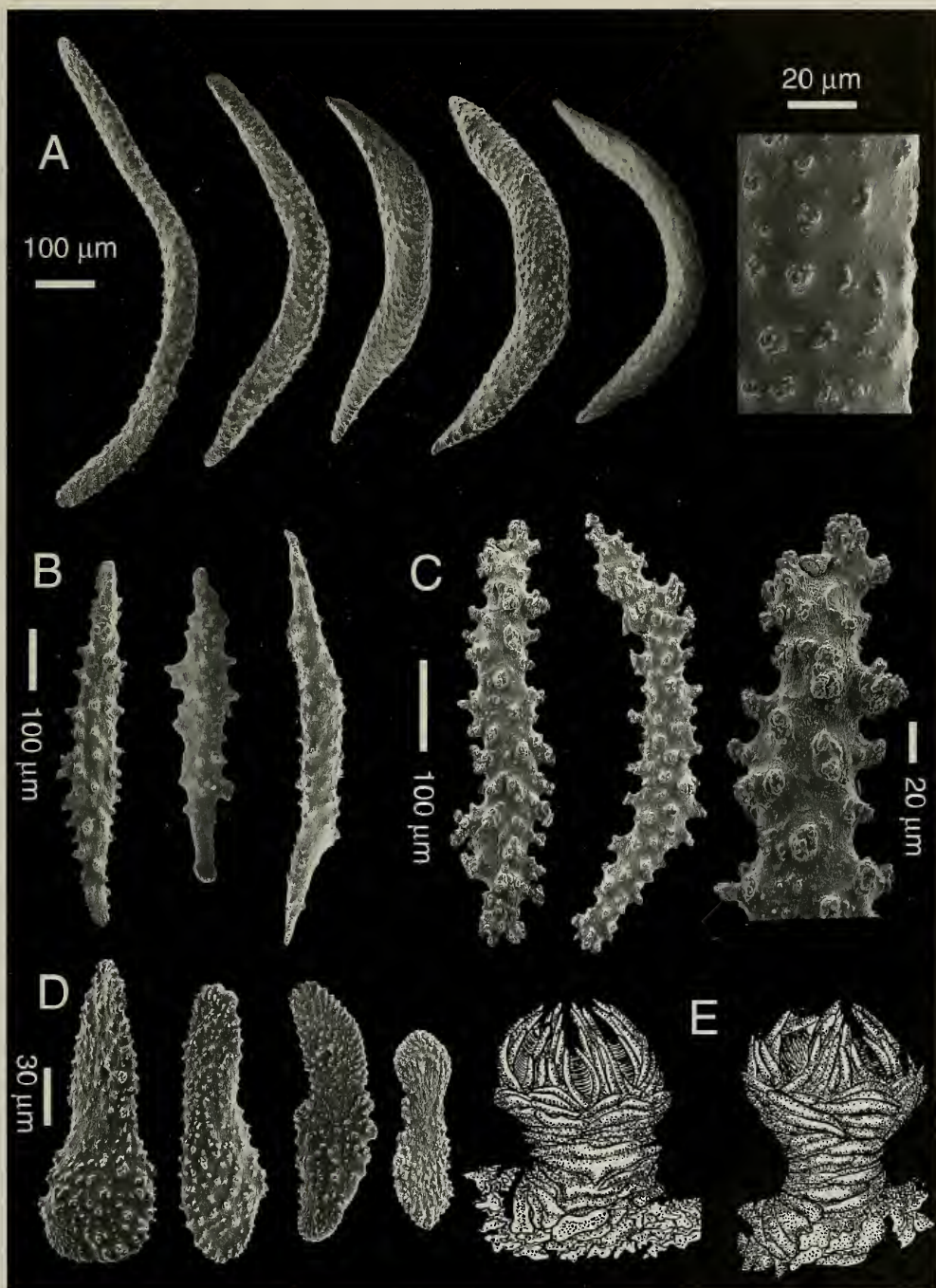


Fig. 8. *Chrysogorgia multiflora*. A–D, sclerites from G-859, USNM 52846. A, six curved spindles from body wall; B, coenenchymal platelets from side branch; C, coenenchymal platelets from main stem; D, pinnular scales. E, two polyps, MCZ “5796”, width of polyps 0.68 mm (from Verrill, unpublished plates).

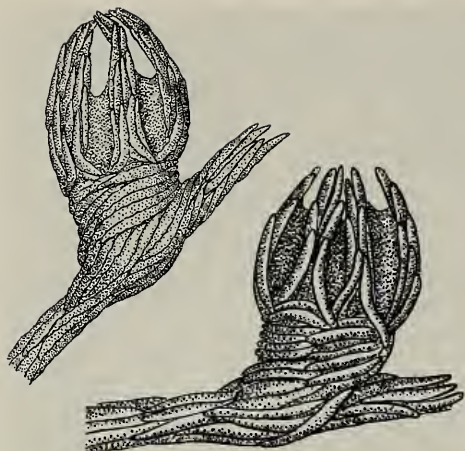


Fig. 9. *Chrysogorgia fewkesii*, two polyps from lectotype, MCZ 4850, polyps 0.5–0.7 mm in width (from Verrill, unpublished plates).

although may be up to 10, the first internode being 10–12 mm in length and remaining ones 6–8 mm, resulting in branch lengths of up to 100 mm. Internodes and terminal twigs not arranged in a plane. Two to four polyps occur on each internode, a variable number on terminal twigs. Polyps small, about 1 mm in height. Coenenchymal sclerites of main stem and branches flattened, elongate, pointed plates up to 0.95 mm in length and 0.05–0.06 mm in width, having prominent compound warts on their faces and edges. Body wall sclerites transversely arranged, consisting of curved, slightly flattened spindles, up to 0.71 mm in length and 0.04–0.06 mm in width. Body wall spindles bear multiheaded warts up to 12  $\mu$ m in diameter and often have one or both distal ends strongly flattened. Tentacular sclerites similar to those of body wall but longitudinally arranged and also containing some shorter blunt rods 0.18–0.30 mm in length and 0.04–0.06 mm in diameter. Pinnular sclerites finely granular, rectangular scales 0.10–0.15 mm in greater length.

*Discussion.*—*Chrysogorgia fewkesii* and *C. multiflora*, the two western Atlantic species having transverse sclerites in the body wall and downward projecting branches,

are very similar (Table 3). In fact, the colony form is so similar that the colony figure of *C. multiflora* (Fig. 7) may serve for both species. Deichmann (1936) established the variety *C. fewkesii* var. *multiflora* for several specimens collected off Dominica (BL-190) that differed from typical *C. fewkesii* in three ways: the variety was purported to have a more robust colony, its body wall sclerites were “better developed”, and its coenenchymal sclerites were larger (0.45 vs 0.35 mm in length for the typical form) and more warty. Concerning point one, there seems to be little or no difference in colony size between the two species. Concerning point two, Deichmann’s illustrations of the body wall sclerites of these two taxa showed the variety to have slightly wider sclerites (i.e., 0.07–0.08 mm vs 0.035–0.05 mm for the typical form) but no difference in length. This difference was borne out by re-examination of the type material, the width of the body wall spindles being even greater than Deichmann illustrated (i.e., up to 0.13 mm). Furthermore, the body wall sclerites of *C. fewkesii* are somewhat shorter, slightly flattened, and have very flattened, rounded distal ends; those of *C. multiflora* are rotund with pointed ends. Concerning point three, the coenenchymal scales of both *C. multiflora* and *C. fewkesii* are warty and of approximately the same size; no difference in degree of “wartiness” could be discerned, although it was noted that the coenenchymal scales on the main stem of *C. multiflora* were more warty than those on the branches. Indeed, the coenenchymal scales of *C. fewkesii* are, in general, longer (not shorter) than those of *C. multiflora* (see Table 3).

The few specimens of *C. fewkesii* reported from the eastern Atlantic by Thomson (1927) and Tixier-Durivault & d’Hondt (1974) were based on fragmentary specimens or were simply listed without description or comment. In view of the subtle differences among the chrysogorgiid species, these records are not accepted until the original specimens can be examined.



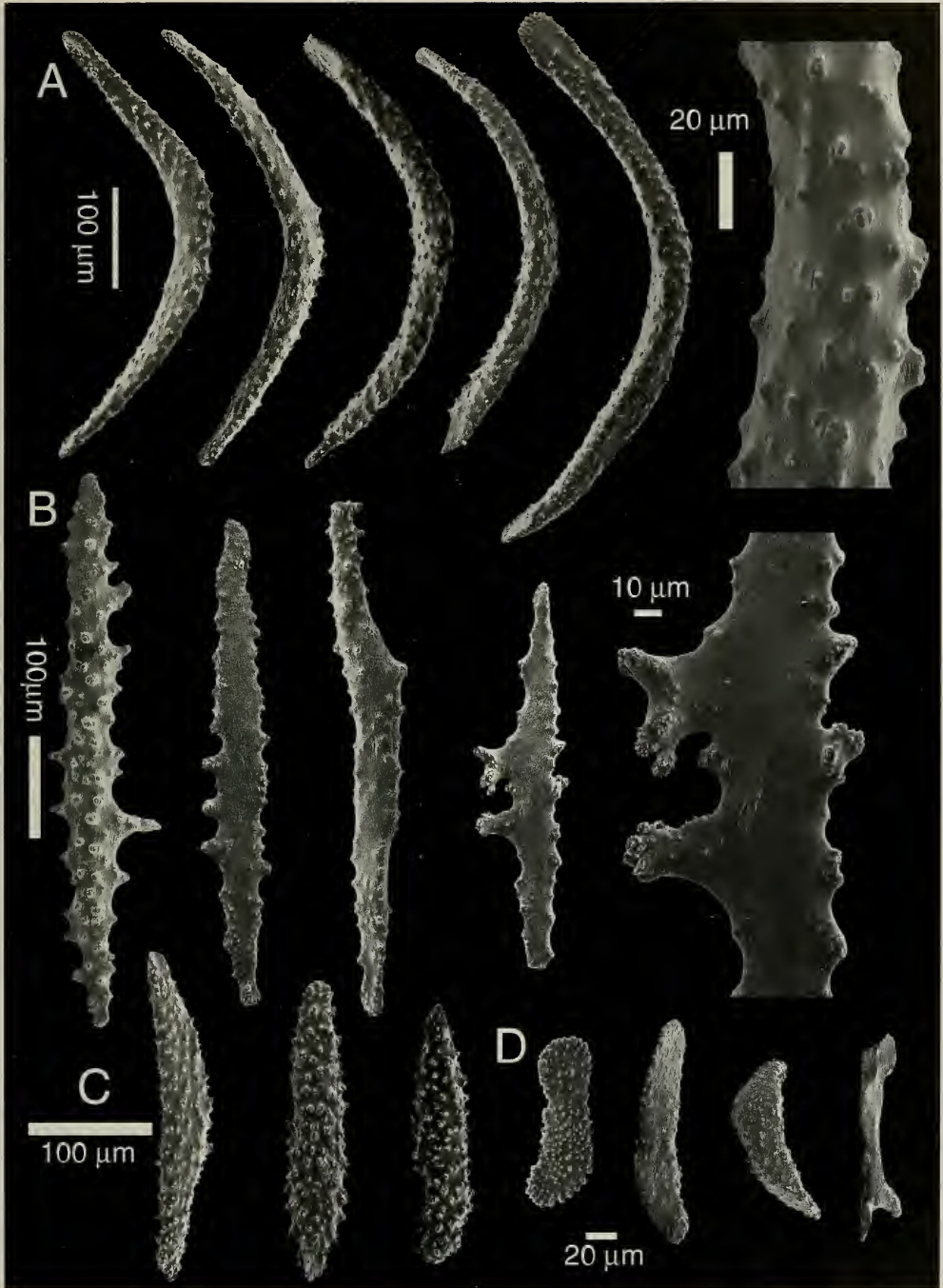


Fig. 10. *Chrysogorgia fewkesii*, sclerites from lectotype, MCZ 4850. A, six spindles with flattened tips from the body wall region; B, five coenenchymal scales; C, three tentacular rods; D, four pinnular scales.

*Material examined.*—BL-190, 1, USNM 49317 (former MCZ 4852); G-190, 1, USNM 52789; G-936, 1, USNM 52807; P-391, 1, USNM 52845; P-689, 5, USNM 52848; P-984, 3, USNM 52835; P-1262, 4, USNM 52843; specimens reported by Deichmann (1936); types of *C. fewkesii* (see below).

*Types.*—In his original description, Verrill (1883: 26) cited several specimens from *Blake-227*, as well as material from “several other localities in the same region, and off Cuba”, the Cuban specimen probably the one described by Pourtalès (1868) from *Bibb-22*, which Verrill later identified as *C. fewkesii*. However, Deichmann (1936) designated the “type” as MCZ 4850, a specimen from *BL-227*, which restricts the type locality. However, there is more than one specimen from the type lot of *BL-227*; it includes 2 colonies, several branches, and a slide to which a branch is glued. Thus, one of the colonies is chosen as lectotype (MCZ 4850); the other specimens from this station becoming paralectotypes (MCZ 4850a). The specimens from *Bibb-22* are also considered as paralectotypes, but could not be found at the MCZ in 2001. No other paralectotypes can be unequivocally determined. Type locality as restricted by lectotype: 13°10'10"N, 61°18'15"W (off southwestern St. Vincent, Lesser Antilles), 1048 m.

*Distribution.*—Western Atlantic: Straits of Florida, Northwest Providence Channel, Jamaica, Lesser Antilles, off Guyana, off Colombia; 430–1200 m.? Eastern Atlantic: purportedly (see Discussion) from Azores and off Morocco; 1022–2165 m (Thomson 1927, Tixier-Durivault & d'Hondt 1974).

*Chrysogorgia desbonni* Duchassaing & Michelotti, 1864  
Figs. 11-12

*Chrysogorgia Desbonni* Duchassaing & Michelotti, 1864: 13 (107), 21 (115), pl. 1, figs. 7–8, pl. 4, fig. 5.—not Pourtalès, 1868: 131–132 (= *C. fewkesii*).—Duchas-

saing, 1870: 17.—Verrill, 1883: 25–26, pl. 2, figs. 6, 6a, 6b.

*Chrysogorgia desbonni*: Wright & Studer, 1889: 24.—Hargitt & Rogers, 1901: 281, pl. 1, figs. 1–5.—Versluys, 1902: 85–86.—Kükenthal, 1919: 532; 1924: 404.—Deichmann, 1936 (in part: not specimens from *BL-101*, *BL-297* or *BL-“XIII”* (the latter actually *BL-55*) and not pl. 35, fig. 1, which are *C. thyrsoformis*), 228–230, pl. 22, fig. 5, pl. 23, figs. 19–27.—Bayer, 1954: 280 (listed); 1958: 389 (listed).

*Chrysogorgia occidentalis* Versluys, 1902: 56, 86.—Kükenthal, 1919: 523–524, fig. 232; 1924: 398. [new synonym]

*Chrysogorgia desbonni* (sic): Grygier, 1984: 165.

*Description.*—Colonies biflabellate, two equal-sized, parallel to slightly convex, roughly circular flabella originating 15–20 mm above the base; colonies up to 16 cm in height and 12 cm in width. Holdfast encrusting, disc-shaped. Main stem up to 1.6 mm in diameter. Main stem bronze to dark brown; branches paler. Branching sequence 2/5R, but present only in basal 15–20 mm of colony, the two major and several minor flabella being uniplanar and dichotomously branched; anastomosis of branches common, sometimes producing a fine reticulum. Branches extremely closely spaced, only about 0.6–1.0 mm apart, producing an orthostiche interval of about 5 mm; only 3 or 4 orthostiche intervals occur before the distal, dichotomously branched flabella originate. In large colonies, up to 40 nodes may be present in each flabellum, the internodes being 3–4 mm in length, resulting in flabellar branches up to 12–15 cm in length. Flabellar branches gradually decrease in diameter, being quite thick proximally (as thick as the main stem) and decreasing to about 0.12 mm on terminal twigs, resulting in a wiry construction. Dichotomous branching usually unequal, one side of each dichotomy usually much thicker than the other. One polyp, sometimes 2, present on

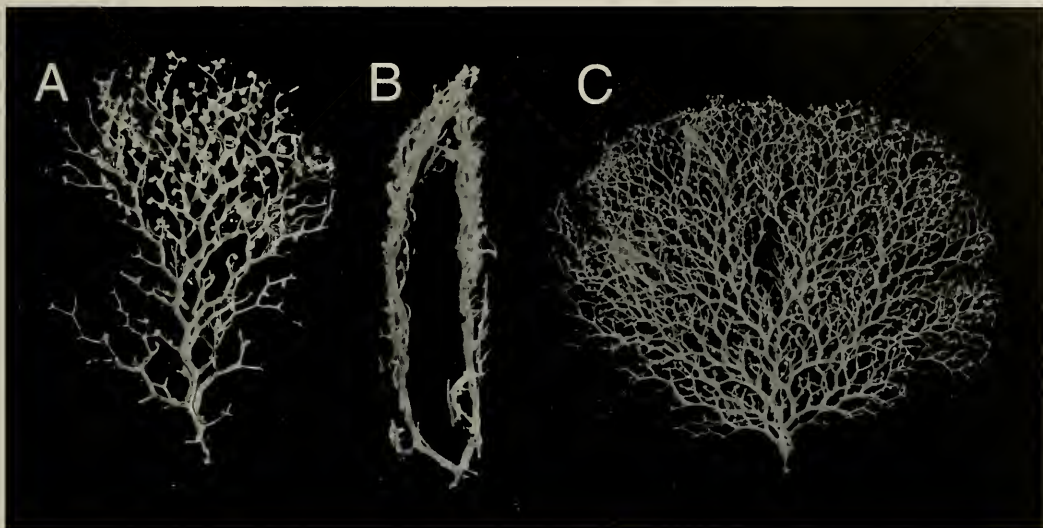


Fig. 11. *Chrysogorgia desbonni*. A–B, neotype, BL-232, MCZ 4839, lateral and edge views, colony 5.5 cm tall. C, colony from G-391, USNM 52797, height 10 cm, two galatheid crabs attached within flabella.

each internode, the polyps usually oriented such that they project perpendicular to the flabella and in an outward direction. Polyps small, cylindrical, about 1.5–1.8 mm in height. Coenenchymal sclerites elongate, warty scales with very irregular margins, up to 0.71 mm in length and 0.06 mm in width, although most scales are shorter, i.e., 0.42 mm in length. Warts of coenenchymal scales about 11–17  $\mu\text{m}$  in diameter and multiheaded. Body wall sclerites transversely arranged spindles, often strongly curved and somewhat flattened, their distal ends being pointed or sometimes flattened like a scale. Body wall sclerites up to 0.75 mm in length and 0.05–0.07 mm in width, bearing small, compound warts 7–9  $\mu\text{m}$  in diameter. Tentacular sclerites straight and rod-shaped, up to 0.24 mm in length and 0.02–0.04 mm in diameter. Pinnular sclerites typical rectangular scales, most 0.11–0.14 mm in length and 0.02 mm in width, often slightly medially-constricted.

*Discussion.*—When a colony is held on edge, a space 5–10 mm wide can often be seen between the two parallel flabella, or an enclosed cavity may be detected in those specimens that have convex flabella. In the latter case, the flabella resemble the two

halves of a clam, the enclosed space sometimes providing refuge for galatheid crabs. Aplacophoran mollusks are also sometimes found attached to the branches of the flabellum (e.g., O-5419).

*Chrysogorgia desbonni* is easily recognized as the only western Atlantic species to have a flabellate colony form (Table 3). Comparisons to *C. thyriformis* are made in the discussion of that species.

For reasons not understood, Duchassaing & Michelotti (1864) described the genus *Chrysogorgia* and its type species *C. desbonni* twice independently in the same publication, as species 18 and 87. Both specimens were from Guadeloupe and both descriptions might even have been based on the same specimen; however, species 18 was reported as 10–13 cm tall, whereas species 87 as 8 cm tall. Duchassaing (1870) later confirmed that both descriptions pertained to the same species. The relatively shallow purported depth at which the specimen(s) was collected (300–400 m, see Duchassaing & Michelotti 1864: 101) would suggest only two possibilities: *C. desbonni* or *C. thyriformis*. The brief French and Latin descriptions of the species are not adequate to distinguish the two, and the types

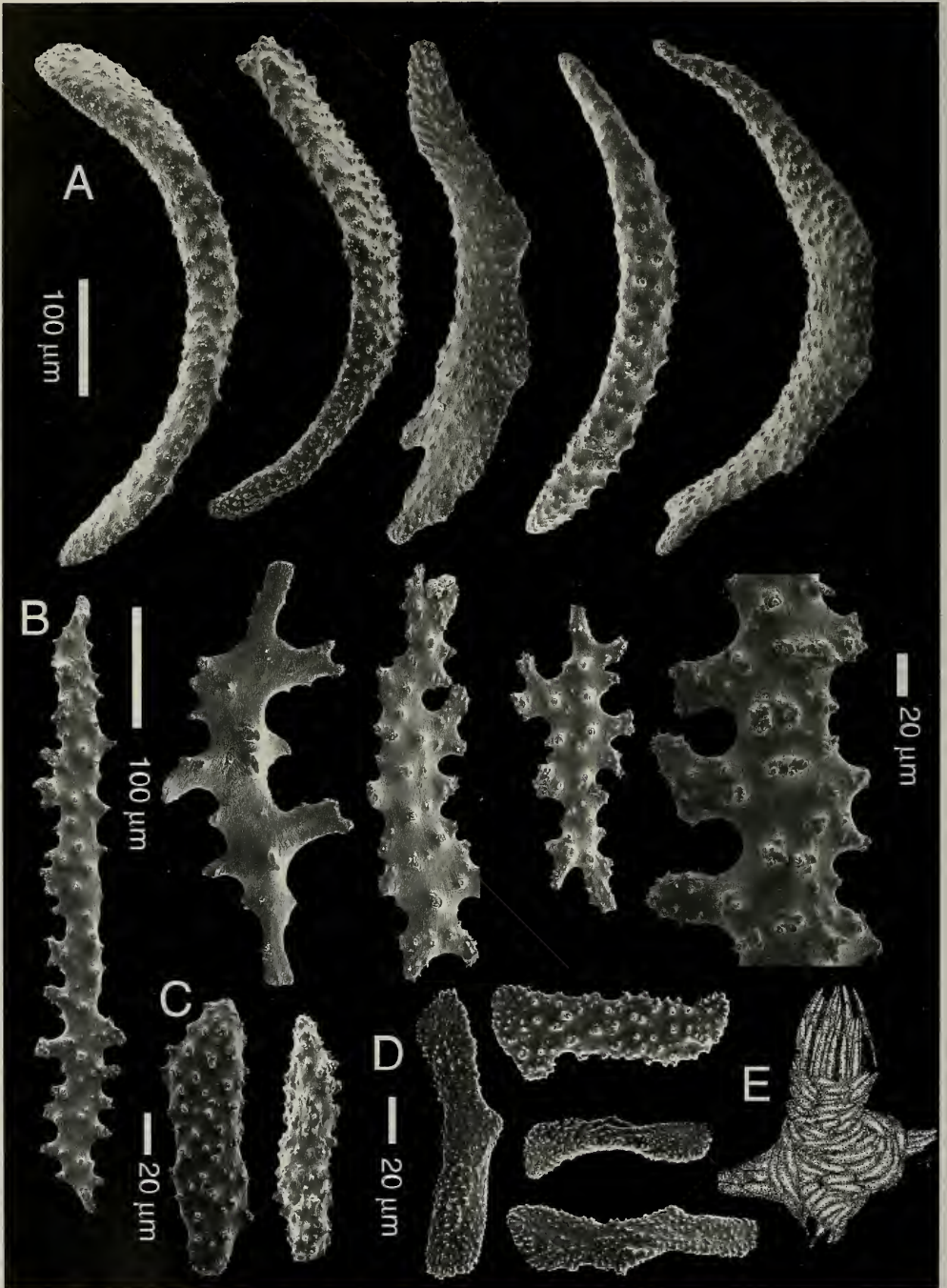


Fig. 12. *Chrysogorgia desbonni*. A–D, sclerites from neotype, MCZ 4839. A, five curved spindles from body wall; B, five coenenchymal scales; C, two tentacular rods; D, four pinnular scales. E, polyp from neotype, width 0.67 mm (from Verrill, unpublished plates).

are lost (Wright & Studer 1889), but the figure of the colony of species 87 appears to be the biflabellate taxon (i.e., *C. desbonni* as understood in this paper and *C. occidentalis* sensu Versluys and Kükenthal), and the number of polyps per internode as well as the length and number of internodes are also consistent with that species. Consequently a neotype of the biflabellate species collected near the type locality has been chosen to represent the species (see Types).

Verrill (1883) also recognized *C. desbonni* as a flabellate species, reporting it from “numerous” but largely unspecified locations in the Caribbean (see Types of *C. occidentalis*, below). Wright & Studer (1889) were convinced that Duchassaing & Michelotti (1864) had described two very different species under the same name, opting to recognize the second of the descriptions, the flabellate species 87, as the name bearer. Hargitt & Rogers (1901) clearly reported the biflabellate form as their *C. desbonni*. However, based purely on the literature, Versluys (1902) concluded that Verrill’s *C. desbonni* was a different species from the one described by Duchassaing & Michelotti, proposing the name *C. occidentalis* for Verrill’s specimens. Versluys did not designate type specimens for *C. occidentalis* nor did he actually see any specimens, but simply relied on the specimens examined of *C. desbonni* by Verrill, all of which must be considered as syntypes of *C. occidentalis* (see “Types”). Kükenthal (1919) followed the taxonomy of Versluys and apparently examined at least one of Verrill’s specimens at the MCZ and illustrated a branch, but he still did not have a firm comprehension of true *C. desbonni*. Comparing crude illustrations and poor descriptions without recourse to examining specimens is ill-advised as a basis in taxonomy. But, since the types of *C. desbonni* are lost, the nomenclatural issue may be simply resolved by designating a biflabellate specimen from the syntype series of *C. occidentalis* as the lectotype of that species as well as the neotype of *C. desbonni*, making *C. occidentalis* a

junior objective synonym of *C. desbonni*. Such a specimen is chosen from BL-232 (MCZ 4839).

Because *C. desbonni* has flattened spindles in its body wall and tentacles, it belongs to *Chrysogorgia* (Group “Spiculosae”).

*Material examined*.—Alb-2342, 3, USNM 44139; Alb-2347, 1, USNM 44140; Atl-2980B, 1, MCZ 3866; Atl-2999, 3, MCZ 3867; Atl-3326, 9, MCZ 3719-22; Atl-3436, 1, MCZ 3705; Atl-3437, 1, MCZ 3698; Atl-3438, 3, MCZ 3752; Atl-3479, 1, MCZ 3756; Caroline-43, 2, USNM 43791; Combat-447, 1, USNM 50802; G-232, 1, 52816; G-235, 1, USNM 52791; G-241, 3, USNM 52792; G-242, 1, USNM 52793; G-246, 2, USNM 52794; G-261, 1, USNM 52795; G-387, 1, USNM 52796; G-391, 6, USNM 52797; G-678, 2, USNM 52799; G-679, 1, USNM 52817; G-692, 2, USNM 52800; G-798, 1, USNM 52801; G-889, 2, USNM 52802; G-897, 1, USNM 52804; G-898, 1, USNM 52834 (specimen reported by Grygier, 1984); G-899, 1, USNM 52805; G-925, 2, USNM 52806; G-927, 1, USNM 52819; G-936, 2, USNM 52807; G-1125, 1, USNM 52905; G-1312, 2, USNM 52833; G-1314, 1, USNM 52832; Eastward-31281, 1, USNM 80097; Nutting Iowa Bahama Expedition, 1893, 1, off Havana, USNM 91861; O-4940, 1, USNM 52813; O-10849, 1, USNM 52837; P-200, 2, USNM 52808; P-208, 1, USNM 52824; P-209, 1, USNM 52809; P-594, 3, USNM 52810; P-610, 5, USNM 52811; P-611, 1, USNM 52812; P-857, 1, USNM 52826; P-877, 1, USNM 52827; P-890, 2, USNM 52828; P-931, 1, USNM 52830; P-1141, 2, USNM 52836; SB-440, 2, USNM 51263; off Sanibel Island, Florida, depth unknown, 3, USNM 52814; specimens reported by Verrill (1883), Deichmann (1936), and Grygier (1984); neotype.

*Types*.—The type of *C. desbonni* is not present at the Museo Regionale di Scienze Naturali, Torino (Wright & Studer 1889, L. Levi, pers. comm., 2001) or the Museum of Florence, and thus is presumed to be lost.

Indeed, none of the specimens reported by Duchassaing & Michelotti (1864) have ever been found (F. M. Bayer, pers. comm.). To resolve the taxonomic confusion about this species (see Remarks), a neotype of 5.5 cm height is chosen from *BL-232* (MCZ 4839). Original type locality: Harbor of Moule, Guadeloupe, Lesser Antilles (depth 300–400 m?). Type locality (as redefined by neotype): 13°06'45"N, 61°06'55"W (east of St. Vincent, Lesser Antilles), 88 fms (=161 m).

The syntypes of *C. occidentalis* Versluys, 1902, must be considered to be the material reported by Verrill (1883: 26) as *C. desbonni*, which reads: "numerous localities in the Caribbean Sea and among the Antilles, in 88 to 163 fathoms, by the *Blake*, in 1878–1979, and off Cuba, in 288 fathoms, in 1880." From the station list of the *Blake*, at least three stations correspond to these requirements: *BL-232* (the shallow end range), *BL-241* (the deep end range), and *BL* (Bartlett)-V (the Cuban specimen). Thirteen additional *Blake* stations are listed by Deichmann (1936), all of which Verrill probably examined. Specimens from all of these stations are still present at the MCZ, except for *BL* (Bartlett)-V. A lectotype is chosen from *BL-232* (MCZ 4839), which corresponds to one of the extremes of the bathymetric range reported by Verrill, and certainly one of the specimens he examined. Because it is the same specimen chosen for the neotype of *C. desbonni*, *C. occidentalis* becomes a junior objective synonym of *C. desbonni*. Type Locality: same as listed for *C. desbonni* above.

*Distribution*.—Fairly continuous distribution from off Turneffe, Belize, clockwise throughout the Antilles to Grenada, including the Bahamas; 155–595 m.

*Chrysogorgia thyriformis* Deichmann,  
1936 new rank  
Figs. 13-14

*Chrysogorgia desbonni* var. *thyriformis*  
Deichmann, 1936: 230.

*Chrysogorgia desbonni*: Deichmann, 1936:  
in part (*BL-101*, *BL-297*, *BL-55*, the latter  
reported as *BL-XIII*), pl. 35, fig. 1.

*Chrysogorgia elisabethae* Bayer, 1951:  
269–272, pl. 9, figs. 56–57; 1952: 189  
[new synonym]; 1954: 280 (listed).

*Description*.—Colonies bushy, rarely more than 8 cm in height and 8–9 cm in width. Holdfast encrusting, disc-shaped. Main stem slender (1.1–1.7 mm in diameter), straight, and rarely more than 3 cm in length; color of main stem golden-brown or bronze. Branching sequence 2/5R; branches extremely closely spaced, only about 0.5–0.7 mm apart, producing an orthostiche interval of 2.7–3.5 mm on lower part of colony and about 5 mm near distal portion of main stem. First two internodes of each branch form a plane that is roughly horizontal to the substrate (i.e., perpendicular to the main stem); however, at the second internode the orientation of the branch is usually twisted 45–90°, the plane of the remaining branch, which usually remains uniplanar to the terminal twigs, being vertical (i.e., parallel to the main stem). This twisting of the plane of branching and equal development of branches around the main stem produces a bushy colony form. Well-developed branches consist of about 10–12 internodes, each 5–8 mm in length, resulting in branch lengths of up to 75 mm. Dichotomous branching usually results in equal-sized sub-branches throughout each branch; angle between sub-branches fairly small (about 30°). Branches arise from the main stem oriented in an upward direction, about 45° from the vertical; branch anastomosis rare. Branches quite thick near main stem but gradually decrease in thickness, ending in terminal twigs of 0.12 mm in diameter; general tensile strength wiry. Two to 3 polyps occur on each internode, often more on the terminal twigs. Polyps small (up to 1.2 mm in height) and often have a highly constricted base; they project perpendicular to the branches or sometimes appear to angle backward toward the main



Fig. 13. *Chrysogorgia thyriformis*, stereo view of lectotype, MCZ 4849, height 5.5 cm.

stem. Sclerites similar to those of *C. desbonni*. Coenenchymal sclerites elongate, warty scales (warts about  $8\ \mu\text{m}$  in diameter)  $0.36\text{--}0.54\ \text{mm}$  in length and  $0.05\text{--}0.08\ \text{mm}$  in width, having pointed distal ends and highly irregularly-shaped edges. Body wall sclerites transversely arranged, curved and/or irregularly-shaped, finely-warty spindles up to  $0.71\ \text{mm}$  in length and  $0.06\text{--}0.07\ \text{mm}$  in width. These sclerites are slightly flattened, particularly at their distal ends, but are not interpreted to be scales. Tentacular sclerites longitudinally arranged rods similar in shape to those of body wall but smaller (i.e.,  $0.21\text{--}0.42\ \text{mm}$  in length). Pinnular sclerites typical rectangular scales  $0.18\text{--}0.21\ \text{mm}$  in length.

*Discussion.*—Although described as a variety of *C. desbonni*, *C. thyriformis* differs from that species in several consistent characters, warranting its elevation to the species level. *C. thyriformis* differs in having a bushy colony (not flabellate), fewer and longer internodes (see Table 3), more polyps per internode, slightly shorter and flatter body wall spindles, and more nu-

merous irregularly-shaped spindles in the body wall (in addition to the curved, regularly-shaped, flattened spindles). As described above, although the branches of *C. thyriformis* are basically uniplanar, there is often a twisting of the orientation at the second node, and the distalmost 8–12 branches that diverge from the main stem produce major branches. In contrast, all branches that diverge from the main stem of *C. desbonni* are exclusively uniplanar, only the distalmost two forming the two large uniplanar flabella having numerous nodes. Because *C. thyriformis* has flattened, curved spindles in its body wall and tentacles, it should, along with *C. desbonni*, be placed in *Chrysogorgia* (Group Spiculosae). Bayer (1951:272) placed *C. thyriformis* (as *C. elisabethae*) in the “Squamosae aberrantes”, apparently interpreting the flattened tentacular spindles/rods as scales, although he clearly noted in his description that both body wall and tentacles possessed rods, which would place it in Group A.

Aplacophoran mollusks are sometimes

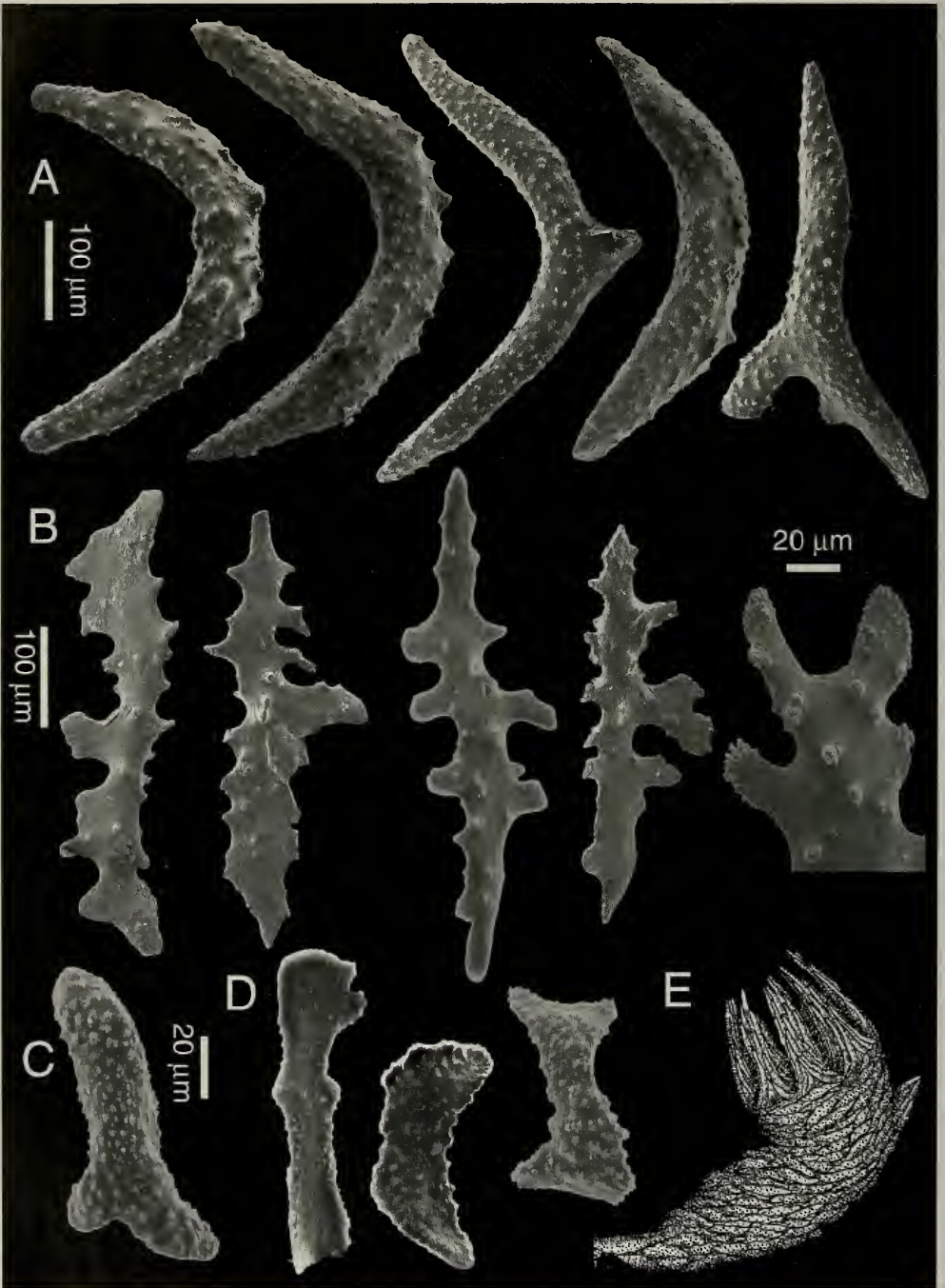


Fig. 14. *Chrysogorgia thyrsoformis*. A–D, sclerites of lectotype, MCZ 4849. A, five curved spindles from body wall; B, five coenenchymal scales; C, a tentacular rod; D, three pinnular scales. E, polyp of lectotype, 1 mm in width (from Verrill, unpublished plates).



found attached to branches of this species (e.g., *G-503*).

*Material examined*.—*Alb-2655*, 4, USNM 44129; *Atl-3320*, 1, MCZ; *Atl-3480*, 1, MCZ 3670; *BL*-(Sigsbee), 2 miles east of Havana, 1, USNM 49501; *Caroline-102*, 2, USNM 100888; *R/V Cape Florida*, 27°31'N, 79°15'W, 350–400 m, 2, USNM 73940; *CI-37*, 2, USNM 54816; *G-168*, 1, USNM 52788; *G-233*, 10, USNM 52790; *G-503*, 5, USNM 52798; *G-705*, 1, USNM 52818; *G-893*, 1, USNM 52803; *G-936*, 1, USNM 100886; *Eastward-26549*, 7, USNM 100889; *O-2655*, 2, USNM 59807; *O-5021*, 2, USNM 52821; *O-5419*, 1, USNM 53034; *P-200*, 3, USNM 100887; *P-739*, 6, USNM 52815; *P-848*, 2, USNM 52825; *P-907*, 2, USNM 52829; *P-991*, 1, USNM 52831; *P-1410*, 1, USNM 54815; *SB-3497*, 1, USNM 100890; University of Iowa, off Havana, 1, USNM 49489 (reported by Bayer, 1952); types of *C. thyriformis* and *C. elisabethae*; specimens reported as *C. desbonni* by Deichmann (1936).

*Types*.—Deichmann cited a type of this variety from a *Hassler* station off Barbados (MCZ 4849) and another specimen from *BL-281* (MCZ 4867); however, there are two specimens in lot 4849. Thus one specimen from MCZ 4849 is chosen as the lectotype, the other becoming a paralectotype (MCZ 4849a). The specimen from *BL-281* is also considered to be a paralectotype. Type Locality: “off Barbados,” 183 m.

The holotype of *C. elisabethae* was collected at *Alb-2129*, and is deposited at the USNM (7552). Type locality: 19°56'04"N, 75°48'55"W (off Santiago, Cuba), 501 m.

*Distribution*.—Fairly continuous distribution from Grand Bahama Bank throughout the Antilles to Isla Tortuga, Venezuela, including Yucatan Peninsula (off Cozumel) and the Bahamas; 146–526 m.

*Chrysogorgia agassizii* (Verrill, 1883)

Figs. 15-16

*Dasygorgia Agassizii* Verrill, 1883: 22–23, pl. 2, figs. 4, 4a–b(c–e); 1884: 220; 1885:

511–512, pl. 9, fig. 199.—Agassiz, 1888: 143–144, fig. 455.—?Roule, 1896: 304–305.

*Chrysogorgia agassizii*: Versluys, 1902: 60.—not Nutting, 1912: 55–56.—Kükenthal, 1919: 530, fig. 233; 1924: 403.—Deichmann, 1936: 222, 233–234, pl. 23, figs. 34–40, but not pl. 34, figs. 1–2 (= *C. elegans*).—Madsen, 1944: 49–54, figs. 42–47.—?Tyler & Zibrowius, 1992: 217.

*Chrysogorgia agassizi*: Kinoshita, 1913: 3 (listed).—?Tixier-Durivault & d'Hondt, 1974: 1409.—?Grasshoff, 1982a: 748 (map 4); 1982b: 949, figs. 22–24.—Vinogradov, 2000: 101–103, figs. 1–2.

?*Chrysogorgia pentasticha*: Thomson, 1927: 22.

?*Chrysogorgia (sic) agassizi*: Pasternak, 1985: 32.

*Description*.—Colony bottlebrush-shaped, up to 41 cm in height, and attached by an encrusting or rhizoidal holdfast. Main stem up to 2.5 mm in diameter; golden-brown in luster. Branching sequence consistently 2/5R: branches closely spaced, one every 1.5–2.0 mm; orthostiche interval 10–12 mm; branches diverge from main stem at about 70° from the vertical. Terminal twig branch diameter quite small (0.1 mm), producing a flexible, limp colony. Number of nodes per branch ranges from 2–5, but are usually 3, the first 2 internodes being short (2–4 mm), the third 4–6 mm, and the terminal twigs being up to 50 mm in length, combining to produce a total branch length of 60–65 mm. Branching dichotomy not always symmetrical, the internodes and terminal twigs of a branch usually arranged in a horizontal plane. Polyps usually absent from first 2 internodes, one occurring near the third internode, and up to 11 polyps on the terminal twigs. Polyps cylindrical, up to 2.5 mm in height and about 0.75 mm in diameter, obliquely arranged on the branches. Coenenchymal sclerites smooth, elongate scales with rounded distal ends and finely serrate edges, up to 0.36 mm in length and 0.04 mm in width. Body wall

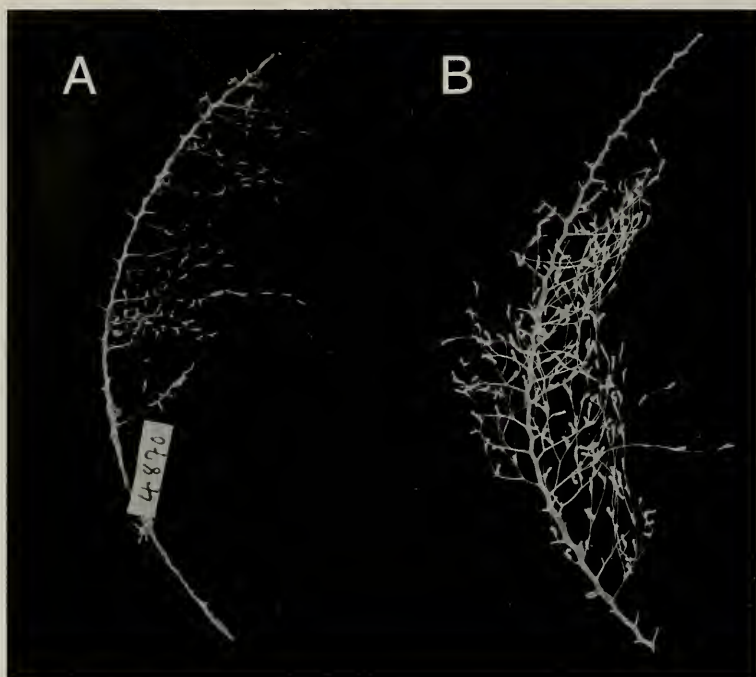


Fig. 15. *Chrysogorgia agassizii*. A, lectotype, BL-308, MCZ 4870, height 15 cm; B, paralectotype, BL-308, MCZ 5748, height 10.5 cm.

sclerites similar to coenenchymal sclerites but slightly larger: 0.42–0.48 mm in length and 0.06–0.07 mm in width. Body wall scales longitudinally arranged, with smooth to finely granular (but not warted) faces and finely serrate edges. Bluntly-tipped, finely-granular, straight rods 0.42–0.60 mm in length and 0.08–0.13 mm in width occur at the base of the tentacles, but are quite rare, perhaps occurring with a frequency of one per tentacle. Tentacular rods bear small compound warts, each about 8  $\mu\text{m}$  in diameter, which are composed of smaller elements. Pinnular sclerites smooth elongate scales up to 0.21 mm in length and 0.04 mm in width, having finely-serrate edges.

*Discussion.*—This species is exhaustively described, figured, and discussed by Madsen (1944), based on several specimens collected south of Iceland; however, the eastern Atlantic records of *C. agassizii* (see “Distribution”) have been little more than unfigured and undescribed listings of the

species. Since I have not examined them, their synonymy records are queried.

It is of interest to note that the specimens from the four *Albatross* stations reported herein were originally identified but not reported by A. E. Verrill.

Based on repeated photographs of a specimen attached to the bow rail of the *R. M. S. Titanic*, Vinogradov (2000) calculated the growth rate of this species to be about 1 cm per year.

*Material examined.*—*Alb*-2034, 1, USNM 9150; *Alb*-2035, 4, USNM 17253; *Alb*-2220, 1, USNM 7920; *Alb*-2573, 2, USNM 11854; *Knorr* 58-I-827, 1, USNM 59808; *Gyre* MA2:04, 1, USNM 88109; Nutting’s (1912) misidentification, *Alb*-5080, USNM 30170; types of *D. agassizii* (see below).

*Types.*—The larger of the two syntypes is deposited at the MCZ (4870) and a smaller one is at the USNM (5748). Deichmann (1936), in designating MCZ specimen 4870

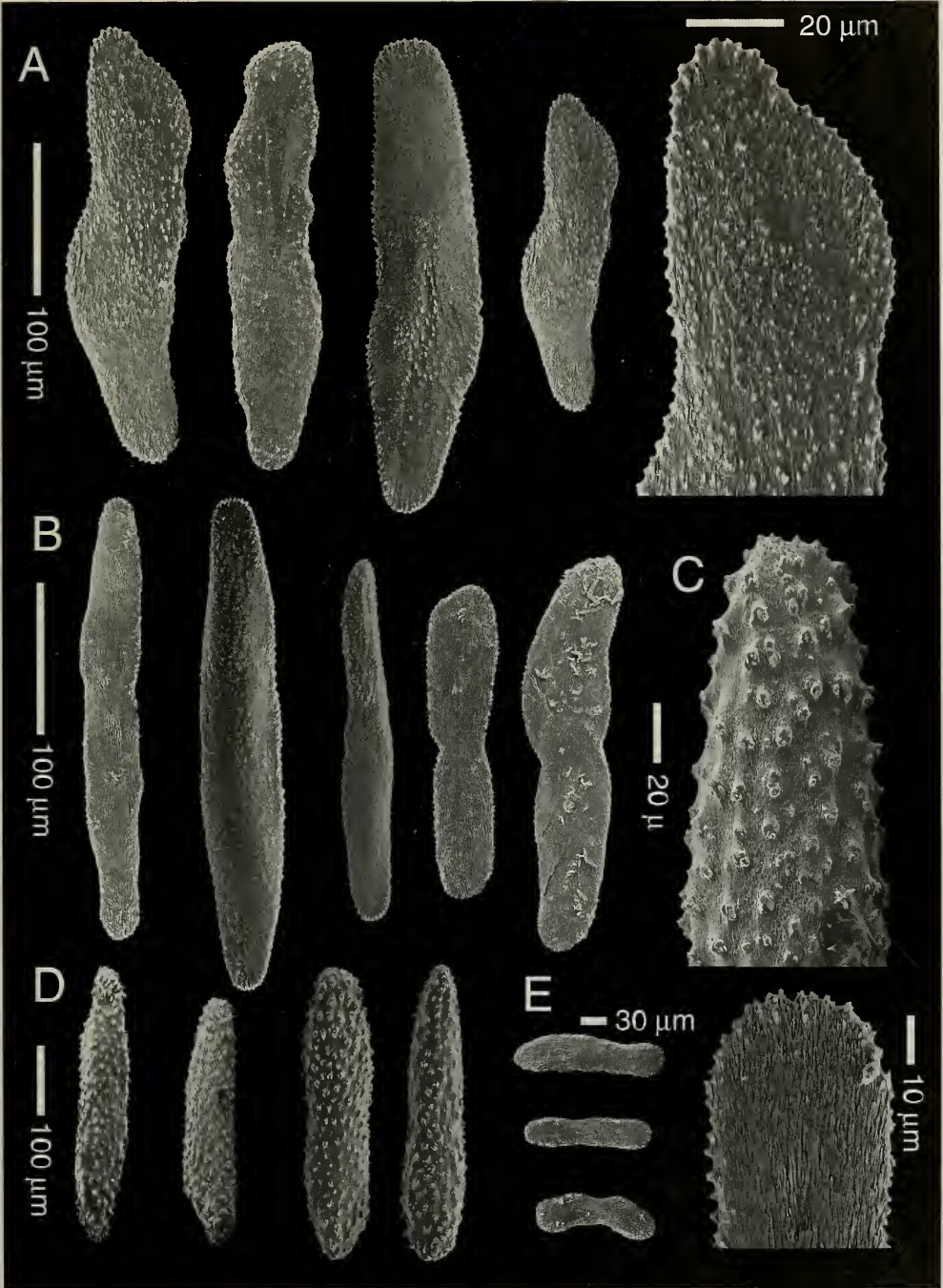


Fig. 16. *Chrysogorgia agassizii*, sclerites from paractotype, BL-308, MCZ 5748. A, five scales from body wall; B, five coenenchymal scales; C, enlargement of tip of tentacular rod; D, four tentacular rods; E, four pinnular scales.



Fig. 17. *Chrysogorgia squamata*, lectotype, BL-283, MCZ 4862, height of colony 10.5 cm.

as the type, effectively makes it the chosen lectotype for the species, the USNM specimen thus becoming a paralectotype. Type Locality: Blake-308: 41°04'45"N, 65°35'30"W (off Georges Bank), 2271 m.

*Distribution.*—Western Atlantic: off continental slope of northeastern United States and Newfoundland from 39–42° N latitude, 1928–3700 m. North and eastern Atlantic: off Iceland (Madsen 1944);? west of Ireland (Tyler & Zibrowius 1992);? Bay of Biscay (Roule 1896, Grasshoff 1982a);? Azores (Thomson 1927);? Atlantis Seamount (Pasternak 1985); 1425–2860 m.

*Chrysogorgia squamata* (Verrill, 1883)

Figs. 17–18

*Dasygorgia squamata* Verrill, 1883: 24.

*Chrysogorgia squamata*: Versluys, 1902: 85.—Kükenthal, 1919: 538; 1924: 408.—Deichmann, 1936: 232–233, pl. 22, fig. 8, pl. 23, figs. 28–33.

*Description.*—Colonies bottlebrush-shaped, up to 20 cm in height and 6 cm in

width, attached by an encrusting holdfast. Main stem up to 1.6 mm in diameter, yellowish-amber in luster, and, along with the internodes, covered with numerous, slender cnidal papillae up to 0.2 mm in height. Branching sequence predominantly 1/5R, although the occasionally the sequence shifts to 1/6 or even 1/7R. Branches occur every 2.1–3.0 mm, resulting in an orthostiche interval for the 1/5 sequence of 8.5–12.0 mm. Branches diverge from main stem at 70–90° from the vertical. Distal branch diameter 0.25 mm; branches and colony wiry in construction. Number of nodes per branch 2 or 3. First internode 4–8 mm in length; second, 4–5 mm; third, 4–5 mm, and terminal twigs up to 10 mm, resulting in a total branch length up to 28 mm. Polyps sparse, usually absent from the first 2 internodes, only 1 on the third internode, and 1 or 2 on the terminal twigs. Polyps cylindrical, up to 1.8 mm in height. Coenenchymal sclerites elongate (up to 0.45 mm in length and about 0.07 mm in width), smooth scales, rounded on their distal ends, with finely serrate edges, and often slightly constricted medially. Body wall sclerites transversely arranged, elongate (up to 0.54 mm in length and 0.08–0.09 mm in width), smooth scales, also with rounded distal ends and finely serrate edges, the apices of the serrations of uniform height (1–2  $\mu\text{m}$ ) and quite regularly spaced (every 3–4  $\mu\text{m}$ ). Backs of tentacles, adjacent to the naked space at the base of each tentacle, filled with longitudinally-placed, warty rods, up to 0.42 mm in length and 0.07 mm in diameter. Smaller rods (0.20–0.25  $\times$  0.06 mm) occur in the distal tentacles. Pinnular scales quite small, somewhat rectangular and usually slightly medially constricted. Pinnular scales up to 0.17 mm in length and 0.09 mm in width, but may be much smaller, e.g., 0.08  $\times$  0.02 mm.

*Discussion.*—Deichmann's (1936) redescription of this species, which must have been based on the type material, was somewhat misleading, in that she indicated a branching sequence of 1/7, branches with

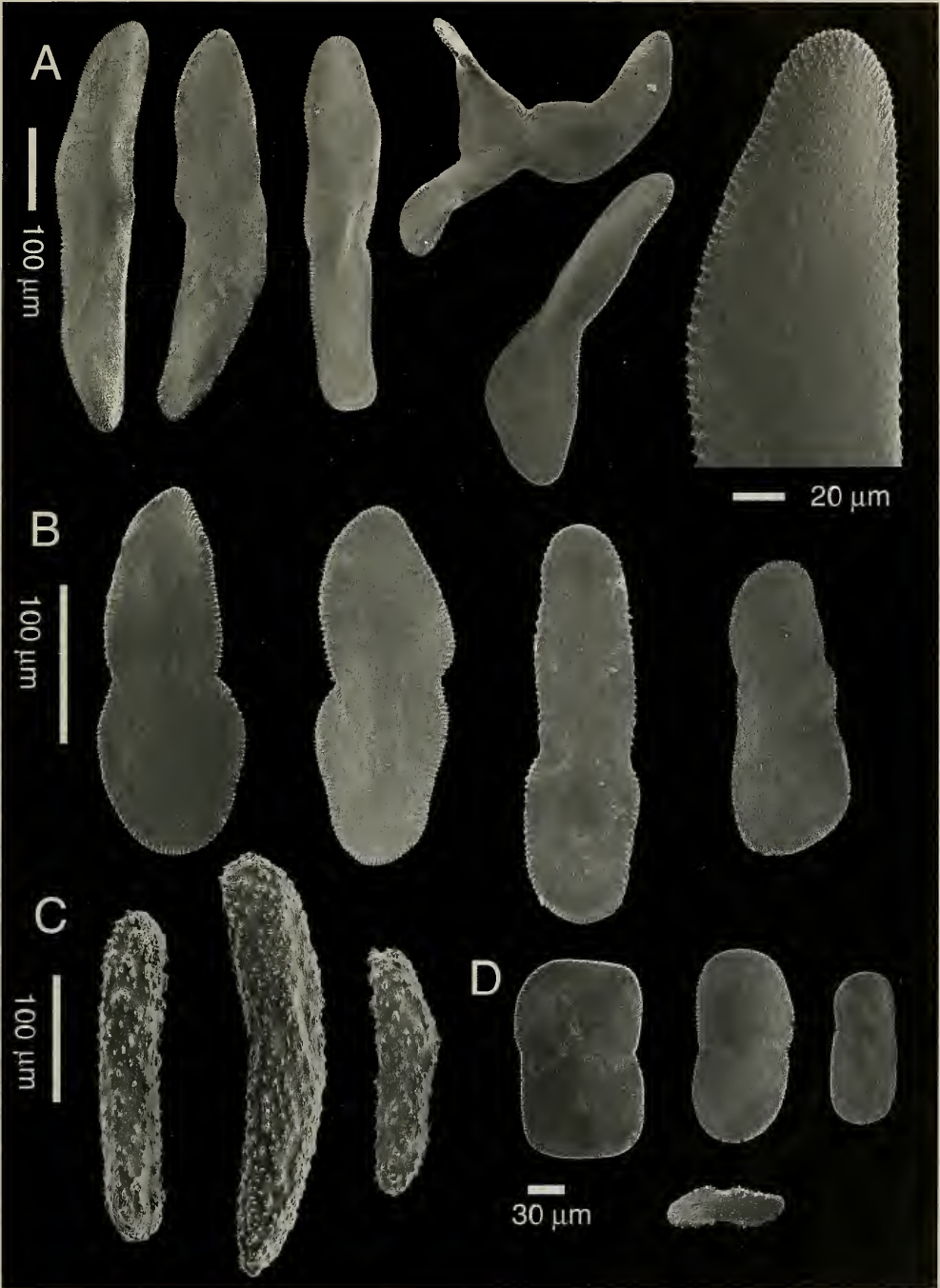


Fig. 18. *Chrysogorgia squamata*, sclerites from lectotype, MCZ 4862. A, six scales from body wall; B, four coenenchymal scales; C, three tentacular rods; D, four pinnular scales.

5–6 nodes, and longitudinally arranged body wall sclerites. As reported in the description, the branching sequence is predominantly 1/5, branches usually have 2–3 nodes, (never as many as 6), and body wall sclerites are transversely arranged. Versluys (1902) tentatively placed *C. squamata* in the group “Squamosae typicae”, but acknowledged that he did not have knowledge of the tentacular sclerites. Since the tentacles of this species contain well developed rods, it thus belongs in the group “Squamosae aberrantes”.

*Chrysogorgia squamata* is a very rarely collected species, the specimens listed below being the first new records since its original description. It is easily distinguished from other western Atlantic species by having a 1/5R branching sequence and cnidal papillae. Indeed, no other species in the “Squamosae aberrantes” group has a 1/5R branching sequence (Table 1).

*Material examined.*—Atl-3326, 1, MCZ (unnumbered); P-607, 1, USNM 52840; types of *D. squamata* from BL-283 (see below).

*Types.*—Verrill reported three specimens from two Blake stations, which must be considered as syntypes: one from BL-227 and two from BL-283 (MCZ 4862). Deichmann (1936) restricted the type locality to BL-283, but did not designate a lectotype. Thus, one of the three (not two) specimens from BL-283 (MCZ 4682) is herein designated as the lectotype: not the largest colony of 20 cm height, but the smaller of 12 cm height that is attached to the substrate. The remaining two specimens from BL-283 (MCZ 4682a) and that from BL-227 are thus paralectotypes; however, the latter specimen could not be found at the MCZ in 2001. Type locality: 13°05'05"N, 59°40'50"W (off southwestern Barbados, Lesser Antilles), 431 m.

*Distribution.*—off Banco Chinchorro, Yucatan Peninsula; southwestern Cuba; Lesser Antilles (Barbados and St. Vincent); 431–1046 m.

### Key to the western Atlantic species of *Chrysogorgia*

The two previous keys (Deichmann 1936; Bayer 1951) to the western Atlantic species of *Chrysogorgia* relied on the position and/or kind of sclerites in the body wall as the first couplet. The following key emphasizes the more gross and easily recognized characters such as colony shape and branching sequence, reserving characteristics of sclerite position, shape and size for the terminal couplets.

1. Colones bottlebrush-shaped; distance between branches over 1 mm . . . . . 2
- 1'. Colonies bushy or flabellate; distance between branches less than 1 mm . . . . . 8
2. Sclerites of body wall longitudinally arranged . . . . . 3
- 2'. Sclerites of body wall transversely arranged . . . . . 6
3. Branching sequence 2/5R . . . . . 4
- 3'. Branching sequence 3/8R *C. herdendorfi*, n. sp.
4. Body wall sclerites exclusively scales . . . . . *C. agassizii*
- 4'. Body wall sclerites includes spindles and/or rods . . . . . 5
5. Number of nodes per branch 0–2, usually 1; distance between branches 2.5–3.0 mm . . . . . *C. herdendorfi*, n. sp.
- 5'. Number of nodes per branch 1–3, usually 2; distance between branches 1.0–1.5 mm. . . . . *C. elegans*
- 5". Number of nodes per branch 3–6, usually 4; distance between branches 3.5–4.5 mm . . . . . *C. spiculosa*
6. Branching sequence 2/5R . . . . . 7
- 6'. Branching sequence 1/5R . . . . . *C. squamata*
7. Body wall sclerites cylindrical spindles up to 0.06 mm in width . . . . . *C. fewkesii*
- 7'. Body wall sclerites flattened spindles up to 0.13 mm in width . . . . . *C. multiflora*
8. Colony bushy; up to 12 internodes per branch . . . . . *C. thyriformis*
- 8'. Colony flabellate (biflabellate); up to 40 internodes per branch . . . . . *C. desbonni*

### Acknowledgments

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## Reevaluation of *Tropidopathes saliciformis* Silberfeld: A hydroid originally identified as an antipatharian coral

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*Abstract.*—*Tropidopathes saliciformis* Silberfeld (1909) was originally identified as an antipatharian coral growing over a hydroid colony. A re-examination of the type specimen revealed no evidence of any antipatharian skeletal material on the hydroid, and it is assumed that the lower parts of the hydrocauli of the hydroid, which lacked hydrocladia, had been mistaken for antipatharian sclerenchyme. The hydroid was subsequently identified by Stechow (1913) as *Halicornaria ishikawai* Stechow, 1907 (now known as *Gymnangium ishikawai*). Therefore, the genus *Tropidopathes* is herein removed from the Antipatharia, and for nomenclatural purposes, *Tropidopathes saliciformis* Silberfeld is considered a junior subjective synonym of *Gymnangium ishikawai* (Stechow).

In 1909, Silberfeld described a new genus and new species of antipatharian coral, *Tropidopathes saliciformis*. She reported that it was growing over a hydroid colony, and because of the epizotic habit, she referred the genus to the subtribe Crustosae which had been established by Schultze (1896) for *Savagliopsis pedata* (Gray). Brook (1889) had reported that the lower parts of the corallum of the type specimen of *Antipathes pedata* Gray appeared to be growing over a gorgonian axis, and Schultze (1896) considered this sufficient reason for establishing a new genus for the species. (NOTE: recent re-examination of the type specimen of *A. pedata* deposited in the Natural History Museum, London, revealed no evidence of an epizotic habit). In Schultze's revised classification of the Antipatharia, the subtribe Crustosae was placed in an unnamed tribe characterized by the lack of peristomal folds; the tribe was placed in the subfamily Dekamerota (characterized by polyps with ten septa); and the subfamily was placed in the family Antipathidae. Van Pesch (1914) applied the name Apuchaeophora to Schultze's un-named tribe contain-

ing the Crustosae. Pax (1918, 1987) did not recognize Schultze's subdivisions of the family and, although he retained *Tropidopathes* as one of seven genera in the Antipathidae, he noted that the systematic position of the genus was unclear. There is no evidence that any later antipatharian worker had re-examined the type specimen of *Tropidopathes saliciformis* after Silberfeld's original description appeared in 1909.

In Silberfeld's description of *Tropidopathes saliciformis*, she mentions that the branches of the antipatharian arise singly from a reticulum ("Geflecht") which is also overgrown by bryozoans, sponges, and balanids. She reported that the branches were light brown in color, reached a maximum length of 14 cm, and that each had two rows of very thick spines. The spines were described as being 285  $\mu\text{m}$  wide at the base, up to 357  $\mu\text{m}$  in height, rounded at the apex, and up to 535  $\mu\text{m}$  apart in the same row. She further reported that on the side opposite the spines, there was a long crest-like ridge, 178  $\mu\text{m}$  in thickness. The illustrations given by Silberfeld (1909, figs. 3–4) showed protuberances on either side of

the stem which were arranged bilaterally and alternately. These protuberances differed from typical antipatharian spines in that they appeared slightly concave on one side.

*Re-examination of the type specimen.*—Figure 1 shows the complete holotype of *Tropidopathes saliciformis* Silberfeld in the collections of the Zoologische Staatssammlung Muenchen. Numerous unbranched “stems” arise from a tangled hydrorhizal mass. At the top of some of these “stems” there are small pinnately branched structures that Silberfeld had identified as a hydroid (Fig. 2A). A close examination of one stem (Fig. 2B) reveals that Silberfeld had mistakenly identified the apophyses of the hydrocauli of the hydroid as antipatharian spines. Associated with each apophysis are three openings on the hydrocaulus corresponding to cauline nematothecae. The hydroid was subsequently identified by Stechow (1913) as *Halicornaria ishikawai* Stechow, 1907. A complete redescription of the hydroid is given below.

### Systematic Treatment

Plumularioidea McCrady, 1859

Aglaopheniidae Marktanner-Turneretscher,  
1890

Gymnangiinae Calder, 1997

*Gymnangium ishikawai* (Stechow, 1907)  
Figs. 1–3

?*Aglaophenia balei* Marktanner-Turneretscher, 1890:272, pl. 7, figs. 19–20 (sensu Ritchie, 1910:22–23, pl. 4, fig. 12 (see Stechow, 1913).

?*Halicornaria flava* Nutting, 1905:955, pl. 13, figs. 11–12 (see Stechow, 1913).

*Halicornaria ishikawai* Stechow, 1907: 198; 1909:100–101; 1913:95.

*Tropidopathes saliciformis* Silberfeld, 1909:19–20, figs 3–4.

*Gymnangium ishikawai*.-Stechow, 1923:19; Yamada, 1959:84; Hirohito, 1995:290.

*Material examined.*—Zoologische Staatssammlung Muenchen, No. 121a of

the collection of Doflein, Japan, Sagami Bay, near Jogashima Island, 150 m, 31 Oct 1904; holotype of *Tropidopathes saliciformis* Silberfeld (1909) (schizoholotype, USNM 100479).

*Description.*—Unbranched monosiphonic hydrocauli arising from complex root-like hydrorhiza (Fig. 1). Hydrocauli up to 14 cm long and up to 520  $\mu\text{m}$  in diameter; separated into internodes about 900  $\mu\text{m}$  in length by faint diagonal constrictions. Each internode with two frontal lateral hydrocladial apophyses (Fig. 2). Apophyses distally inclined, alternately arranged; surrounded at base by three cauline nematothecae, one median inferior and two axillary (Fig. 2B). Frontal axillary nematotheca very wide, leaf-like. Longitudinal crest extending down hydrocauli on side opposite apophyses. Hydrocladia present at top of some, but not all hydrocauli. Hydrocladia simple, in two rows, bilaterally arranged. Hydrothecae in single series on inner side of hydrocladia (Fig. 3A). Upper part of hydrotheca tube-shaped in lateral view (Fig. 3B); margins flared outward, usually forming a single weak cusp on each lateral side; adcauline margin straight or slightly concave: abcauline margin convex. Hydrothecal aperture approximately 160  $\mu\text{m}$  in diameter from adcauline to abcauline wall. Each hydrotheca with three nematothecae; one median inferior, and two lateral (Fig. 3A, B). Median inferior nematotheca tube-like in shape, narrowing at apex; lateral nematothecae bowl-shaped and relatively wide at apex. Terminal aperture of median inferior nematotheca facing distally; apertures of lateral nematothecae facing distally and somewhat medially (i.e., towards each other). Distal side of median inferior nematotheca mostly free, not adnate to the abcauline wall of hydrotheca, and not extending beyond abcauline margin of hydrotheca. Abcauline intrathecal septum extending about a third of the way across interior cavity of hydrotheca. Distinct crest-like ridge extending down the side of the hydrocladia di-



Fig. 1. *Gymnangium ishikawai* (Stechow). Holotype of *Tropidopathes saliciformis* Silberfeld (1909); approximately 15 cm tall.

rectly opposite side on which hydrothecae occur. Gonosomes not present.

*Remarks.*—The length of the hydrocauli (maximum 14 cm) and the size, shape and spacing of the apophyses match very closely the description given by Silberfeld of the “antipatharian” *Tropidopathes saliciformis*, and there is little doubt that Silberfeld was describing the lower parts of the hydroid colony as an antipatharian. In 1913 Stechow identified the hydroid as *Halicor-*

*naria ishikawai* Stechow (1907), and listed as the “Untergrund” or substrate, the antipatharian *Tropidopathes saliciformis*, in contradiction to Silberfeld’s description of the hydroid being the substrate for the antipatharian. Stechow apparently did not review Silberfeld’s original description.

*Comparisons.*—When Stechow (1913) identified Silberfeld’s specimen as *Halicornaria ishikawai* (Stechow), he noted that the median inferior nematothecae were sig-

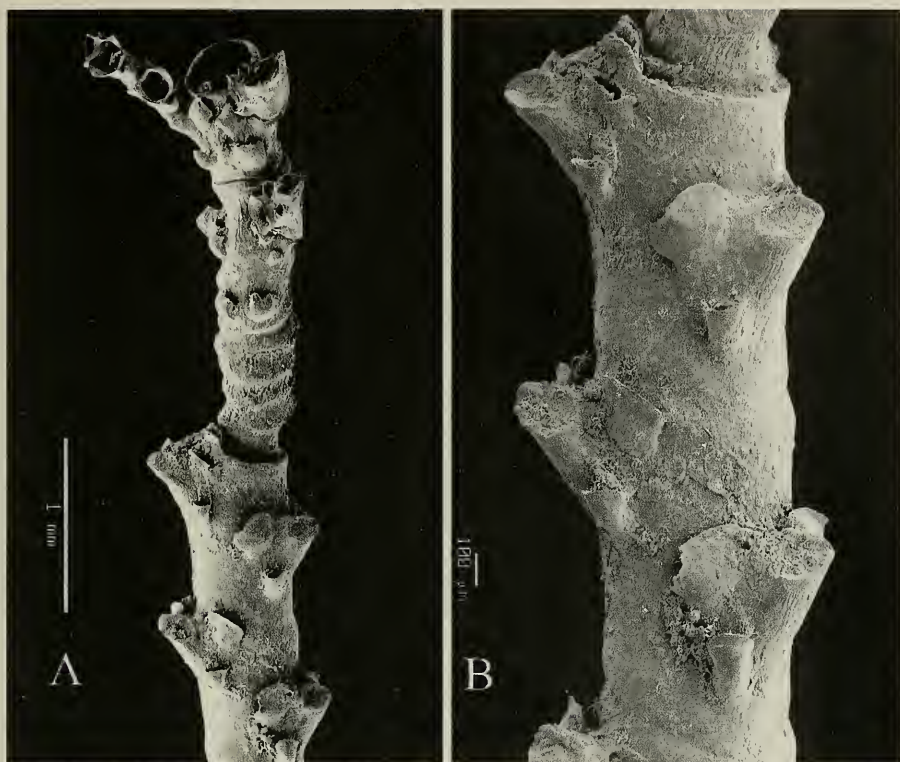


Fig. 2. *Gymnangium ishikawai* (Stechow); schizoholotype of *Tropidopathes saliciformis* Silberfeld (1909), USNM 100479. A, Upper part of hydrocaulus showing basal part of one hydrocladia. B, Enlarged view of hydrocaulus.

nificantly shorter than those in the type specimen of *H. ishikawai* that he had illustrated in 1909. Because of this, Stechow (1913) suspected that the specimen might be referable to *Aglaophenia balei* Marktanner-Turneretscher, 1890, as described by Ritchie (1910), or to *Halicornaria flava* Nutting, 1905. Stechow (1913), however, also mentioned that the margin of the hydrotheca in *H. ishikawai* was less serrated than in either of these two species; in particular, he noted that there was no denticle on the front or back central areas as described by Nutting.

*Gymnangium balei* (Marktanner-Turneretscher) was synonymized with *G. hians* (Busk) by Vervoort & Vasseur (1977). In describing a specimen of *G. hians*, Rees & Vervoort (1987) note that the length of the medial nematotheca varied considerably de-

pending on its location on the hydrocladium (usually longer on the part of the hydrocladium closest to the hydrocaulus). In the specimen of *G. hians* described by Vervoort & Vasseur (1977), the hydrothecal margin was reported to have only a single cusp on either side, similar to the situation in *G. ishikawai*; however, in the specimen of *G. hians* described by Rees & Vervoort (1987), the hydrothecal margin was reported to have three cusps on either side. As noted by Calder (1997), not only the length of the median inferior nematotheca, but also the dentition of the hydrothecal margin are quite variable in species of *Gymnangium*. Hirohito (1995) reported and illustrated material of *G. ishikawai* and *G. hians* from Sagami Bay, Japan. Both species were described as having median inferior nematothecae extending beyond the hydrothecal

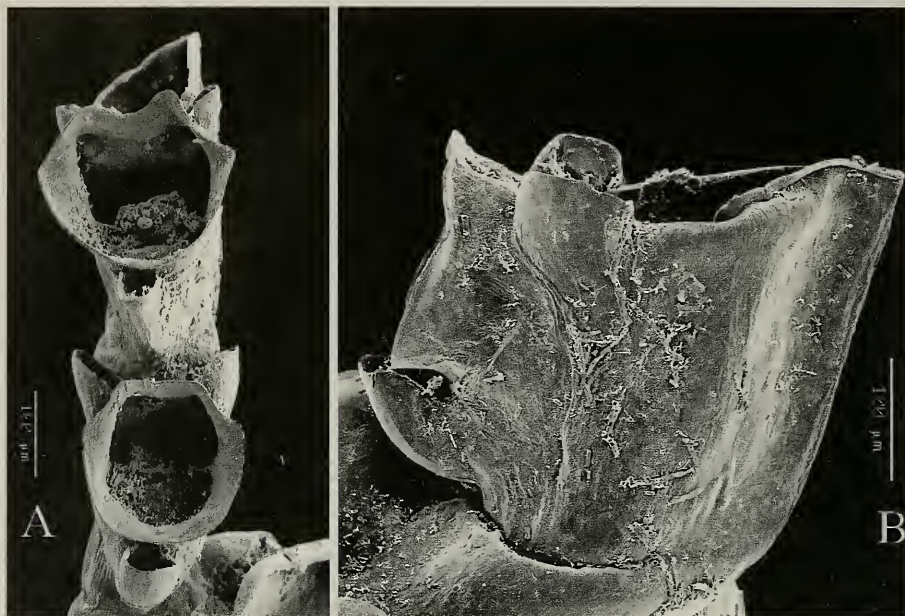


Fig. 3. *Gymnangium ishikawai* (Stechow); upper part of the schizoholotype of *Tropidopathes saliciformis* Silberfeld (1909), USNM 100479. A, Lower portion of hydrocladium, frontal view with two hydrotheca. B, Lateral view of hydrocladium showing a single hydrotheca and associated nematotheca.

margin; differentiated mainly on the basis of the serration of the hydrothecal margin (inconspicuous in *G. ishikawai*, and very conspicuous in *G. hians*). According to Calder (personal communication), *G. ishikawai* is distinct from *G. hians* Busk. In the type material of *Tropidopathes saliciformis* the dentition along the hydrothecal margin is relatively weak, suggesting that Silberfeld's specimen should be referred to *G. ishikawai*, however, the median inferior nematotheca is relatively short and its adcauline side is not adnate to the abcauline hydrothecal body wall, suggesting that Silberfeld's specimen may be distinct from both *G. ishikawai* and *G. hians*.

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## East Pacific Mexican *Tethya* (Porifera: Demospongiae) with descriptions of five new species

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**Abstract.**—Seven species of Tethyidae (Porifera: Demospongiae: Hadromerida) inhabiting the Pacific waters of Mexico, including the Gulf of California, were studied. Five of them, *Tethya ensis*, *T. mexicana*, *T. ovum*, *T. paroxeata*, and *T. socius* are new species. The remaining two, *T. taboga* De Laubenfels and *T. californiana* De Laubenfels, are new records for the area.

This is the first published report on species of the genus *Tethya* (Porifera: Demospongiae) coming from the Pacific coast of Mexico. A total of 242 collected *Tethya* specimens yielded five new species and two other species recorded for the first time. *Tethya taboga* (De Laubenfels) was known only for the Pacific coast of Panama, and *T. californiana* De Laubenfels, 1932, re-described by Sarà & Corriero (1993), is recorded here for a more southern site in Mexico. Only four species of *Tethya* were previously known for the whole Pacific coast of America: *T. californiana* De Laubenfels from California, *T. taboga* (De Laubenfels) from Panama, *T. papillosa* Thiele from Calbuco (Chile) and *T. sarai* Desqueyroux-Faúndez & van Soest, 1997 from the Galápagos Islands. This small number of American Pacific species, now amounting to nine, is probably due both to a real scarcity of species and to the poverty of records from this area. *Donatia multifida* Carter, 1882 from Acapulco (Mexico), examined by Sarà (1994) on spicular slides of the British Museum of Natural History (BMNH) is currently regarded as incertae sedis, given the scarcity of the material. Moreover, it is impossible to know if it belongs to a species of the *Tethya seychellen-*

*sis* group or if it should be considered as representative of a new genus of Tethyidae.

### Materials and Methods

Samples of *Tethya* (242 individuals) represent part of several collections obtained along the Pacific coast of Mexico, including the Gulf of California at different depths (Table 1, Fig. 1). Sponges were collected with SCUBA diving and with a trawl aboard the R/V *El Puma*. Thirty-eight trawls, covering almost all the Gulf of California from 31°15'9"N, 114°21'7"W to 20°49'N, 105°42'W, from 22 to 120 m depth, were performed in March, July, August, and October of 1985. Several dives off the coast of Mazatlán took place from 23°15'N, 106°29'W to 23°11'30"N, 106°25'W in May 1981 and June 1987 at a depth of 0 to 15 m. Trawls and dives from Guerrero were performed in February (Winter) and April (Spring) of 1982, in the continental shelf, from the coastline to the beginning of the continental slope, at 200 m depth (102°15'N, 98°W), including the Balsas river delta. Sponges, once aboard, were preserved first in 95% alcohol and then in 70%. Techniques to analyze internal structures follow Sarà (1992), and scanning electron microscopy (SEM) follow Gómez



(1998). Spicular data reported are based on 50 measurements from each spicular trait. Main and auxiliary megascleres, generally, stronglyxeas, were distinguished by a conventional 1000  $\mu\text{m}$  length figure. For two species, a third category of "sword" stronglyxeas was considered. *Micraster* nomenclature is traditionally based on observations taken at the light microscopic level. Yet, the difference between oxyasters, strongylasters and tylasters (Sarà 1994) is only partially due to the ray shape. It depends largely, as shown by SEM micrographs, on the distribution and strength of the spines. The holotypes are deposited in the Natural History Museum of Genoa (Italy) (MSNG), some paratypes are deposited in Laboratorio de Ecología de Bentos ICML collection of Mazatlán (Mexico).

*Study area.*—The Gulf of California belongs to the subtropical regime with marked fluctuations in climatic conditions all year long. It is positioned between two dry continental environments that cause wide ranges in temperature, low humidity, and high evaporation rate. The yearly mean temperature value at the surrounding coast is 24°–26°C. Rainfall is abundant at the east coast of the Gulf as well as in the south, whereas at the west coast rainfall is lower. Maximum rainfall is from June to October, becoming dry at winter and at the beginning of spring. This brings about coastal upwelling along the western side in summer and at the eastern side in winter (INEGI 1984, Molina-Cruz 1986). Mazatlán is located at the mouth of the Gulf of California, in a tropical and subtropical semi-humid climate, bathed by the Gulf of California current and causing different water changes according to the nearby inlets, islands, and breakwaters. Yearly mean temperature is from 25°C to 28°C, yearly mean rainfall reaches 850 mm (Álvarez-León 1980). Guerrero has a tropical semi-humid climate, yearly mean temperature of 27.5°C, yearly mean rainfall 1117 mm, and a permanent influx of freshwater in Petacalco Bay that

Table 1.—Sampling stations of *Teriyya* species along the Pacific coast of Mexico. Collecting parameters.

Locality	Gulf of California			Mazatlán		Guerrero	
	Puerto Libertad	Cabo San Miguel	Punta Arboleda	Punta Chile	Petacalco Bay & Pta. Maldonado		
Coordinates	29°59'0"N 112°45'0"W	28°10'2"N 112°48'2"W	26°51'9"N 110°00'9"W	23°12'28"N 106°25'50"W	17°55'N, 102°01'W 16°13'N, 98°44'W		
Depth (m)	Intertidal	25	22	5 & 8	45 both		
Collecting date	Oct 1985	Mar 1985	Jul 1985	May 1981 & Jun 1987	Feb & Apr 1982		
Temperature (°C)	17	14	29.5	22	21.7 & 23.5		
Oxygen (ml/l)	6.16	4.0	4.8	3.5	2.97		
Salinity (‰)	35.56	35.3	35.5	34.4	34.2		
Bottom	Sand	Rock-sand	Irregular	Rock	Sandy-mud, clay		



Fig. 1. Map of collecting areas and distribution of *Tethya* species: Puerto Libertad, Cabo San Miguel and Punta Arboleda inside the Gulf of California, Mazatlán at the mouth, and Petacalco Bay as well as Punta Maldonado at Guerrero, southern Mexico, tropical East Pacific.

comes from the Balsas river (Amezcu-Linares 1996).

The study area, except the Gulf of California, represents the transition zone between the mixture from the North Californian current and the South Perú current with the North equatorial counter-current, it marks the limits between the Californian Province with the Panamic one, now subdivided in Cortez Province, Mexican Province, and Panamic Province (Hendrickx 1995).

#### Systematics

Order Hadromerida Topsent, 1900

Family Tethyidae Gray, 1867

Genus *Tethya* Lamarck, 1815

*Type species.*—*Tethya aurantium* Pallas, 1766.

*Diagnosis.*—Spherical or subspherical body not supported by a stalk, well devel-

oped cortex distinct from the choanosome, megascleres bundles radiate from the center of the sponge ending in tubercles on the surface. Main and auxiliary megascleres are usually strongyloxeas, auxiliary may be also styles, megasters are spherasters or oxyspherasters, micrasters are tylasters, strongylasters (chiasters) or oxyasters; these two are distributed in the cortex as well as in the choanosome (Sarà 1994).

#### *Tethya ensis*, new species

Figs. 2A, B, 3, 4, 15A, Table 2

*Material examined.*—Holotype: MSNG 50191; paratype: LEB-ICML 255; 46 specimens Punta Maldonado (Guerrero), Feb 1982, 45 m depth.

*Description.*—The type has an elongated hemispherical shape, 1.5 by 2.5 cm, with the irregular flattened basis covered by robust filamentous stolons. On the whole, the

shape is elongated hemispherical (Fig. 2A, B), 0.8–2.6 by 0.7–3 cm. Two specimens were attached to the next *Tethya* species described herein. Color: not recorded in vivo, creamy white in ethanol. Consistency slightly compressible. Surface sparsely and irregularly tuberculate, partially smooth. The best distinguished tubercles are finely hispid, flattened, 1–2 mm in diameter, 1 mm in height (Fig. 2A), sharp and stout filamentous stolons on the basis and the edges of the sponges are 2 cm long. Some tubercles on the edge of the sponges produce also 3 mm elongated buds. Cortex thickness, without tubercles, 0.5–1 mm.

*Skeleton*.—Megasclere bundles radiate from center to cortex sometimes in a coiled way as in the holotype. Bundles, 245–325  $\mu\text{m}$  in diameter, ending in compact cortical fans without subdivisions (Fig. 3A). Megasters regularly distributed in the middle and, more densely, in the lower cortex, forming a belt around the choanosome. Some smaller megasters in the outer choanosome (Fig. 15A).

*Spicules*.—Table 2 summarizes measurements taken from 5 specimens. Megascleres (Figs. 3B, D, 4A) are: main strongyloxeas (maximum size 2312 by 47  $\mu\text{m}$ ), peculiar shortened fusiform strongyloxeas (“sword” like) in the cortical fans and among the subcortical interstitial megascleres, 225–965  $\mu\text{m}$ , with a slender head 4–8  $\mu\text{m}$  thick and a thickness of generally 15–25  $\mu\text{m}$ , in the central and distal parts of the spicule and auxiliary megascleres, from slender strongyloxeas to thin styles.

Megasters (Figs. 3D, 4D): Spherasters heterogeneous in size and shape, with some slight differences among the specimens and a main size range 50–90  $\mu\text{m}$  (maximum diameter 115  $\mu\text{m}$ ). The R/C main range is 0.5–0.9, sometimes in the larger spicules it is 1–1.1. Ray number: 14–16.

Micrasters (Figs. 3C, 4B, C): Mainly strongylasters but variable from slightly knobbed tylasters to slightly tyloxyasters 9–13  $\mu\text{m}$  in diameter (minimum 5.9 and maximum 16.5  $\mu\text{m}$ ) with 12 thin spiny

rays. Similar in the cortex and in the choanosome.

*Etymology*.—From Latin *ensis* = sword, in reference to the sword-like appearance of the short fusiform strongyloxeas; here used as a noun in apposition.

*Remarks*.—*Tethya ensis* is characterized by a peculiar shape and the occurrence in the cortex of the sword shortened fusiform strongyloxeas. The species is akin to a group of Mexican species subsequently described herein and to *T. californiana* De Laubenfels, 1932 (Sarà & Corriero 1993). *Tethya ensis* differs from *T. californiana* in body shape and cortical structure and in some significant spicular traits: the megascleres are strongyloxeas instead of anisostrogyles (but a Mexican population of *T. californiana* subsequently described herein also has strongyloxeas); the occurrence of peculiar sword shortened strongyloxeas which are absent in *T. californiana*; and the larger size and the lower R/C of its megasters that are spherasters instead of oxy-spherasters.

*Tethya mexicana*, new species  
Figs. 2C–G, 5–7, 15C, Table 3

*Material examined*.—Holotype: MSNG 50192; paratype: LEB-ICML 256; 75 specimens from Punta Maldonado (Guerrero), Feb 1982 and 10 specimens from Petacalco Bay (Guerrero), Apr 1982, 45 m depth. Adhered to bryozoans and calcareous fragments on sand and sand-mud-clay bottom; 43 specimens from Punta Arboleda (Gulf of California), Jul 1985, 22 m depth.

*Description*.—The type is irregularly ellipsoidal, cushion-like, with two opposite faces 3 by 2 cm, both covered by irregularly rounded tubercles, 1–3 mm in diameter, 0.5–2 mm in height. The thickness of the cushion is 1.5 cm. Long filamentous rooting processes are at one side of the faces, suggesting that in life the specimen was erect 2 cm high and 3 cm broad. Some elongated tubercles with spear like buds are on the top. On the whole, body variable in shape,

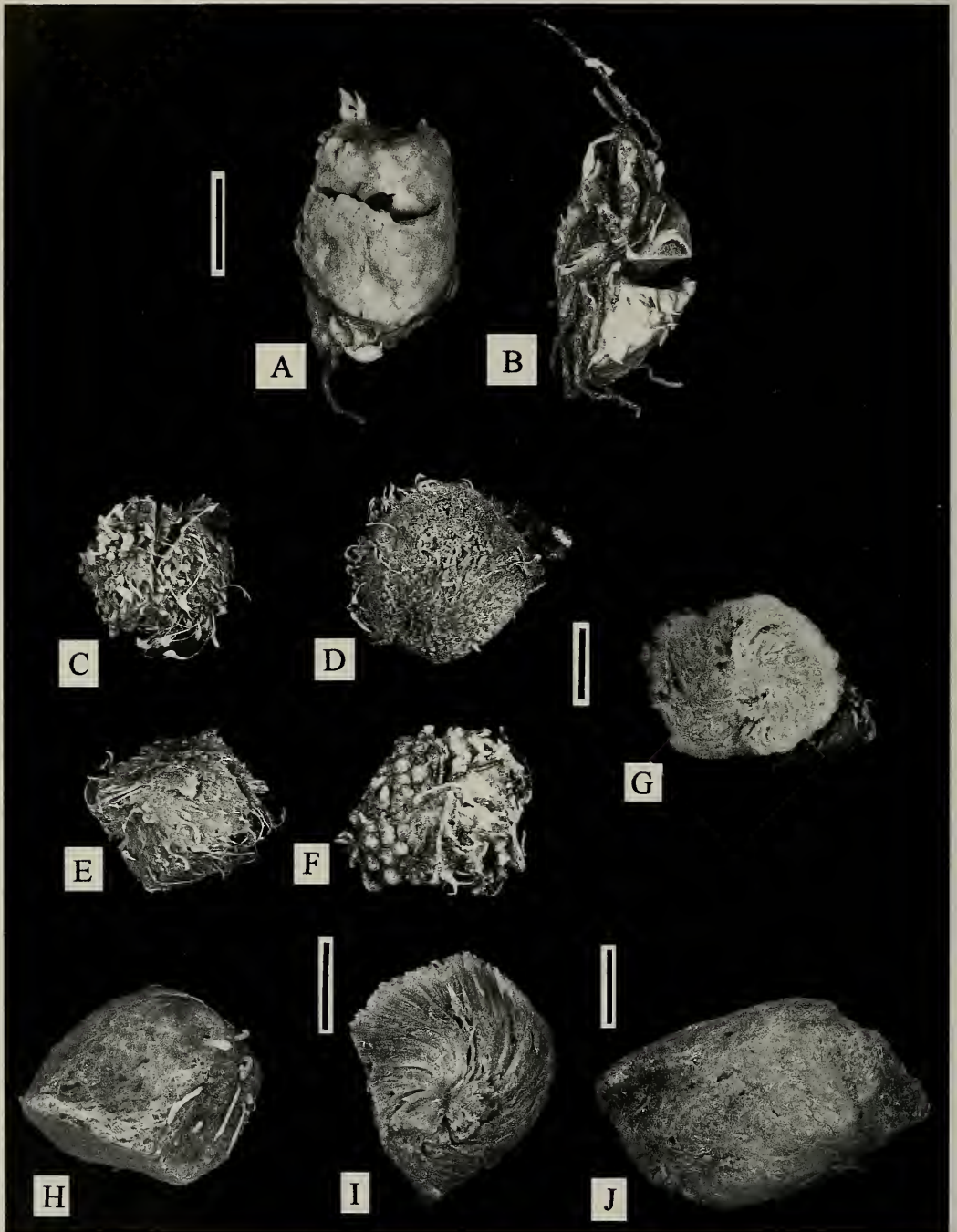


Fig. 2. A, B: *Tethya ensis*, new species. A, Holotype; B, Paratype. C–G: *Tethya mexicana*, new species. C–E, Three specimens from Gulf of California; F, Holotype from Guerrero; G, Transverse section of another specimen from Guerrero showing coiled skeleton and a central nucleus. H–J: *Tethya paroxeata*, new species. H, Holotype lateral view; I, Holotype, transverse section showing a coiled skeleton radiating from an asymmetrical center; J, Another specimen, lateral view. Scale bars = 1 cm.

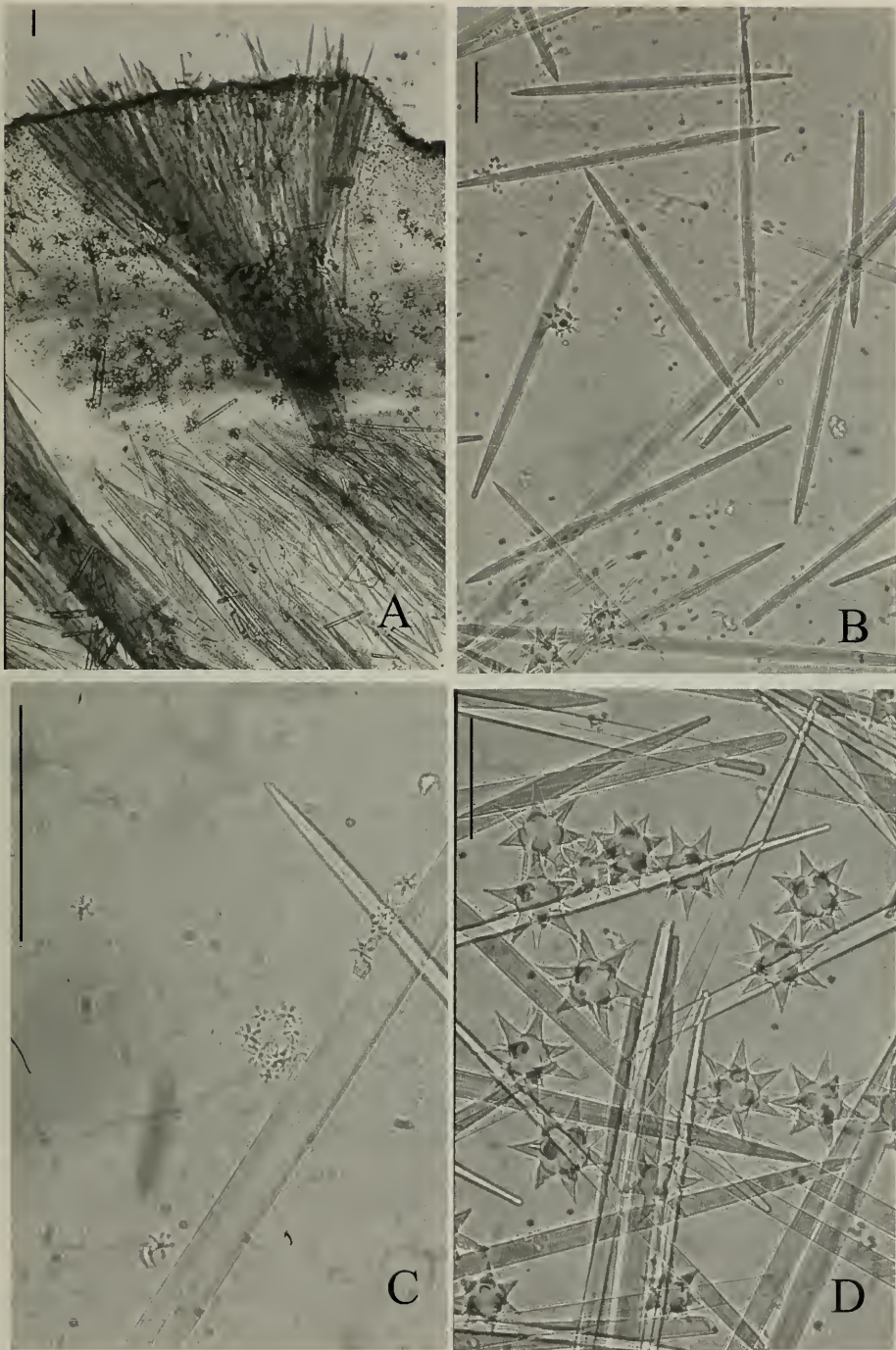


Fig. 3. *Tethya ensis*, new species. Light microscopic photographs. A, Skeletal structure of tubercle; B, Fusiform strongyloxeas and some megasters; C, Micrasters; D, Megasters and megasclere endings. Scale bars = 100  $\mu\text{m}$ .

Table 2.—Measurements of spicules of *Tethya ensis* ( $\mu\text{m}$ ). Underlined numbers indicate mean values.

Specimens	Megascleres						R/C	Micrasters Diameter
	Main		Auxiliary		Megasters			
	Length	Width	Length	Width	Diameter			
1 (Holotype)	1056-1611-2115	15-30-47	319-443-609	12-17-26	381-571-972	37-81-106	0.4-0.7-1.0	5.9-10.5-16.5
2	1006- <u>1623</u> -2312	8-24-45	364- <u>510</u> -720	11-17-24	318- <u>603</u> -980	27- <u>87</u> -115	0.4-0.6-0.8	8.3- <u>11.6</u> -15.3
3	1005- <u>1586</u> -2280	6-26-36	270-493-780	10-15-22	300- <u>545</u> -970	42- <u>77</u> -106	0.5-0.7-1.1	9.0- <u>12.1</u> -14
4	1342-1714-2290	18-29-35	247- <u>513</u> -777	10-16-21	260- <u>551</u> -990	46- <u>76</u> -98	0.4-0.6-0.9	10.0- <u>11.9</u> -13.5
5	1000-1599-2100	10-27-36	225-472-965	10-15-23	390- <u>735</u> -985	34- <u>67</u> -106	0.4-0.6-0.8	8- <u>11.6</u> -13

with irregularly hemispherical, ellipsoidal or polyhedral specimens, 0.8–4 cm in diameter and 0.5–2.5 cm in height (Fig. 2C–G). Color orange when alive, dirty white or brownish in ethanol. Consistency firm, slightly compressible. Surface tuberculate, with irregularly rounded or roughly polygonal tubercles 1–3 mm in diameter, 0.5–2 mm in height irregularly spaced and unevenly developed in Guerrero specimens, sometimes flattened, sometimes papillose, covered by sand in the Gulf of California specimens, others are scarcely visible with a surface covered by several stalked buds 2 cm long, and several with visible oscules. Specimens from Guerrero, as in the type, have on the basis and edges of the body flattened or filamentous rooting processes 10–16 mm long by 1–10 mm wide. Cortex (Fig. 5C, D), including tubercles, 2–4 mm thick. Spicular tufts hispidating the tubercles supported by bundles of strongyloxeas with a diameter of 300–480  $\mu\text{m}$  in the cortex and 350–950  $\mu\text{m}$  in the choanosome.

*Skeleton*.—The megasclere tracts branch at different levels of the choanosome (Fig. 5B). The interstices among the tracts in the upper part of the choanosome are filled with bundles of auxiliary megascleres. Megasters are placed densely in the central and lower parts of the cortex that shows several lacunes (Fig. 15C), although it is less lacunar than *Tethya californiana*. In some specimens the megasclere tracts are coiled and sometimes they depart from a central nucleus (Fig. 2G). The nucleus, about 5 mm in diameter, is made up of an irregular network of small styles and subtylostyles (Fig. 5A).

*Spicules*.—Table 3 summarizes measurements taken from three specimens of Guerrero and three specimens from the Gulf of California. Megascleres (Figs. 6A, 7B) are main strongyloxeas and auxiliary (cortical) strongyloxeas with intermediates among the two categories. Maximal length is 2130  $\mu\text{m}$  and thickness 41  $\mu\text{m}$ . The nucleus of some specimens presents heterogeneous styles

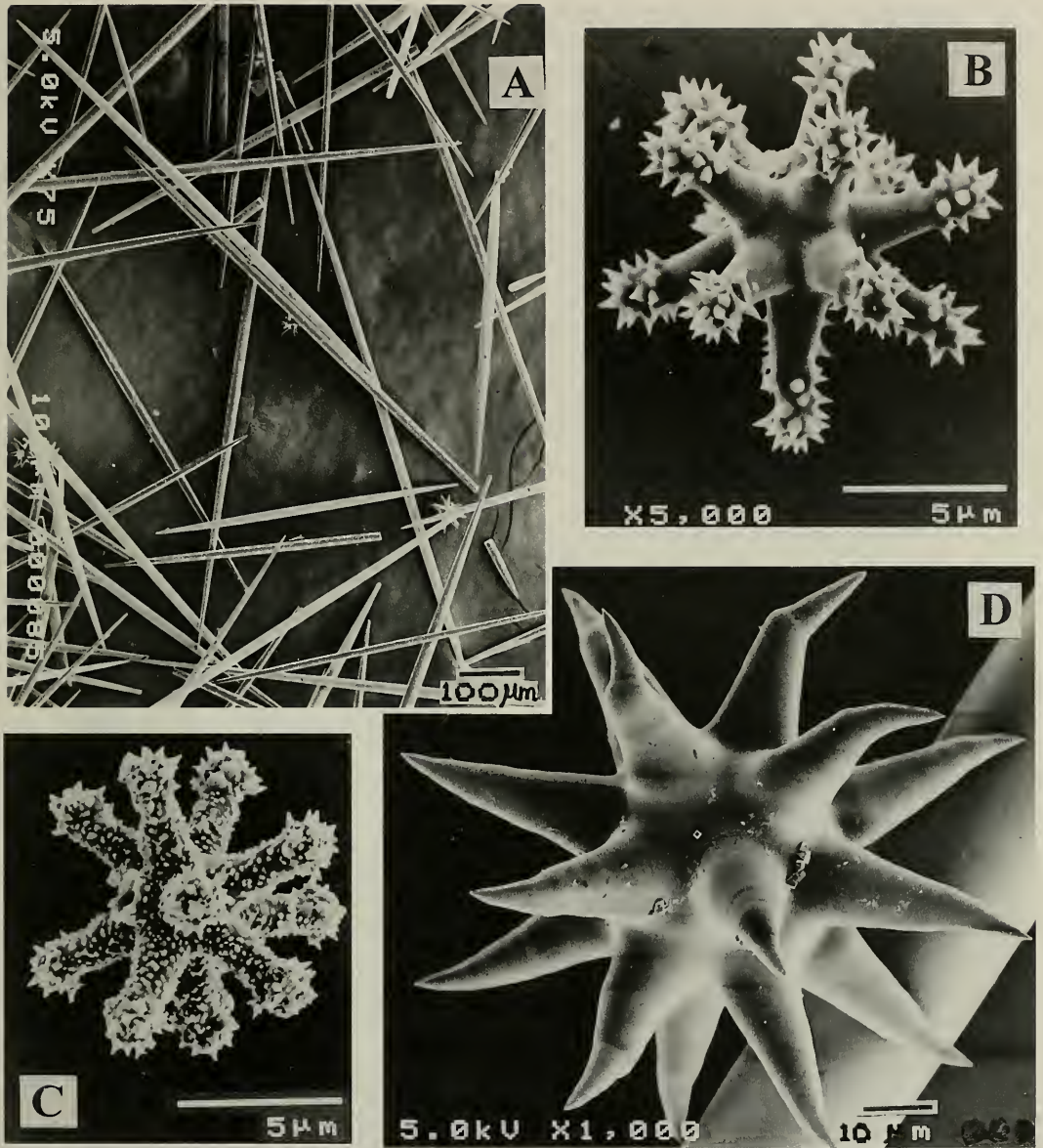


Fig. 4. *Tethya ensis*, new species. SEM micrographs. A, Megascleres and some megasters; B, Tyloster (more frequent); C, Chiaster (less frequent); D, Spheraster.

and subtylostyles frequently somewhat curved, 300–800 by 10–18  $\mu\text{m}$ .

Megasters (Figs. 6A, 7C) are spherasters-oxyspherasters: heterogeneous in size and shape, they vary also among the species. The main size range is 70–120  $\mu\text{m}$  (maximum 128  $\mu\text{m}$ ) and R/C range 0.7–1.2 (maximum 1.4). Two specimens from Punta

Arboleda (Gulf of California) show sharp differences. The main size range is 60–75  $\mu\text{m}$  and the main R/C range respectively, 0.5–0.7 and 0.7–0.9. Ray number 16–18, frequently bent, sometimes twisted or forked.

Micrasters: Mainly strongylasters (chiasmers) but variable from slender tylostasters with

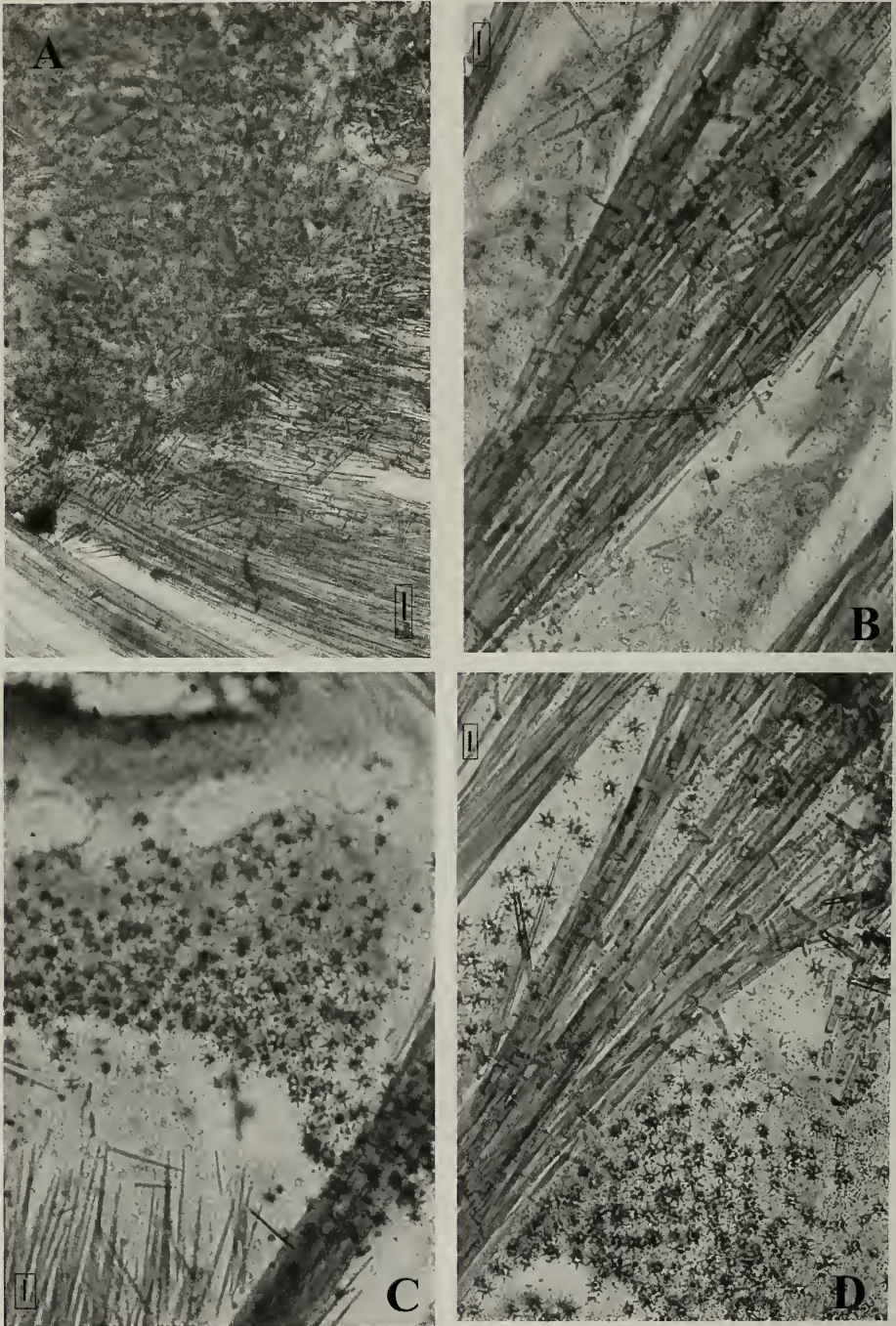


Fig. 5. *Tethya mexicana*, new species. Details of structure. A, Nucleus skeleton; B, Branching of a megasclere bundle in the choanosome; C, Cortical structure; D, Cortical structure with megasclere fans. Scale bars = 100  $\mu\text{m}$ .



Table 3.—Measurements of spicules of *Tethya mexicana* ( $\mu\text{m}$ ). Underlined numbers indicate mean values.

Specimens	Megascleres				Megasters		R/C	Micrasters Diameter
	Main		Auxiliary		Diameter	R/C		
	Length	Width	Length	Width				
1 (Holotype) (Guerrero)	1020-1339-2010	14-23-40	339-547-971	4-14-26	48-97-127	0.5-0.8-1.2	6.8-11.4-15.5	
2 (Guerrero)	1000-1522-2070	14-26-36	359-670-990	5-16-38	36-85-108	0.7-1.0-1.4	8.0-11.6-15.5	
3 (Guerrero)	1033-1428-1820	18-29-39	360-656-985	5-15-23	70-102-130	0.6-0.9-1.4	8.5-11.6-15.5	
4 (P. Arboleda)	1000-1564-2105	16-29-41	347-745-990	4-12-23	49-64-78	0.3-0.6-1.0	8.0-11.3-15.0	
5 (P. Arboleda)	1000-1568-2130	9-28-39	250-725-978	4-12-21	23-59-93	0.5-0.7-1.1	8.0-11.3-15.0	
6 (P. Arboleda)	1002-1340-2021	10-20-34	494-808-999	6-15-24	59-99-128	0.6-0.9-1.3	5.2-8.7-12.5	

slightly knobbed rays to slightly tylote oxyasters. Sometimes with a more or less developed center. They are in the cortex and in the choanosome alike, generally 8–13  $\mu\text{m}$  in diameter (maximum 15.5 and minimum 5.2), with 8–14, generally 12, thin rays (Figs. 6B, 7A, D).

*Etymology*.—Named after its origin, the Mexican waters.

*Remarks*.—*Tethya mexicana* is characterized by a variable, generally depressed, body shape, uneven tuberculate cortex, sometimes with long stolons as in *T. ensis*, sometimes with buds, large and variable in size, spherasters-oxyspherasters with rays frequently bent, micrasters similar in the cortex and in the choanosome varying from a slightly tylote oxyaster to strongylaster shape or true slender tylasters. There is some intraspecific variability in spiculation, with differences especially among the specimens of Guerrero and Punta Arboleda. One of the Arboleda specimens (6) is characterized by smaller megascleres and micrasters (Table 3). The general structure and the spicular traits have several affinities with *T. ensis* but also some remarkable differences: the body shape even if variable, is not elongated hemispherical as in *T. ensis*; the skeletal structure shows a branching of megasclere tracts and interstitial strongyloxeas which are absent in *T. ensis*; the sword-like strongyloxeas of *T. ensis* are lacking in *T. mexicana*; the megasters (spherasters-oxyspherasters) are considerably larger in *T. mexicana* and with a greater R/C than in *T. ensis*. *Tethya mexicana* is also similar to *T. californiana* but differs in some important traits: the body shape is not spherical, has uneven tubercles and different cortical structure; the denser distribution of megasters in the lower cortex; the presence of strongyloxea instead of anisotstrongyle type of megasclere; a greater size, lower R/C and lower ray number of its megasters; the more slightly tylote oxyaster type of its micrasters; and the lack of spherules.

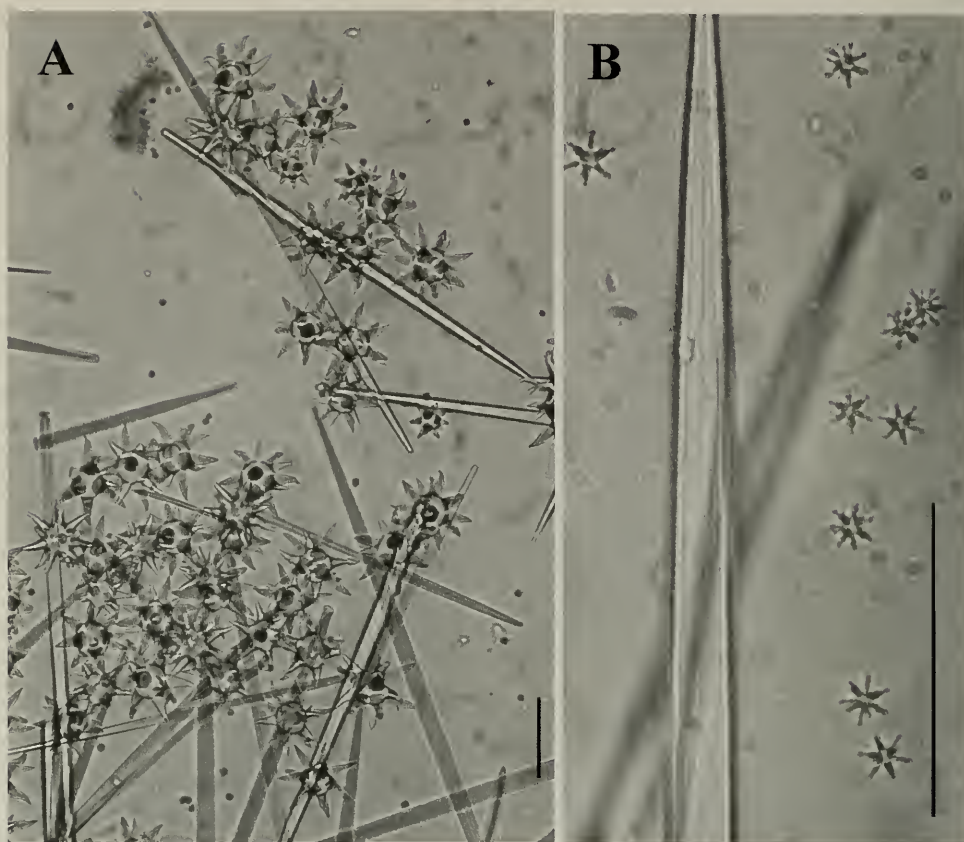


Fig. 6. *Tethya mexicana*, new species. Light microscopic photographs. A, Megasters; B, Micrasters. Scale bars = 100  $\mu$ m.

*Tethya ovum*, new species

Figs. 8A, B, 9, 10, 15B, Table 4

*Material examined.*—Holotype MSNG 50193; paratype: LEB-ICML 257; 4 specimens from Petacalco Bay (Guerrero), Apr 1982, 45 m depth.

*Description.*—The type is ovoidal 11 mm in diameter and 17 mm in height. On the whole, 10–17 mm in diameter, 15–25 mm in height (Fig. 8A). Color, not recorded alive, dirty white in ethanol. Consistency hard. Surface strongly tuberculate, tubercles irregularly spaced, uneven, microhispid, sometimes smooth: 1–4 mm in diameter, 1–2 mm in height. Cortex, including tubercles, 3–4 mm thick.

*Skeleton.*—Megasclere bundles less than 500  $\mu$ m in diameter, sometimes a little

coiled, radiating from the center to the cortex (Fig. 8B). Smaller fusiform subtylote strongyloxeas occur in the tubercle fans. Megasters are placed mainly in the lower cortex as a narrow continuous belt around the choanosome (Fig. 15B). Micrasters are similar in the cortex and in the choanosome.

*Spicules.*—Table 4 summarizes measurements taken from two specimens. Main and auxiliary megascleres are slightly subtylote strongyloxeas. Maximum size of main megascleres is 1885 by 39  $\mu$ m. Shortened cortical sword-like megascleres are fusiform, with the head 8–10  $\mu$ m thick and the greater thickness 10–27  $\mu$ m, in the central and distal parts of the spicule (Figs. 9A, 10A).

Megasters: Spherasters and oxyphas-

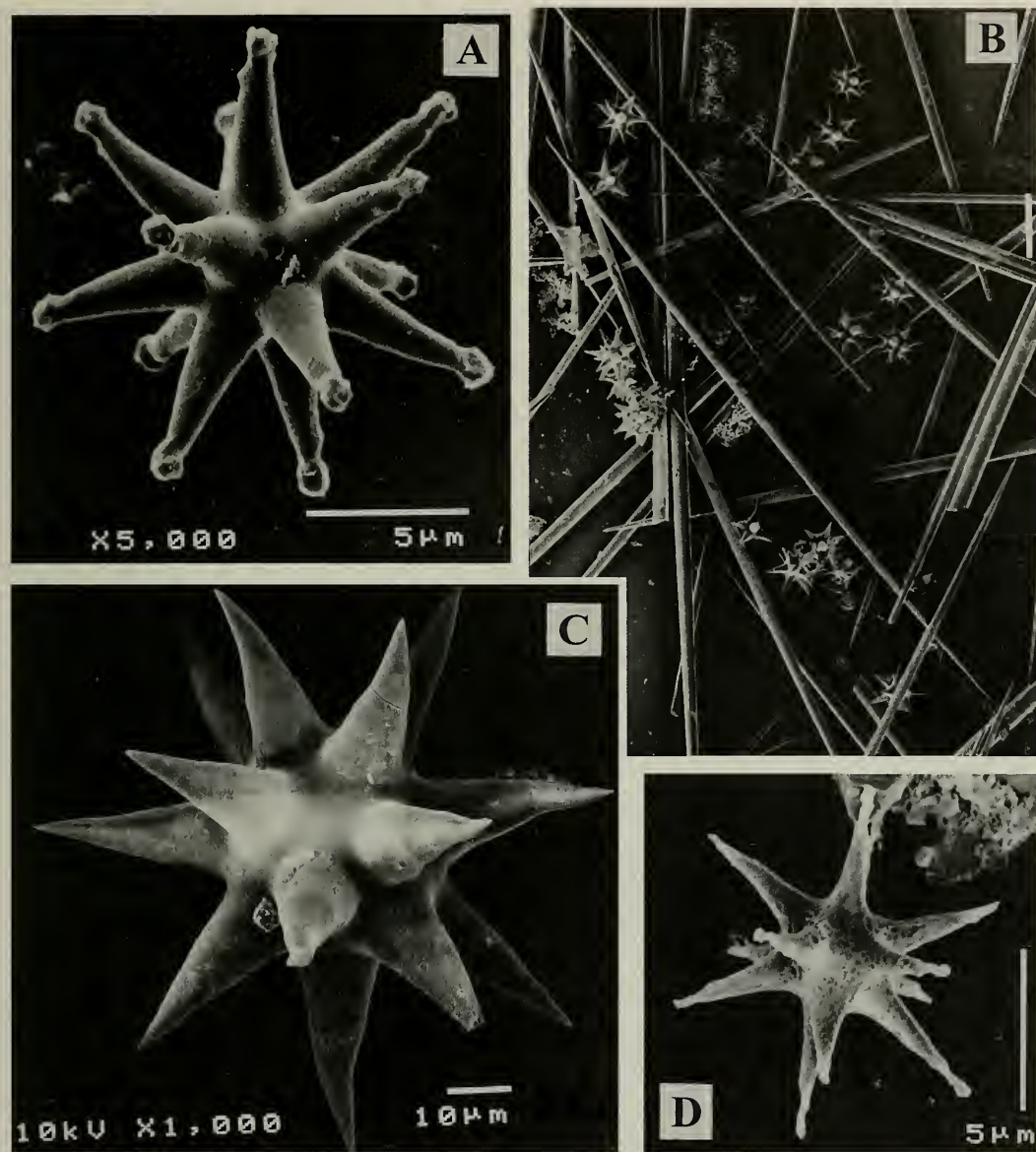


Fig. 7. *Tethya mexicana*, new species. SEM micrographs. A, D. Oxyasters with slightly tyloate ends (more frequent); B, Megascleres and several megasters; C, Megaster.

ters show a main size range of 75–100 μm (maximum 110 μm), and R/C 0.7–1.2 (maximum 1.5), with about 18 rays generally bent and frequently spined or bifid (Figs. 9B, 10D).

**Micrasters:** Mainly strongylasters (chiasmasters), but they vary from slender tylasters with slightly knobbed rays to slightly tyloate

oxyasters. Size: 8–13 μm in diameter, with about 12 thin rays, in the cortex and choanosome alike (Figs. 9C, 10B, C).

**Etymology.**—From latin *ovum* = egg, in reference to the ovoid shape of the body, an unusual character in *Tethya*; here used as a noun in apposition.

**Remarks.**—*Tethya ovum* is similar to *T.*

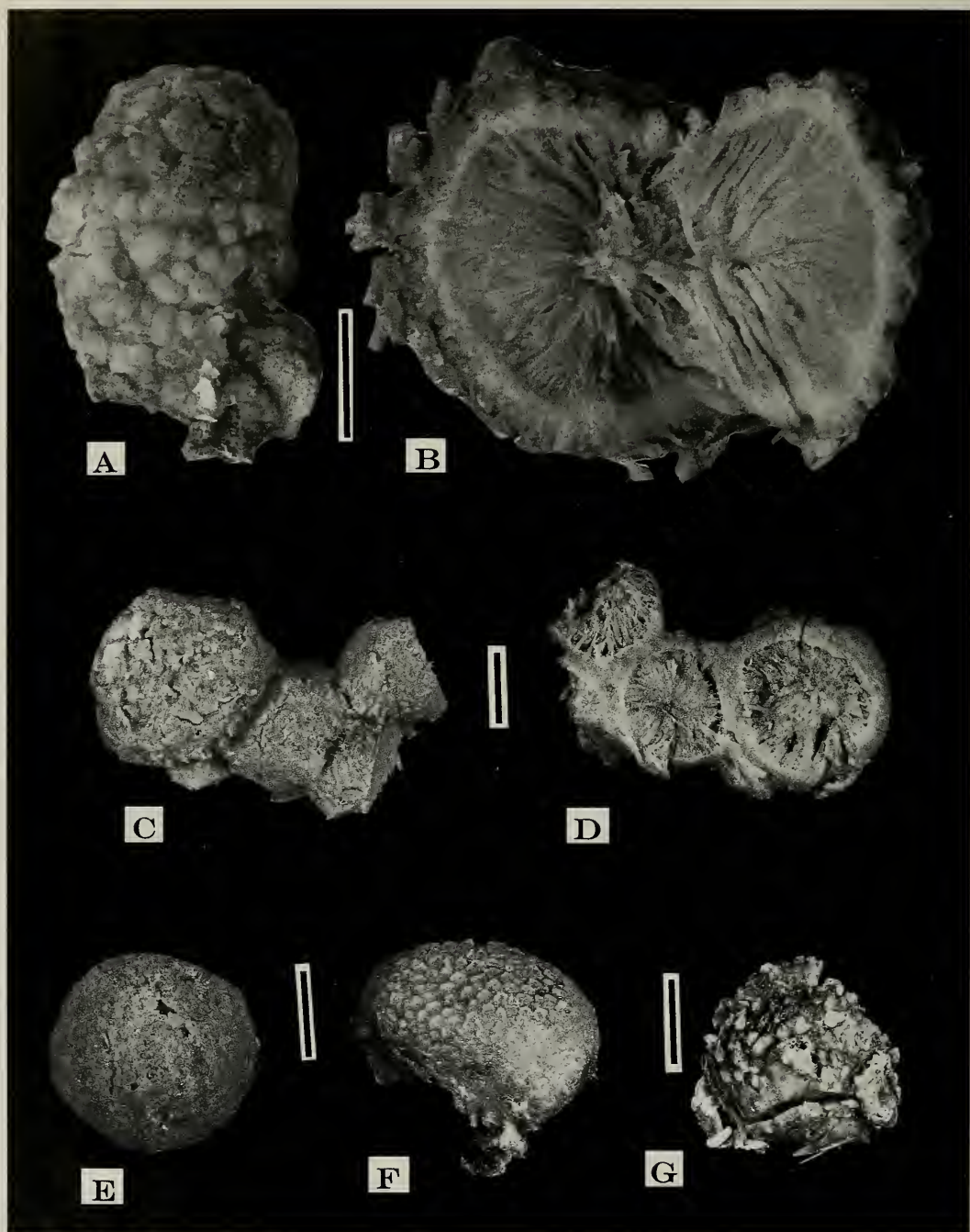


Fig. 8. A, B: *Tethya ovum*, new species. A, Lateral view of paratype; B, Transverse section of the same. C, D: *Tethya socius*, new species. C, Upper view of holotype; D, Basal view of the same. E, F: *Tethya californiana* De Laubenfels, two specimens showing differences of tuberculate surface. G: *Tethya taboga* (De Laubenfels) upper view. Scale bars = 1 cm.

Table 4.—Measurements of spicules of *Tethya ovum* ( $\mu\text{m}$ ). Underlined numbers indicate mean values.

Specimens	Megascleres						Megasters		Micrasters Diameter
	Main		"Sword" stronglyloxeas		Auxiliary		Diameter	R/C	
	Length	Width	Length	Width	Length	Width			
1 (Holotype)	1007-1375-1693	8-23-36	357-573-996	10-15-23	400-696-996	2-7-10	28-77-106	0.2-0.8-1.2	6.3-9.7-13.2
2	1005-1490-1885	14-30-39	385-649-960	10-19-27	754-814-875	8-8-8	70-92-110	0.7-1.0-1.5	8.0-11.1-13.0

*ensis* and to *T. mexicana* but is well characterized by its ovoidal shape and strongly tuberculated surface. It shares with *T. ensis* the sword-like category of stronglyloxeas, but these are clearly distinct because their head diameter is 8–10  $\mu\text{m}$  instead of 4–8  $\mu\text{m}$ . The megasters are spherasters-oxyspherasters similar to those of *T. mexicana* but generally bent and frequently adorned by forks and spines while the skeleton structure is more alike to *T. ensis*. *Tethya ovum* differs from *T. californiana* in all the traits discussed for *T. ensis* and *T. mexicana*.

*Tethya paroxeata*, new species  
Figs. 2H–J, 11, 12, 15D, Table 5

*Material examined*.—Holotype MSNG 50194; paratype LEB-ICML 258; 6 specimens from Punta Arboleda (Gulf of California), Jul 1985, 22 m depth.

*Description*.—The type is irregularly polyhedral 2 cm high with flattened basis and six faces, 2 by 2 cm. The origin of the radiate bundles of the megascleres is a central nucleus near the surface of a lateral face, and the bundles are then strongly coiled towards the opposite face (Fig. 2I). In other four specimens, the body shape is irregularly polyhedral 1.5–3 cm at the base, 1–2.5 cm in height (Fig. 2H,J), and in two specimens hemispherical with a diameter of 2.5 cm. Color orange when alive. Consistency compact but not hard. Surface with small flattened and contiguous tubercles, 1–1.5 mm in diameter in two specimens, larger (2 mm) but more flattened and surface nearly smooth in the other three specimens. Many sand particles on the surface. With stalked buds (stalks 1 cm long). Tubercles 0.5 mm high, cortex (without tubercles) 1.5 mm thick, very lacunar under the sponge surface (Fig. 15D).

*Skeleton*.—Megasclere tracts, 280–630  $\mu\text{m}$  thick, run compact to the tubercles forming little-developed fans (Figs. 11A, 15D). Some tracts, however, branch in the inner part of the choanosome. Auxiliary

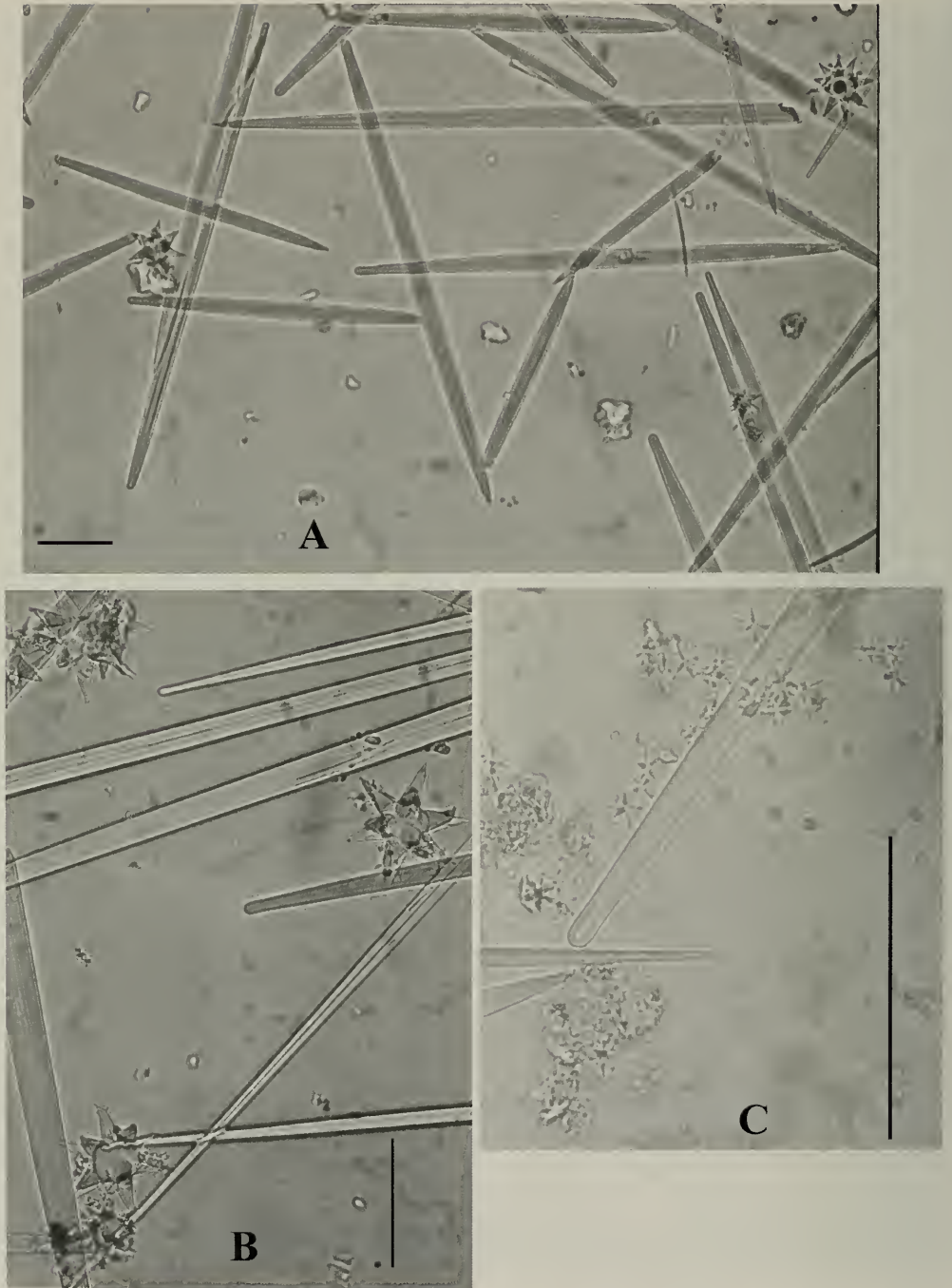


Fig. 9. *Tethya ovum*, new species. Light microscopic photographs. A, Fusiform strongyloxeas and three megasters; B, Spined and forked megasters with parts of megascleres; C, Micrasters and points of megascleres. Scale bars = 100  $\mu\text{m}$ .

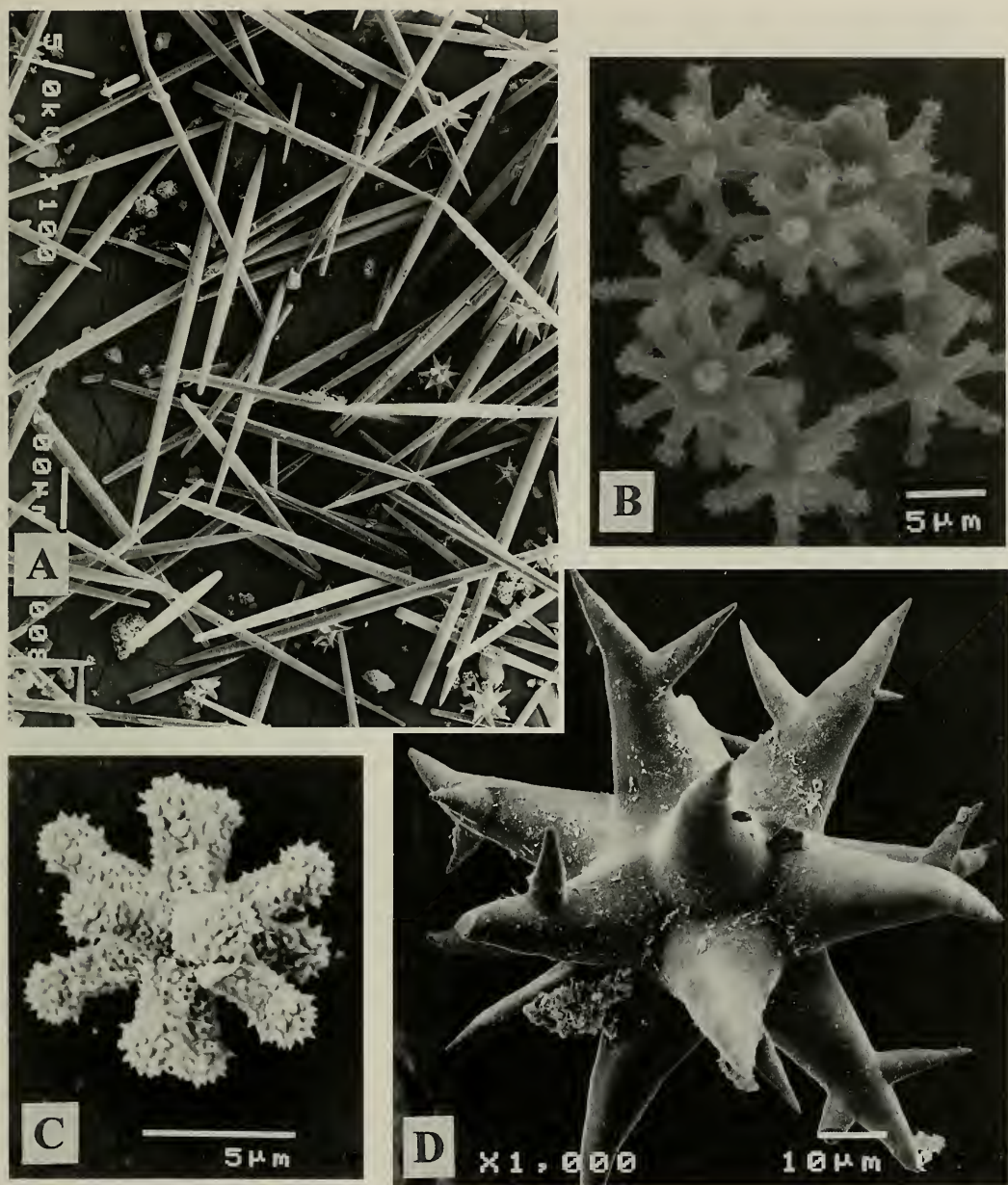


Fig. 10. *Tethya ovum*, new species. SEM micrographs. A, Megascleres and megasters; B, Tylostera (more frequent) with one chiaster at middle left; C, Chiaster (less frequent); D, Megaster.

megasclere bundles occur in the upper choanosome in some interstices among the main megasclere tracts. Megasters are irregularly and not densely distributed in the middle and inner cortex, more dense in the middle part (Fig. 15D). The surface is coated with a dense layer of micrasters.

*Spicules.*—Table 5 summarizes measurements taken from five specimens. Megascleres are fusiform stronglyloxeas. Several middle-sized (1000–1300 by 10–20  $\mu\text{m}$ ), and the great majority of the small (300–1000 by 1–20  $\mu\text{m}$ ) megascleres are oxeiform with a very thin (0.5–3.5  $\mu\text{m}$  thick)

rounded or tylote head (Figs. 11C, 12B). It is not easy to distinguish between main and auxiliary megascleres because there is a continuous range in their length (283–2620  $\mu\text{m}$ ), thickness (1–50  $\mu\text{m}$ ) and head width (0.7–22  $\mu\text{m}$ ), and these parameters are not always correlated. Moreover, large and small megascleres are associated in the same bundle. Some measurements (head thickness in brackets): 2620 by 45  $\mu\text{m}$  (15), 2500 by 45  $\mu\text{m}$  (18), 2250 by 50  $\mu\text{m}$  (20); 1880 by 40  $\mu\text{m}$  (10); 1840 by 40  $\mu\text{m}$  (10); 1550 by 38  $\mu\text{m}$  (22); 1240 by 10  $\mu\text{m}$  (2), 950 by 20  $\mu\text{m}$  (5); 900 by 7  $\mu\text{m}$  (1.5); 830 by 8  $\mu\text{m}$  (2.5); 770 by 6  $\mu\text{m}$  (1); 670 by 5  $\mu\text{m}$  (1). There are also strongyles, (one with the rounded head of the transformed strongyloxa a little tylote, 1050 by 35  $\mu\text{m}$  (20), another 1135 by 35  $\mu\text{m}$  (15) and anisotrongyles. The measurements reported in Table 5 refer to a conventional figure to distinguish between main and auxiliary megascleres at a length of 1000  $\mu\text{m}$ . The larger megascleres (maximum size 2620 by 50  $\mu\text{m}$ ) have a head generally slightly tylote thick 10–22  $\mu\text{m}$ , and a distal end generally well pointed, sometimes slightly rounded. In contrast, the middle-sized and smaller megascleres are also fusiform, but looking like oxes for their very thin (0.5–3.5  $\mu\text{m}$ ) and generally slightly tylote head.

Megasters (Figs. 11D, 12A): Spherasters, sometimes oxyspherasters, with the main range 40–70  $\mu\text{m}$  (maximum 91  $\mu\text{m}$ ) in diameter. R/C range, more frequently 0.6–1 (maximum 1.5). Ray number: 16–20, rays sometimes slightly bent or bifid. Spherasters, not abundant, are variable in size and shape in the same specimen and among the specimens.

Micrasters (Figs. 11B, 12C, D): Similar in the cortex and in the choanosome. Mainly strongylasters (chiasters) but variable from tylasters with slightly knobbed rays to slightly tylote oxyasters. Size: 8–13  $\mu\text{m}$  (minimum 4, maximum 15.5  $\mu\text{m}$ ) in diameter. Ray number: 12–14. Often a center is more or less developed.

*Etymology.*—From the Greek prefix *para*

Table 5.—Measurements of spicules of *Tethya paraxeata* ( $\mu\text{m}$ ). Underlined numbers indicate mean values.

Specimens	Megascleres			Megasters		Micrasters Diameter	
	Main Length	Width	Length	Auxiliary Width	Diameter		R/C
1 (Holotype)	1010-1369-2620	10-21-50	315-682-998	1-7-20	19-50-71	0.4-0.8-1.1	4.7-8.9-13.5
2	1014-1344-1963	9-20-32	419-718-982	6-11-18	26-55-69	0.3-0.7-1.0	4.0-7.6-11.8
3	1000-1616-2289	8-31-48	420-687-980	8-14-23	26-53-83	0.5-0.6-1.0	8.0-11.9-15.5
4	1000-1572-2280	8-28-43	400-733-995	5-13-24	28-53-70	0.5-0.8-1.3	8.0-11.5-15.0
5	1000-1513-2120	21-27-36	283-678-990	5-12-21	27-62-91	0.5-0.8-1.5	8.0-11.6-15.0



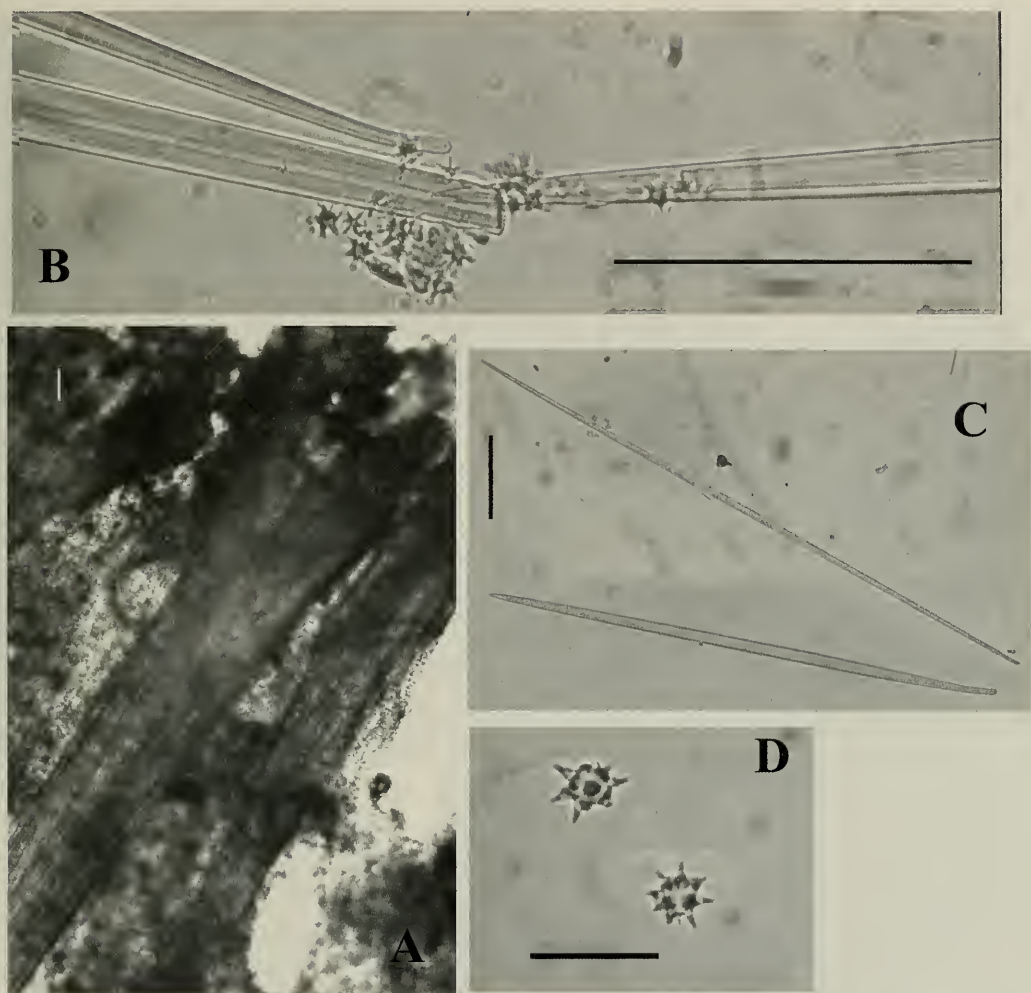


Fig. 11. *Tethya paroxeata*, new species. Light microscopic photographs. A, Cortical structure; B, Micrasters; C, Slender stronglyxeas; D, Megasters. Scale bars = 100  $\mu$ m.

= beside, nearby + *oxeata* = relating to an oxea, Neolatin from Greek *oxys* = sharp, in reference to the ends, both thin, of the small megascleres.

*Remarks.*—*Tethya paroxeata* is similar to *T. ensis*, *T. mexicana* and *T. ovum* but is clearly distinguished by its peculiar polyhedral shape and even surface. The same type of shape and surface may occur rarely in some specimens of *T. mexicana* from the same locality (Punta Arboleda) but less pronounced. *Tethya paroxeata* is clearly distinguished from similar species

by the peculiar oxeiform shape of the greater majority of the shorter megascleres. The spherasters, rarely oxyspherasters, are smaller than in *T. ensis*, *T. mexicana* and *T. ovum*. Spicular intraspecific variability is shown by specimen two which is characterized by smaller micrasters (Table 5). *Tethya paroxeata* differs from *T. californiana* in body shape, cortical surface and structure and occurrence of the oxeiform megascleres, in addition to the other traits listed for *T. ensis*, *T. mexicana* and *T. ovum*.

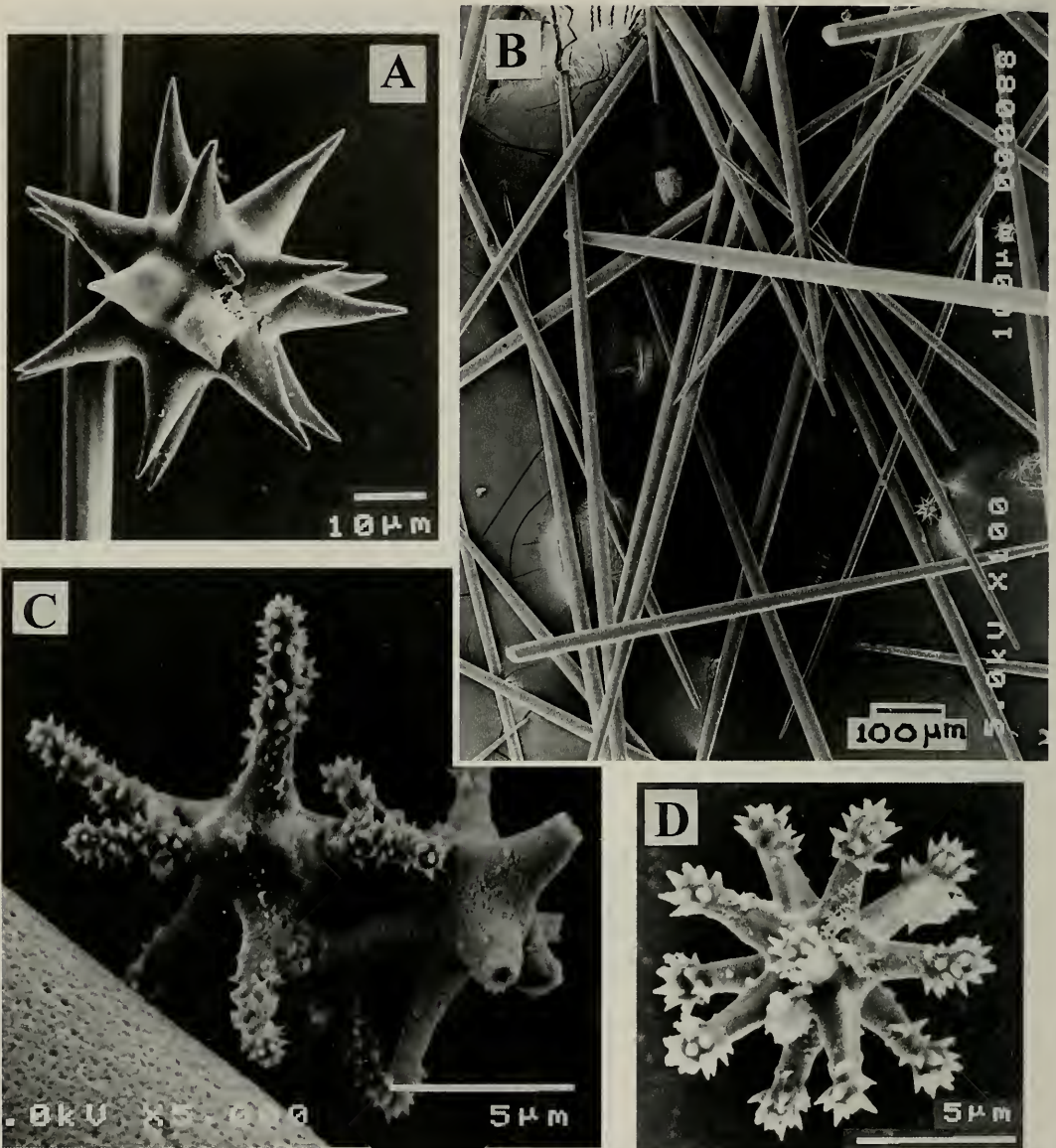


Fig. 12. *Tethya paroxeata*, new species. SEM micrographs. A, Megaster; B, Megascleres; C, Strongylasters (less frequent); D, Tylaster (more frequent).

*Tethya socius*, new species

Figs. 8C, D, 13, 14, 15E, Table 6

*Material examined*.—Holotype MSNG 50195; 1 specimen (composed of 4 fused individuals) from Puerto Libertad (Gulf of California), Oct 1985, intertidal.

*Description*.—The type is made by 4 fused spherical depressed individuals of 2,

1.5, 1.2 and 1 cm in diameter and 1–1.2 cm in thickness. On the whole, the specimen measures 4 by 3 by 1–1.2 cm in thickness (Fig. 8C, D). Color: pale pink in ethanol. Consistency soft, rather compressible. Lacunes in the outer cortex and in the outer choanosome under the cortex (Fig. 15E). Surface with contiguous tubercles of irreg-

ular shape and different size, 1–3 mm wide, flattened and with slightly winding outlines. Cortex with the tubercles, 2–2.5 mm thick. The body of all the individuals has a strong central nucleus, about 6 mm in diameter, from which the megasclere bundles radiate.

*Skeleton.*—The megasclere tracts may split, as in *T. mexicana*, before reaching the cortex. Different megasclere bundles may also support the same tubercle. Terminal fans are little developed. Auxiliary megasclere bundles fill the interstices among the main tracts in the upper choanosome. Spherasters are distributed in all the cortex, more densely in the basal part, especially at the boundary with the choanosome. Some smaller megasters are in the outer part of the choanosome. The skeleton of the nucleus is made by a dense and irregular network of small styles and subtylostyles (Fig. 15E).

*Spicules.*—Table 6 summarizes measurements taken from the holotype. Megascleres (Fig. 14A): strongyloxeas little fusiform without a clear distinction between the main and auxiliary. In the table the two categories are conventionally separated on the basis of a 1000  $\mu\text{m}$  length figure. Some measurements (head thickness in brackets): 1700 by 30  $\mu\text{m}$  (10); 1350 by 18  $\mu\text{m}$  (10); 1315 by 18  $\mu\text{m}$  (10); 1250 by 22  $\mu\text{m}$  (12); 1040 by 8  $\mu\text{m}$  (5); 1030 by 18  $\mu\text{m}$  (5); 700 by 2  $\mu\text{m}$  (1). An anisostrongyle: 1460 by 28  $\mu\text{m}$  (15; 10). Maximal sizes 1700  $\mu\text{m}$  in length and 30  $\mu\text{m}$  in thickness, on the whole: 440–1700  $\mu\text{m}$  by 2–30  $\mu\text{m}$  (1–12). In the center small styles or subtylostyles heterogeneous in length and thickness and sometimes with the basal third a little curved: 150–400 by 5–20  $\mu\text{m}$ .

Megasters (Figs. 13B, C, 14B, D): Oxy-spherasters: generally 60–100 (max. 118  $\mu\text{m}$  in diameter); R/C generally 1.2–1.7 (max. 1.8, min. 0.7). Ray number: about 14, frequently bent, twisted, blunt, bifid or with spines on the rays.

Micrasters (Figs. 13B, 14C): Mainly strongylasters but variable from slightly knobbed tylasters to slightly tylote oxyasters. They are similar in the cortex and in

Table 6.—Measurements of spicules of one specimen of *Tethya socitius* ( $\mu\text{m}$ ). Underlined numbers indicate mean values.

Specimens	Megascleres				Megasters		Micrasters Diameter
	Main Length	Width	Auxiliary Length	Width	Diameter	R/C	
1 (Holotype)	1003-1206-1700	8-18-30	439-768-992	2-9-19	20-71-118	0.7-1.3-1.8	6.5-10.1-14.6

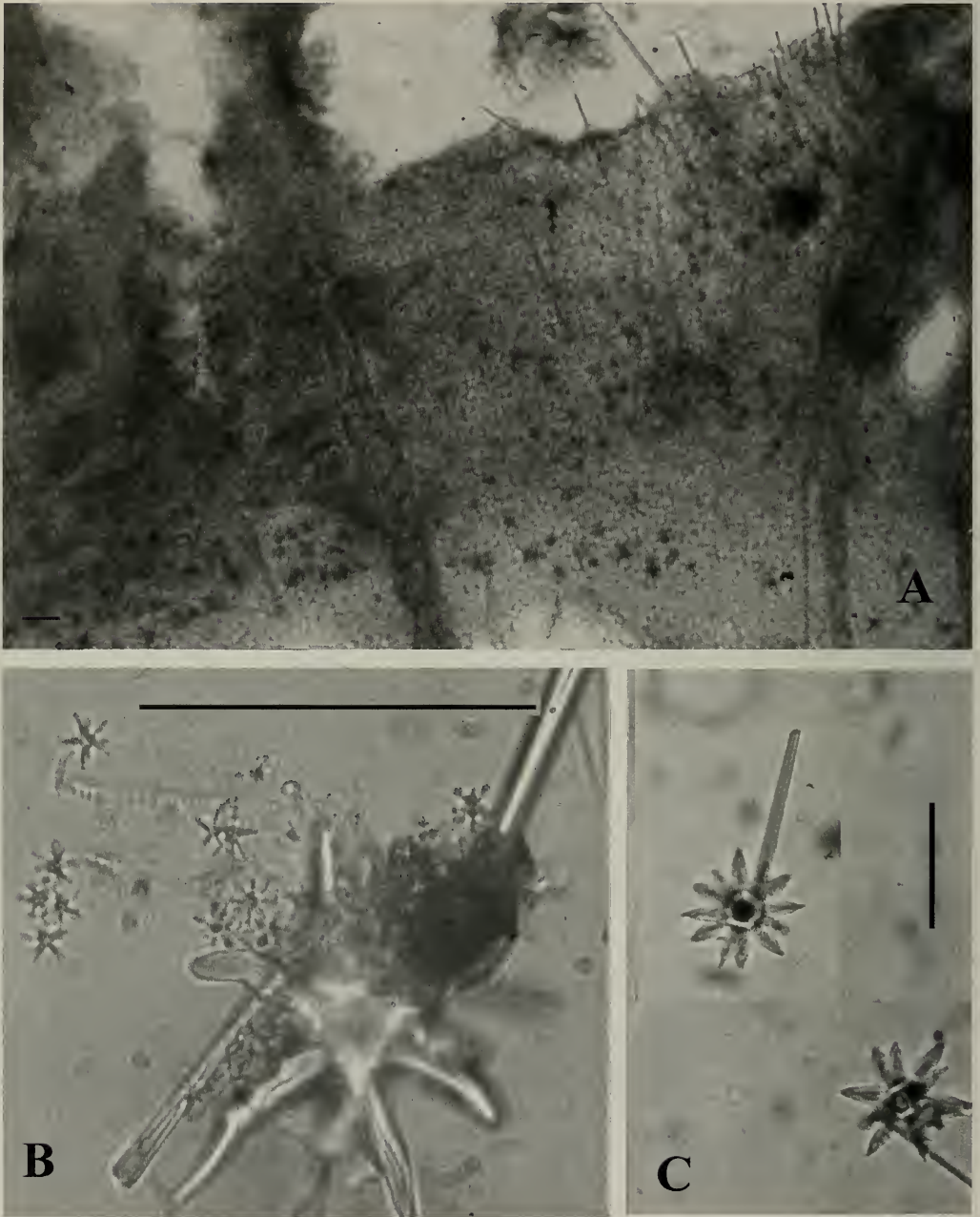


Fig. 13. *Tethya socius*, new species. Light microscopic photographs. A, Cortical structure; B, Micrasters and one megaster; C, Megasters. Scale bars = 100  $\mu$ m.

the choanosome, generally 8–12  $\mu$ m in diameter. Ray number 10–14.

*Etymology*.—From Latin *socius* = companion, in reference to the fusion of different individuals to form one specimen, un-

usual in *Tethya*; here used as a noun in apposition.

*Remarks*.—*Tethya socius* is well distinguished from the other Mexican species here described for the smaller size of the

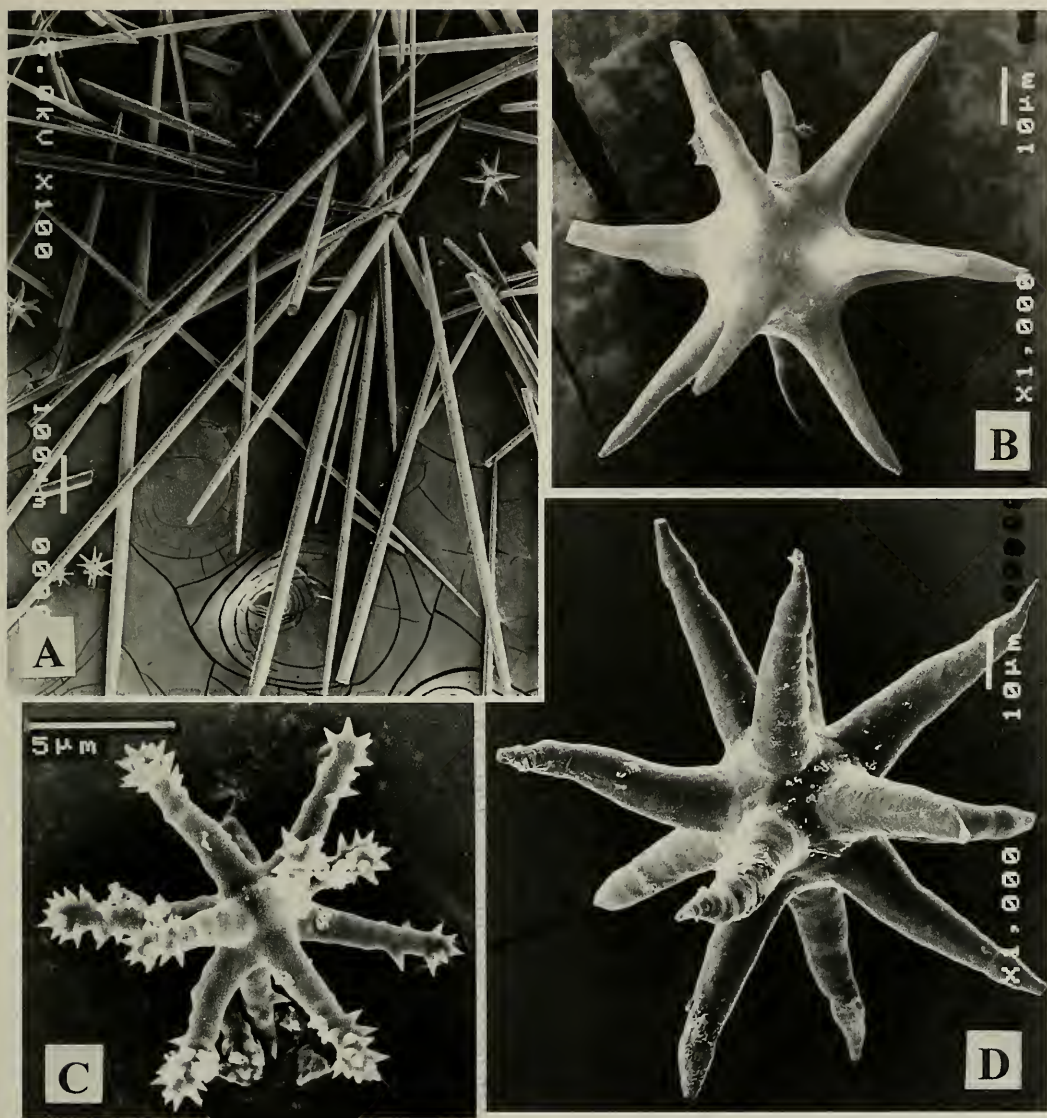


Fig. 14. *Tethya socius*, new species. SEM micrographs. A, Megascleres; B, Megaster; C, Micraster (more frequent); D, Megaster.

megascleres, the very high R/C of its oxyspherasters with rays frequently twisted, bent, blunt, bifid or with spines. Only the micrasters, similar in the cortex and in the choanosome as in the other Mexican species, are roughly alike to those of *T. ensis*, *T. mexicana*, *T. ovum*, and *T. paroxeata*. The frequent oxyasters with a small swelling at the ray tips, which occur in all these

Mexican species and also in *T. californiana*, may be compared to a similar trait in the eastern Indian Ocean *T. affinis* Kirkpatrick, 1900 and to the western Pacific *T. deformis* Thiele, 1905. Yet, in *T. affinis* the rays are longer and slenderer, and in *T. deformis* the micrasters have a well developed center. Other spicular traits of both these species are clearly different by the Mexican

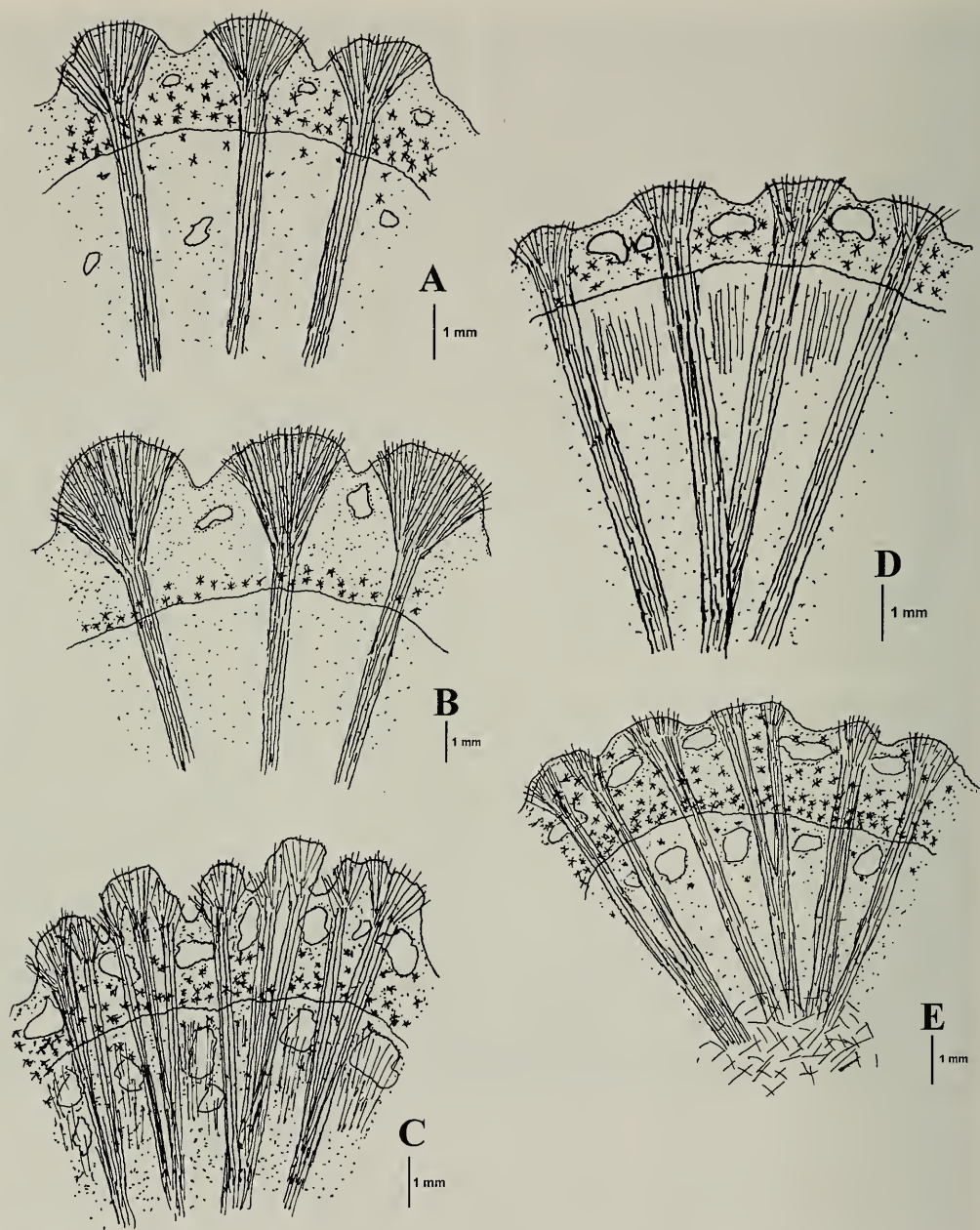


Fig. 15. Reconstruction of skeletal patterns from transverse sections of the new species of *Tethya*. A, *T. ensis*; B, *T. ovum*; C, *T. mexicana*; D, *T. paroxeata*; E, *T. socius*.

species. *Tethya socius* is also characterized by the fusion of the subspherical individuals which show a well marked central nucleus. A similar fusion of individuals is found in *T. communis* Bergquist & Kelly-

Borges, 1991 from S.E. Australia. But *T. communis* lacks the central nucleus and has oxyspherasters with shorter rays and polyrhabs, absent in *T. socius*, among the microscleres. A central nucleus has been

found also in some specimens of *T. mexicana*.

*Tethya californiana* De Laubenfels, 1932  
Fig. 8E, F, Table 7

*Tethya aurantia* var. *californiana* De Laubenfels, 1932:44

*Tethya californiana*.—Sarà & Corriero, 1993:204

*Material examined*.—54 specimens from Cabo San Miguel (Gulf of California), Mar 1985, 25 m depth.

*Description*.—Body shape spherical or sub-spherical, 0.6–3.8 cm in diameter. Surface smooth due to the very even tubercles. Color ochre yellow to orange when alive. Some specimens have round to irregular oscules on top. Consistency soft in ethanol. Cortex including the tubercles 2–2.5 mm thick. Tubercles 0.5–1.5 high, 1–3 mm broad. The irregular outlines of tubercles and the lacunar structure of the cortex and the choanosome correspond to those in the redescription of *T. californiana* in Sarà & Corriero (1993).

Megasclere bundles 300–800 μm in diameter.

*Spicules*.—Measurements of 5 specimens are summarized in Table 7. Megascleres are main and auxiliary strongyloxeas with intermediates between the two categories. Maximal size of strongyloxeas is 2375 by 43 μm. Medium-sized and small strongyloxeas have often the proximal part (head and neck) a little bent on the axis of the spicule.

Megasters: are mostly spherasters with a wide range in size and in R/C, even in the same specimen. Generally measuring between 45 and 60 μm, but minimal and maximal diameters are 20 and 83 μm. R/C generally between 0.6 and 0.8 but minimal and maximal R/C are 0.3 and 1.2. The conical rays about 24, are sometimes bifid or blunt.

Micrasters: similar in the cortex and in the choanosome are mainly microspined strongylasters, frequently as a strongylasteroxyaster type, with moderately pointed

Table 7.—Measurements of spicules of specimens of *Tethya californiana* (μm). Underlined numbers indicate mean values.

Specimens	Megascleres						Micrasters Diameter	Spherule Diameter
	Main		Auxiliary		Megasters			
	Length	Width	Length	Width	Diameter	R/C		
1	1053-1373-2017	12-21-36	407-725-983	1-4-18	25-50-68	0.4-0.7-1.2	7.9-11.3-14.8	
2	1010-1742-2375	7-26-43	286-686-976	1-7-22	23-51-66	0.4-0.7-1.1	6.7-10.0-13.5	
3	1000-1402-2090	10-26-40	270-738-995	3-11-22	26-54-83	0.4-0.6-1.0	8.0-11.8-15.5	
4	1000-1576-2340	10-26-40	307-698-990	3-11-18	21-54-78	0.4-0.7-1.1	9.0-12.3-15.5	
5	1000-1604-2100	10-29-40	270-777-995	4-13-28	20-55-75	0.3-0.6-0.09	7.5-11.7-15.0	

rays, and, less frequently, as a strongylaster-tylaster type, with slightly knobbed rays. Ray number 10–14 and, sometimes, a small center. More frequent size: 10–13  $\mu\text{m}$  (max. 15.5 and min. 6.7).

Spherules 8–13  $\mu\text{m}$ , are present in the cortex.

*Remarks.*—The Mexican population was identified as *Tethya californiana* after comparison with the type material of the species. However, it differs considerably in two traits: the megascleres are strongyloxeas instead of anisostrongyles and the megasters are generally spherasters, with R/C lower than 1, instead of oxyspherasters. Yet, some oxyspherasters with R/C = 1–1.2 occur also in the Mexican population. Other slight differences between the Mexican population and the Pacific *T. californiana* are the smaller body size, the smoother surface, and the greater spherule diameter. These differences may be due to the different geographic location of the samples. The type material comes from the Pacific coast of California, north of Los Angeles, whereas the ones described here are from the Mexican coast of the Gulf of California.

*Tethya taboga* (De Laubenfels, 1936)

Fig. 8G, Table 8

*Taboga taboga* De Laubenfels, 1936:452

*Tethya aurantia* sensu Green & Gomez, 1986:284

*Material examined.*—Punta Chile (Matatlán), 7 specimens, May 1981, 8 m depth, 2 specimens, Jun 1987, 5 m depth.

*Description.*—Body shape hemispherical, 2.5 cm in diameter, 1.5 cm in height. Surface with rounded tubercles 1–1.5 mm high and broad. Cortex including the tubercles, 2–2.5 mm thick.

Megasclere bundles are sometimes coiled from the center to the cortical surface.

*Spicules.*—Measurements of three specimens are summarized in Table 8. Megascleres are generally strongyloxeas, sometimes with stepped ends. Maximal size found for strongyloxeas is 1680 by 34  $\mu\text{m}$ .

Table 8.—Measurements of spicules of specimens of *Tethya taboga* ( $\mu\text{m}$ ). Underlined numbers indicate mean values.

Specimens	Megascleres			Megasters		Oxysasters Diameter
	Main Length	Width	Auxiliary Length	Diameter	R/C	
1	1000-1355-1680	16- <u>27</u> -34	182-698-980	30-57-70	0.3-0.5-0.8	11.5-45.6-67.5
2	1002-1329-1641	12-18-28	262-587-987	19-48-65	0.2-0.4-1.0	22.3-42.9-58.5
3	1026-1309-1602	9- <u>23</u> -32	323- <u>600</u> -987	42- <u>62</u> -74	0.2-0.4-0.6	22.2-39.2-55.0





There are also some strongyles which measured 490 by 16  $\mu\text{m}$ , 1090 by 28.5  $\mu\text{m}$ , 1123 by 27  $\mu\text{m}$ , 1268 by 25  $\mu\text{m}$  and 1450 by 30.5  $\mu\text{m}$ . Several thinner styliform strongyloxeas are slightly sinuous.

Megasters are spherasters, generally 40–60  $\mu\text{m}$  in diameter, 0.3–0.6 in R/C and 16–20 conical rays.

Micrasters are small tylasters in the cortex and larger oxyasters in the choanosome. Cortical tylasters are stout, generally 8–12  $\mu\text{m}$  in diameter with 4–8, sometimes 3, frequently irregular, microspined knobbed rays. Choanosomal oxyasters, generally 25–55  $\mu\text{m}$  in diameter, with 4–8 smooth or spined rays, frequently bent, bifid or twisted.

*Remarks.*—The identification of the Mexican *T. taboga* specimens has been made by comparison with the type material. The two samples of Mazatlán differ slightly in the spheraster diameter and R/C between them and more considerably with the Panama type. The megasters of the type have a greater size, generally 50–80  $\mu\text{m}$  and a lower R/C (0.3–0.5). Micrasters, tylasters and oxyasters, are alike in Mexican and type specimens.

#### General remarks

The Mexican Pacific species of *Tethya* here recorded, with the exception of *T. taboga*, represent a homogenous group, as indicated by the very similar micraster type. This micraster is mainly a slender strongylaster, variable, also in the same specimen, from a slightly knobbed tylaster to a slightly tylote oxyaster. This group of species may be called “californiana” from the first described species *T. californiana* De Laubenfels, 1932 and does not show any evident relationship with *Tethya* species of other regions.

Table 9 summarizes the distinctive and similar traits of these species as well as the differences with *T. taboga*. This last species belongs to the “seychellensis” group, characterized by two types of micrasters, cortical

tylasters and larger choanosomal oxyasters.

#### Acknowledgments

This work was supported financially by the Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, by CONACyT ICECXNA-021996) project and by the Italian Government M.U.R.S.T. funds. Thanks are due to Dr. Martín Merino Ibarra for his support, Jorge Sepulveda Sánchez for the SEM micrographs, Dulce María Flores Sánchez for spicule measurement, Ignacio Palomar Morales and Blanca Rocio Tafoya Fernandez for their help with image processing, Laura Vázquez Maldonado for the *T. ovum* photographs (Figs. 8A–B), and Jorge A. Castro Sánchez for the map drawing; to the anonymous reviewers whose comments improved the manuscript.

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**BIOLOGICAL SOCIETY OF WASHINGTON**  
**128th Annual Meeting, 29 May 2001**

President Brian F. Kensley called the meeting to order in the Waldo Schmitt Room, National Museum of Natural History. Council members present: Roy W. McDiarmid (President Elect), W. Duane Hope, Susan L. Jewett, Rafael Lemaitre, (Elected Council), C. Brian Robbins (Editor), Storrs L. Olson (Custodian of Publications), Richard Banks (Past President), Janet Reid (Past President), Frank D. Ferrari (Associate Editor, Invertebrates), T. Chad Walter (Treasurer), Carole C. Baldwin (Secretary).

Minutes of the 127th Annual Meeting of the Society were approved, and President Kensley then called on Chad Walter for the Treasurer's Report (Table 1). Society income for the period 1 January 2000 to 31 December 2000 was \$105,736.21; expenses for the same period were \$123,796.96. Total assets for the Society as of 15 April 2001 were \$119,733.58, the Society's endowment account declining by \$5,013.39 because of stock-market fluctuations. The Treasurer's report was approved, and President Kensley thanked Duane Hope and Kristian Fauchald for auditing the Treasurer's account records.

Editor Brian Robbins then reported that four issues of Volume 113 of the *Proceedings* were published comprising 108 papers and 1172 pages, the largest volume in recent history. As of 1 May 2001, there were

33 submissions, down from 45 in 2000. There continues to be no backlog for papers accepted in the *Proceedings*.

Revision of the new guidelines for authors is nearing completion, and several options for their publication were discussed, including placing them on the World Wide Web. The Society currently has no presence on the internet, but Kensley and Susan Jewett agreed to investigate development of a Society web site. Of considerable importance is that the new guidelines will include instructions for electronic submission of manuscripts, which will reduce publication costs considerably.

Editor Robbins announced his plans to move to southern California in July 2001, but noted that he is willing to continue serving as editor from his new residence. Details of the arrangement will be addressed in the near future, but the Council agreed that Robbins' continuing as Editor would provide the best chances for uninterrupted production of the *Proceedings*.

Following a brief discussion of who might replace Janet Reid as the Society's representative in the Washington Academy of Sciences, the meeting was adjourned by President Kensley.

Respectfully submitted,  
Carole C. Baldwin  
Secretary

Table 1. Summary Financial Statement for 2000.

	General Fund	Merrill Lynch Fund	Total Assets
ASSETS: JANUARY 1, 2000	42,075.82	88,746.18	130,822.00
TOTAL RECEIPTS FOR 2000	86,496.89	19,239.32	105,736.21
TOTAL DISBURSEMENTS FOR 2000	99,544.25	24,252.71	123,796.96
ASSETS: DECEMBER 31, 2000	29,028.46	83,732.79	112,761.25
NET CHANGES IN FUNDS	(13,047.36)	(5,013.39)	(18,060.75)

**INTERNATIONAL TRUST FOR ZOOLOGICAL NOMENCLATURE**

**Applications published in the *Bulletin of Zoological Nomenclature***

The following Applications were published on 30 March 2001 in Vol. 58, Part 1 of the *Bulletin of Zoological Nomenclature*. Comment or advice on any of these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary (I.C.Z.N.), c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

*Case No.*

- 3149 Proposed conservation of 31 species-group names originally published as junior primary homonyms in *Buprestis* Linnaeus, 1758 (Insecta, Coleoptera).
- 3158 *Helix lucorum* Linnaeus, 1758 and *Helix punctata* Müller, 1774 (currently *Otala punctata*; Mollusca, Gastropoda): proposed conservation of usage of the specific names by the replacement of the syntypes of *H. lucorum* with a neotype.
- 3175 *Ampullaria canaliculata* Lamarck, 1822 (currently *Pomacea canaliculata*; Mollusca, Gastropoda): proposed conservation of the specific name.
- 3132 *Eudorylas* Aczél, 1940 (Insecta, Diptera): proposed conservation of usage by the designation of *Pipunculus fuscipes* Zetterstedt, 1844 as the type species.
- 3157 *Halictoides dentiventris* Nylander, 1848 (currently *Dufourea dentiventris*; Insecta, Hymenoptera): proposed conservation of the specific name.
- 3165 *Parasuchus hislopi* Lydekker, 1885 (Reptilia, Archosauria): proposed replacement of the lectotype by a neotype.
- 3143 *Euphryne obesus* Baird, 1858 (Reptilia, Squamata): proposed precedence of the specific name over that of *Sauromalus ater* Duméril, 1856.
- 3022 *Catalogue des mammifères du Muséum National d'Histoire Naturelle* by Étienne Geoffroy Saint-Hilaire (1803): proposed placement on the Official List of Works Approved as Available for Zoological Nomenclature.

**Opinions published in the *Bulletin of Zoological Nomenclature***

The following Opinions were published on 30 March 2001 in Vol. 58, Part 1 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary, I.C.Z.N., c/o The Natural History Museum, Cromwell Road, London SW7 5BD, U.K. (e-mail: iczn@nhm.ac.uk).

*Opinion No.*

1965. *Euchilus* Sandberger, 1870 and *Stalioa* Brusina, 1870 (Mollusca, Gastropoda): *Bithinia deschiensiana* Deshayes, 1862 and *Paludina desmarestii* Prévost, 1821 designated as the respective type species, with the conservation of *Bania* Brusina, 1896.
1966. *Gnomulus* Thorell, 1890 (Arachnida, Opiliones): *Gnomulus sumatranus* Thorell, 1891 designated as the type species.
1967. *Disparalona* Fryer, 1968 (Crustacea, Branchiopoda): conserved.
1968. *Phytobius* Schönherr, 1833 (Insecta, Coleoptera): placed on the Official List.
1969. *Drosophila rufifrons* Loew, 1873 and *D. lebanonensis* Wheeler, 1949 (currently *Scaptoarosophila rufifrons* and *S. lebanonensis*; Insecta, Diptera): specific names conserved by the designation of a neotype for *D. rufifrons*.
1970. *Odatria keithhornei* Wells & Wellington, 1985 (Reptilia, Squamata): specific name placed on the Official List.

## INFORMATION FOR CONTRIBUTORS

*Content.*—The *Proceedings of the Biological Society of Washington* contains papers bearing on systematics in the biological sciences (botany, zoology, and paleontology), and notices of business transacted at meetings of the Society. Except at the direction of the Council, only manuscripts by Society members will be accepted. Papers are published in English (except for Latin diagnoses/descriptions of plant taxa), with an Abstract in an alternate language when appropriate.

*Submission of manuscripts.*—**Submit three copies of each manuscript in the style of the Proceedings to the Editor, complete with tables, figure captions, and figures** (plus originals of the illustrations). Mail directly to: Editor, Proceedings of the Biological Society of Washington, National Museum of Natural History NHB-108, Smithsonian Institution, Washington, D.C. 20560. (Do not submit manuscripts to an associate editor).

*Presentation.*—Clarity of presentation, and requirements of taxonomic and nomenclatural procedures necessitate reasonable consistency in the organization of papers. Telegraphic style is recommended for descriptions and diagnoses. The style for the Proceedings is described in "GUIDELINES FOR MANUSCRIPTS for Publications of the BIOLOGICAL SOCIETY OF WASHINGTON," a supplement to Volume 103, number 1, March 1990. Authors are encouraged to consult this article before manuscript preparation. Copies of the article are available from the editor or any associate editor.

The establishment of new taxa must conform with the requirements of appropriate international codes of nomenclature. Decisions of the editor about style also are guided by the General Recommendations (Appendix E) of the International Code of Zoological Nomenclature. When appropriate, accounts of new taxa must cite a type specimen deposited in an institutional collection.

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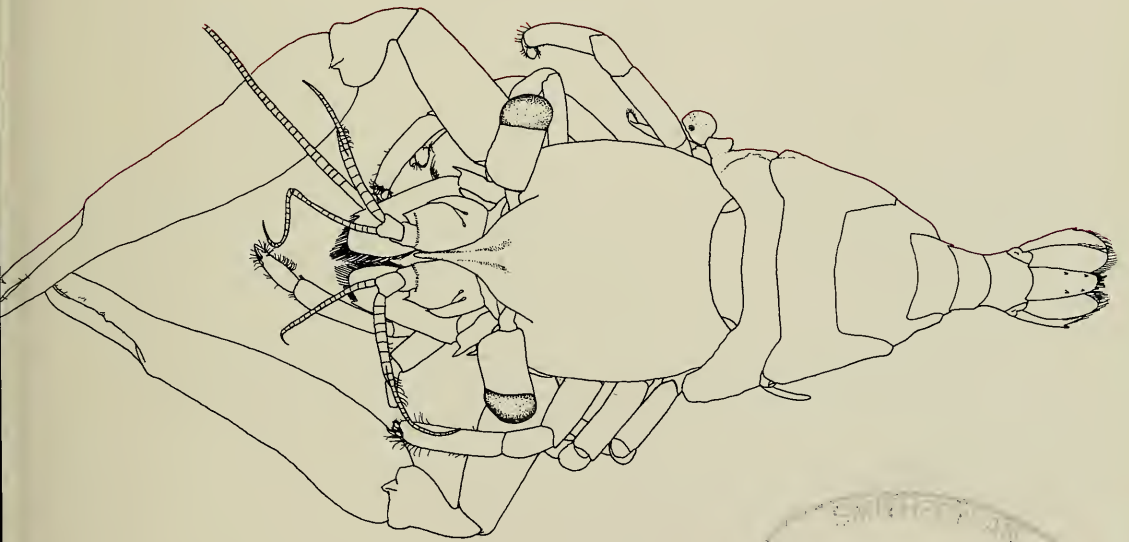
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## **Merotrichous isorhiza, a nematocyst new to the Campanulariidae (Cnidaria: Hydrozoa), and its relevance for the classification of Cnidae**

Alberto Lindner and Alvaro E. Migotto

Centro de Biologia Marinha, Universidade de São Paulo, Caixa Postal 83, 11600-970, São Sebastião, SP, Brazil; and Departamento de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil;

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*Abstract.*—Merotrichous isorhizae, a nematocyst class found in only a few species of Cnidaria, are present in the hydroid *Clytia noliformis*. This nematocyst type is present in the hypostome, gonangium, and hydranth body, near the base of the tentacles but is absent in the tentacles themselves. The undischarged capsules are similar to the B-type microbasic b-mastigophores found in other species of *Clytia*. The presence of a prominent rod in undischarged capsules indicates that changes may be needed in the classification of heteronemes and haplonemes, categories that embrace the great majority of nematocysts.

Within the hydroid family Campanulariidae (Hydrozoa: Leptomedusae), knowledge on the cnidome has been shown to be valuable for the identification of more than 20 species (see Table 1 for references). Information on nematocysts has been crucial in solving taxonomic debates, such as the ones on the validity of *Clytia gracilis* (M. Sars, 1850) and *Obelia longissima* (Pallas, 1766) (Östman 1979a, 1979b, 1982; Cornelius & Östman 1986). Two classes of nematocysts have thus far been reported for the Campanulariidae, i.e., microbasic b-mastigophore and holotrichous isorhiza (sensu Östman 2000). These classes were subdivided into seven and four different types, respectively (Table 1), using intra- and interspecific size differences, as well as the morphology of the capsules and spines (Östman 1979a, 1979b, 1982, 1988, 1999). However, with a few exceptions (e.g., Migotto 1996), most cnidome studies within the Campanulariidae were based on species from temperate waters (e.g., Russell 1938; Kubota 1976, 1978a, 1978b; Östman

1979a, 1979b, 1982, 1988, 1999). By studying the tropical species *Clytia noliformis* auct., we found a nematocyst class not yet reported for the Campanulariidae and present only in a few species of the Phylum Cnidaria: the merotrichous isorhiza.

### Materials and Methods

*Clytia noliformis* was identified according to Calder (1991). Discharged and undischarged capsules of nematocysts of *C. noliformis* were observed by squash preparations (Silveira & Migotto 1984) of living colonies collected along the shallow subtidal coasts of São Sebastião (23°49.72'S, 45°25.52'W) and Ilhabela (23°51.18'S, 45°25.07'W), southeast Brazil, between 1996–1998. Undischarged capsules of the proposed neotype of *C. noliformis* (see Lindner & Calder 2000), fixed in ETOH 70%, from Castle Harbour, Bermuda, were also observed. Nematocysts were measured and photographed by light microscopy. The nomenclature adopted is that of Mariscal (1974) and Östman (2000).

Table 1.—Cnidomes of campanulariid species. Nematocyst classes are in accordance with the classification of Östman (2000). The terminology adopted for the types is in accordance with the revision of Östman (1999). (–) absent; (N) not observed or reported; (MA) free medusa absent.

Species	Nematocyst Class				Source <sup>a</sup>
	Microbasist b-mastigophore		Holotrichous isorhiza		
	Polyp	Medusa	Polyp	Medusa	
<i>Clytia delicatula</i> (Thomely, 1899) <sup>a</sup>	N	A-, C-, D-types	N	I <sub>c</sub> -type	1
<i>Clytia edwardsi</i> (Nutting, 1901) <sup>a</sup>	A-type, B-type	A-, C-, D-types	–	I <sub>c</sub> -type	2, 3
<i>Clytia gracilis</i> (M. Sars, 1850)	A-type, B-type	A-, C-, D-types	–	I <sub>c</sub> -type	4–7
<i>Clytia hemisphaerica</i> (Linnaeus, 1767)	A-type, B-type	A-, C-, D-types	–	I <sub>c</sub> -type	4–10
<i>Clytia linearis</i> (Thomely, 1899)	A-type, B-type	A-, C-, D-types	–	I <sub>c</sub> -type	6, 7, 8, 11
<i>Obelia bidentata</i> Clark, 1875 (from England)	A-type, sB-type	N	–	I <sub>c</sub> -type	6, 7
<i>Obelia cf. bidentata</i> (from Brazil)	A-type	N	?I <sub>p</sub> -, I <sub>r</sub> -types	N	7, 8
<i>Obelia dichotoma</i> (Linnaeus, 1758)	A-type	A-type	I <sub>p</sub> -, I <sub>r</sub> -types	I <sub>p</sub> -, I <sub>r</sub> -types	6, 7, 8, 12
<i>Obelia geniculata</i> (Linnaeus, 1758)	A-type	A-type	I <sub>g</sub> -type	–	6, 7, 9, 12
<i>Obelia longissima</i> (Pallas, 1766)	A-type, F <sub>1</sub> -type	A-type, F <sub>1</sub> -type	–	–	6, 7, 12
<i>Obelia plana</i> (M. Sars, 1835) <sup>a</sup>	A-type, ?F <sub>1</sub> -type	A-type, ?F <sub>1</sub> -type	–	–	2
<i>Orthopyxis asymmetrica</i> Stechow, 1919	A-type, B-type	N	–	N	6, 7, 11
<i>Orthopyxis integra</i> (Macgillivray, 1842)	A-type, B-type	N	–	N	6, 7, 11
<i>Orthopyxis sargassicola</i> (Nutting, 1915)	A-type, sB-type	sB-type	–	–	7, 8
<i>Campanularia hineksii</i> Alder, 1856	A-type, B-type	MA	–	MA	6, 7, 13
<i>Gonothyreae hyalina</i> Hincks, 1866	A-type, sB-type	MA	–	MA	6, 7, 13
<i>Gonothyreae loveni</i> (Allman, 1859)	A-type	MA	–	MA	13
<i>Hartlaubella gelatinosa</i> (Pallas, 1766)	A-type, sB-type	MA	b	MA	6, 7
<i>Laomedea angulata</i> Hincks, 1861	N	MA	b	MA	6
<i>Laomedea exigua</i> M. Sars, 1857	A-type, sB-type	MA	–	MA	6, 7, 14
<i>Laomedea flexuosa</i> Alder, 1857	A-type, E <sub>r</sub> -type	MA	–	MA	6, 7, 9, 12
<i>Rhizocaulus verticillatus</i> (Linnaeus, 1758)	A-type, B-type	MA	–	MA	7, 13

Sources: 1. Kubota 1978a; 2. Kubota 1976; 3. Kubota 1978b; 4. Östman 1979a; 5. Östman 1979a; 6. Östman 1979b; 6. Östman 1987; 7. Östman 1999; 8. Migotto 1996; 9. Weill 1934; 10. Russell 1938; 11. Östman et al. 1987; 12. Östman 1982; 13. Östman 1988; 14. Cornelius & Östman 1987.

<sup>a</sup> Types inferred from descriptions (Kubota 1976, 1978a, 1978b).

<sup>b</sup> According to Östman (1987:77), isorhizae of *H. gelatinosa* and *L. angulata* "... have been identified, but only provisionally."

<sup>c</sup> Besides articles published before Östman's (1979a, 1979b, 1982) descriptions of the types, some publications adopted a slightly different terminology (e.g., Östman 1987). Not all publications dealing with nematocysts of the Campanulariidae are included in the table.

Table 2.—Measurements of undischarged merotrichous isorhiza capsules of *Clytia noliiformis*.

Locality	Length ( $\mu\text{m}$ ) [mean $\pm$ SD (range) (n)]	Width ( $\mu\text{m}$ ) [mean $\pm$ SD (range) (n)]	Number of colonies observed
Brazil, São Sebastião	21.1 $\pm$ 1.6 (18.0–24.0) (37)	5.3 $\pm$ 0.6 (4.0–7.0) (37)	2
Brazil, Ilhabela	20.4 $\pm$ 1.1 (17.0–23.0) (26)	5.1 $\pm$ 0.3 (4.5–6.0) (26)	2
Bermuda	19.8 $\pm$ 0.6 (19.0–21.0) (10)	4.4 $\pm$ 0.3 (4.0–5.0) (10)	1

## Results

Two classes of nematocysts, i.e., microbasic b-mastigophore (sensu Östman 2000) and merotrichous isorhiza (sensu Mariscal 1974), are present in the hydroid *C. noliiformis*. The microbasic b-mastigophores are  $7.1 \pm 0.6 \mu\text{m}$  (mean  $\pm$  SD,  $n = 59$ ) in length and  $2.5 \pm 0.5 \mu\text{m}$  (mean  $\pm$  SD,  $n = 59$ ) in width. These nematocysts are abundant in the entire colony and correspond to the A-type described by Östman (1979a). Merotrichous isorhizae are abundant in the hypostome, gonangium, and hydranth body, near the base of the tentacles but are absent in the tentacles. The undischarged capsule is elongated (ca.  $20 \mu\text{m}$  in length; see Table 2), with rounded ends. In a lateral view, one side is slightly convex and the other approximately straight; a distinct axial rod, corresponding to the region of the armature, is visible inside the undischarged capsule, running longitudinally from its tip to the posterior end (Fig. 1A). The aperture is turned towards the straighter side. The everted tubule forms a  $20\text{--}80^\circ$  angle with the straighter side of the capsule (Fig. 1B). The region with prominent spines (armature) is slightly shorter than one capsule-length ( $17.95 \pm 1.58 \mu\text{m}$ ;  $n = 19$ ); the distance between its distal end and the tip of the capsule is about 4 capsule-lengths ( $80.68 \pm 8.37 \mu\text{m}$ ;  $n = 70$ ). The diameter of the tubule shortly before and after the armature is identical. Medusae of *C. noliiformis* have the same types of nematocysts so far reported for the genus *Clytia* (Table 1)—microbasic b-mastigophores (A-, C- and D-types) and holotrichous isorhizae ( $I_c$ -type).

## Discussion

The A-type microbasic b-mastigophore is the most common nematocyst in the Campanulariidae, showing almost no variation in shape and size in all species studied so far (Östman 1999). In contrast, the B-type microbasic b-mastigophore—another common nematocyst present in all species of *Clytia*, except *C. noliiformis*—differs in shape and size among species and is used for species identification (Östman 1979a, 1987, 1988, 1999; Östman et al. 1987). Undischarged capsules of the latter type are morphologically similar to the merotrichous isorhiza of *C. noliiformis*. With light microscopy, both nematocysts can only be distinguished by the position of the prominent armature in the everted tubule. These nematocysts also have a similar distribution in the colony—absent from the tentacles and abundant in the hypostome, gonangium, and near the base of the tentacles (Östman 1979a, 1988; Lindner 2000). This suggests that, within the Campanulariidae, the merotrichous isorhiza may have evolved from microbasic b-mastigophores (or vice-versa), i.e., the prominent armature possibly “migrated” either from the proximal part of the tubule to a more distal part (microbasic  $\rightarrow$  merotrichous) or from a distal to a proximal position (merotrichous  $\rightarrow$  microbasic).

Instead of merotrichous isorhizae, B-type microbasic b-mastigophores were reported for colonies identified as *C. noliiformis* from Italy (Östman et al. 1987, redefined as sB-type by Östman 1987, 1999). Since these capsules also measured only approximately one-third of the length of the capsules found in colonies of *C. noliiformis* from

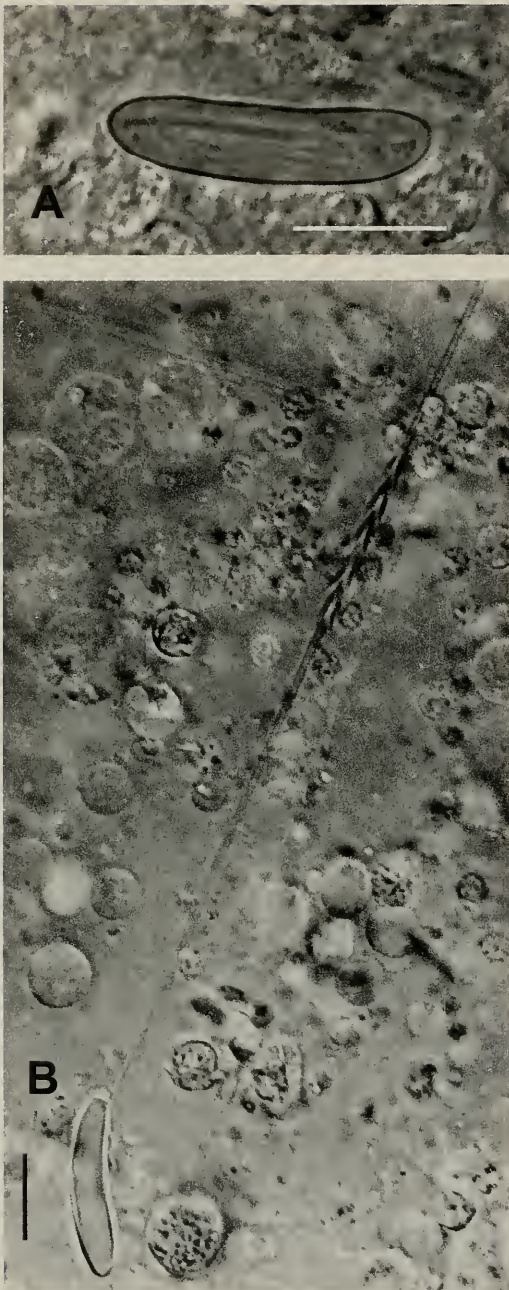


Fig. 1. Merotrichous isorhiza of *Clytia noliformis*. A, undischarged capsule; B, discharged capsule with everted tubule. Scale bars: 10  $\mu\text{m}$ .

Brazil and Bermuda [ca. 7  $\mu\text{m}$  (see Östman et al. 1987:302) and 20  $\mu\text{m}$  (Table 2), respectively], it is possible that the authors based their observations on another species.

Although differences in cnidome may be indicative of different species (see Östman 1982, 1988), the taxonomic relevance of the size differences of nematocysts has not yet been evaluated. However, the mean size of the merotrichous isorhiza among different colonies of *C. noliformis* shows little variation (Table 2). The large size may, therefore, help to identify the species, and it is particularly important for the identification of fixed samples having only undischarged capsules. The slightly smaller size of capsules of nematocysts from Bermuda in comparison to those from Brazil (particularly width, ca. 16% smaller in the colony from Bermuda; see Table 2) is probably due to fixation, a procedure that causes a 15–20% decrease in the width of B-type microbasic b-mastigophores in other species of *Clytia* (Lindner 2000).

Until recently, the merotrichous isorhiza was a nematocyst category reported only for the class Hydrozoa, where it was found in a few species of five families of Leptomedusae (Eirenidae, Eucheilotidae, Lovenellidae, Haleciidae and Tiaropsidae), and in *Halitiara*, a genus of Anthomedusae with features paralleling somewhat features found in the Leptomedusae (Bouillon et al. 1988). According to Bouillon et al. (1988), the presence of merotrichous isorhizae suggests affinities between the families Eirenidae and Eucheilotidae, as well as between the latter family and the Lovenellidae.

Similarly, Boero & Sarà (1987) considered the presence of merotrichous isorhizae in polyps of *Campalecium medusifera* (Torrey, 1902) and *Hydranthea margarica* (Hincks, 1862) (Haleciidae), and in medusae of *Eucheilota maculata* Hartlaub, 1894 (Eucheilotidae), as a further evidence that the families Haleciidae and Campanuliniidae s.l. are phylogenetically related. Werner (1965), who first described this nematocyst class (for *Eucheilota maculata*), and included it in the category haploneme in the system of Weill (1934), also attributed taxonomic value to the presence of merotrichous isorhizae (as “merotriche Haploneme”).

me'') in the cirri of medusae of *Eucheilota* and *Eutima*. However, the presence of merotrichous isorhizae in the scyphomedusa *Cyanea nozakii* Kishinouye, 1891 (see Wang & Xu 1990) and possible misidentifications of this nematocyst class as microbasic or macrobasic mastigophores (as, for example, in *Campalecium medusifera*, see Boero et al. 1987) indicate that merotrichous isorhizae may be actually more common among the Medusozoa. Moreover, this kind of nematocyst may have evolved more than once, and some phylogenetic inferences based on the presence of merotrichous isorhizae may be misleading if not corresponding to appropriate generality levels. Phylogenetic relationships within the class Hydrozoa are poorly understood, and the relevance of merotrichous isorhizae for the systematics of the Leptomedusae (e.g., if they represent or not a synapomorphy of some taxa) can only be assessed after a comprehensive phylogenetic analysis. It is also important to emphasize that the name merotrichous isorhiza refers solely to features of the tubule of the nematocyst; other characters, such as a visible rod in the undischarged capsule and the shape of the capsule, for example, should also be considered when comparing nematocysts of this and other categories.

The presence and absence of an internal axial rod in the undischarged capsule is a key character for the definition of the categories heteronemes and haplonemes in the new classification of Östman (2000). Heteronemes and haplonemes were originally defined by Weill (1934) by the presence and absence, respectively, of a basally enlarged region of the everted tubule, the so-called shaft, seen in discharged capsules. In contrast, Östman (2000), in an attempt to improve the classification of Weill (1934) by incorporating information not available at his time—but without changing the nomenclature—redefined heteronemes and haplonemes by the presence and absence, respectively, of a prominent rod-shaped shaft, corresponding to the region of the prominent

armature, visible inside the undischarged capsule (regardless of the presence of an enlargement of the everted tubule). Since an internal rod is visible inside the undischarged capsule of the merotrichous isorhiza of *C. noliformis*, this nematocyst—a haploneme sensu Mariscal (1974)—must be classified as a heteroneme in the system of Östman (2000).

The presence of an internal rod (inferred by drawings) is also observed in the merotrichous isorhiza of, for example, *Hydranthea margarica* (Boero & Sarà 1987:133), *Lovenella assimilis* (Browne, 1905) (Hirano & Yamada 1985:133) and *Tiaropsidium roseum* (Maas, 1905) (Boero et al. 1987:296). However, in contrast to the classification of Mariscal (1974), the class merotrichous is not applicable in the classification of Östman (2000). Moreover, in adopting the latter classification, the merotrichous isorhiza of *C. noliformis* may be assigned to two distinct classes of heteronemes, since the length of the proximal tubule with prominent armature is variable. Those nematocysts with the proximal tubule with prominent armature slightly shorter than 4 capsule-lengths would be classified as mesobasic, whereas those with the proximal tubule with prominent armature slightly longer than 4 capsule-lengths would be classified, according to Östman (2000), as macrobasic.

Even if the merotrichous isorhiza of *C. noliformis* could be objectively classified as a mesobasic or macrobasic b-mastigophore, we believe that this would represent a hindrance, since nematocysts with distinct armatures (i.e., those with a long region with prominent spines starting at the base of the tubule and those with prominent spines only at a more distal position) would be grouped in the same categories. Since the merotrichous isorhiza is a nematocyst easy to identify and important for species identification, such as *C. noliformis*, it seems more appropriate to maintain it as a category in the classification of cnidae.

Furthermore, we believe that the visibil-

ity of an internal rod may not be a suitable trait to distinguish all heteronemes and haplonemes—two categories that include the great majority of nematocysts. This opinion, however, does not deny that further improvements in the definitions of the nematocysts categories may be needed in the future.

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*Nipponnemertes fernaldi*, a new species of swimming monostiliferous hoplonemertean from the San Juan Archipelago, Washington, U.S.A.

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*Abstract.*—*Nipponnemertes fernaldi*, new species, is described as a member of the order Hoplonemertea, suborder Monostilifera. In general morphology, it appears to be most closely related to the genus *Nipponnemertes* (family Cra-tenemertidae) and the new species is placed in this genus. The significant characters are explained and discussed.

Among numerous nemerteans collected in the San Juan Archipelago, Washington in 1964 were specimens of a monostiliferous hoplonemertean here described as new. This nemertean possesses characters that exclude it from any of the previously described species of *Nipponnemertes*. New information on the morphology of monostiliferans is provided with respect to: the central stylet-basis complex of the proboscis; the cerebral organs (with a sensory canal and a sac-like canal); a pair of middorsal epidermal folds in the anterior region; the stylet bulb of the proboscis, with a plate-like muscular wall and a thick layer of glandular cells; the intestinal caecum, with four branches or pouches and two pairs of lateral diverticula; the nervous system, with large ganglion cells in the brain; and a middorsal nerve extending anteriorly beyond the brain.

Materials and Methods

Two specimens were collected by dredging, and two were collected at a night light. All four were fixed in Bouin's solution (after being anesthetized by addition of menthol or 70% alcohol). Three of them were sectioned at 10  $\mu\text{m}$  (8  $\mu\text{m}$  for the proboscis apparatus of the holotype), and stained with

Delafield's hematoxylin and eosin. An Olympus or Sony video camera with Symphonic monitor television and Sony color video printer, in addition to an Olympus BH-2 microscope, were used for observation of the material.

*Nipponnemertes fernaldi*, new species  
Figs. 1–9, Tables 1, 2

*Generic diagnosis.*—Monostiliferous hoplonemerteans with rhynchocoel nearly equal to body length, proboscis sheath composed of a wickerwork of interwoven circular and longitudinal muscles; body wall musculature, especially longitudinal layer, well developed, with layer of diagonal muscles between the circular and the longitudinal muscles, longitudinal musculature not anteriorly divided; stomach with a small diverticulum or caecal folds; intestinal caecum with short anterior diverticula and with lateral diverticula; cerebral sensory organ large and extending behind the dorsal cerebral ganglia; nervous system without neurochords and neurochord cells; accessory lateral nerves absent; blood vascular system with three longitudinal vessels, mid-dorsal vessel with single vascular plug; frontal organ present; cephalic glands well developed but not reaching posteriorly behind the ce-

rebral ganglia, except as lateral bands; excretory system extending from rear of brain to hind regions of foregut; sexes separate.

*Specific diagnosis.*—Pale brown, without pattern; with two pairs of oblique cephalic grooves and dorsomedial longitudinal grooves; each anterior oblique cephalic groove is subdivided by 21 transverse secondary grooves, 14 dorsal to the opening of cerebral organ canal and 7 on the ventrolateral surface of the head below the canal opening; paired posterior oblique cephalic grooves originating at the end of the dorsomedial longitudinal grooves; dorsomedial longitudinal grooves forming anteriorly a pair of epidermal folds; with numerous large ocelli (76 in the holotype, 78 in paratype 1, and 52 in paratype 3) in four groups; dermis thick; rhynchodeum provided with a circular muscle layer; precerebral septum is of the dissolved type composed of separate muscular bundles; proboscis diaphragm provided with central stylet-basis complex, which includes a basis consisting of ovoid body to which the central stylet is attached, columnar structure (with obliquely oriented projection) posterodorsal to it, and more massive posterior portion resting on muscular bolster; stylet bulb with a plate-like muscular wall and a thick layer of glandular cells; 2 or 3 accessory stylet pouches; proboscis with 14 nerves; mouth small and located on the ventral side of the rhynchodeum; esophagus, anterior to brain, surrounded by longitudinal muscle; intestinal caecum with anterior branches or pouches and two pairs of lateral diverticula; intestinal diverticula branched; brain with neurilemma and large ganglion cells; mid-dorsal nerve extending anteriorly beyond the brain; lateral nerve cords with myofibrillae and large efferent nerves; ventral ganglia not distinctly separated from the dorsal ganglia except posteriorly; dorsal ganglia without bifurcated fiber core; paired midgut, foregut, and esophagus nerves originating from the ventral brain; cerebral sensory organ with neurilemma, the cerebral organ canal, located at the anterior end of

the cerebral sensory organ, branching into the medial sensory canal and lateral sac-like canal with two kinds of glandular masses; glands lacking at the bifurcation of the cerebral organ canal; excretory pores lateral to the nerve cords and situated in the posterior portion of the nephridial region.

*Type material.*—Holotype (USNM 1000131), paratype 1 (USNM 1000132), paratype 2 (USNM 1000133) and paratype 3 (USNM 1000134) are deposited at the National Museum of Natural History, Smithsonian Institution, Washington, DC.

The holotype (female) consists mostly of a set of serial sections mounted on 81 slides. These include transverse sections of the anterior portion of the body, midgut, tail, and proboscis, and frontal sections of the proboscis apparatus. The remainder of the holotype consists of short pieces that were not sectioned. Paratype 1 (male) consists of serial sections mounted on 76 slides. These include transverse sections of the anterior portion of the body, midgut, tail, and proboscis, and frontal sections of the proboscis apparatus. Four pieces were not sectioned. Paratype 2 (male) consists of serial sections mounted on 29 slides, which include horizontal sections of the anterior portion of the body and proboscis apparatus, and transverse sections of the tail and two pieces that were not sectioned. Paratype 3 was not sectioned (it dried once after it was preserved).

*Type locality.*—Holotype: Peavine Pass, between Blakely Island and Obstruction Island, Washington, U.S.A. (48°34.7'N, 122°50.5'W); collected on 21 Sep 1964 by dredging, gravel bottom, depth between 42 and 56 m. Paratypes 1 and 2: Friday Harbor, Washington, U.S.A.; collected by night light in water column, depth 4 m on 12 Sep 1964. Paratype 3: Willow Island (48°32.4'N), Washington, U.S.A.; collected on 10 Sep 1964, gravel bottom, depth between 18 and 33 m.

*Etymology.*—The species name commemorates the late Professor Robert Fernald, former Director of Friday Harbor Lab-

oratories of the University of Washington, who collected two specimens (Paratypes 1 and 2).

### Description

*External features.*—The holotype is 5 cm long and 6 mm wide, but 8 mm wide while moving (Fig. 1a, b); paratype 1 is 8 cm long and 7 mm wide anteriorly and 10 mm wide in the midgut region (Fig. 1c, d); paratype 2 is 6 cm long and 8 mm wide; paratype 3 is 4 cm long and 10 mm wide, but 7 cm long and 5 mm wide when narcotized (Fig. 1h–j). The extruded proboscis of the holotype is 2.7 cm long (Fig. 1a). The proboscises of paratypes 1–3 were not extruded when the specimens were preserved. The proboscises of paratypes 1 and 2 were removed from the body for observation of the proboscis apparatus (Fig. 1d). The head is rounded on the anterior margin and slightly separated from the body by a constriction formed by the anterior oblique cephalic grooves.

In the living state, the body is flattened dorsoventrally, convex on the dorsal side, tapering posteriorly to a blunt tip. The color is pale brown on the dorsal surface, and more pale brown on the ventral side, with a colorless lateral margin. In the middorsal portion of the body, the proboscis extends anteroposteriorly within the large rhyncho-coel (Fig. 1b). The brain is recognizable from above as a pair of reddish markings (Fig. 1e, h).

On the dorsal side of the head there are two pairs of oblique cephalic grooves (Fig. 1e, f, h, i). The anterior grooves extend around the margins of the head end and are continued on the ventral surface; they each have 21 short secondary grooves perpendicular to them; 14 of these secondary grooves lie dorsal to the opening of the cerebral organ canal (Fig. 1i) and 7 short secondary grooves lie below the cerebral organ canal opening on the ventrolateral surface of the head. The posterior oblique cephalic grooves are limited to the dorsal side of the

body, and together they form a V-shaped pattern (Fig. 1e, f, h). Two closely parallel longitudinal grooves are located on the mid-dorsal part of the head, as in some species of *Nipponnemertes* and other cratene-mertids. They intersect the anterior oblique cephalic grooves and extend to the posterior oblique cephalic grooves (Fig. 1e, f, h, i). Their course is actually longer than shown in the figures, but their most anterior portions, which extend to the tip of the head, are evident only in transverse sections. In dorsal view, the anterior portion of each dorsomedial longitudinal cephalic groove has a median darkened line due to an epidermal depression that exhibits double epidermal folds in transverse sections (Figs. 1e, f, h, 2a).

The rhynchodeal opening is a slender lengthwise pore on the anteroventral portion of the head (Fig. 1g, j). In both the holotype and paratype 1, the right and left sides of the head region each have up to 39 large ocelli.

*Body wall, musculature, and parenchyma.*—The epidermis is of uniform thickness both in the cephalic region (average 110  $\mu\text{m}$ ) and in the midgut region (average 50  $\mu\text{m}$ ). Large unicellular glands are distributed over the entire body. Small, slender cyanophilous glands are embedded between the large glands.

Two middorsal epidermal folds in the anterior region are separated by a deep median groove (Fig. 2a), but posteriorly the folds unite and the groove disappears. The epidermis of the folds has only a few cyanophilous glands. The secondary grooves of the anterior oblique cephalic grooves, which run perpendicular to the anterior grooves, cut deeply into the epidermis and are distinguished by a thin epithelium free of glands, and also by comparatively long cilia (Fig. 2b).

The dermis, 20  $\mu\text{m}$  to 150  $\mu\text{m}$  thick, is from one-third to three times the thickness of the epidermis. It has fibrils that are predominantly circular, and contains numerous cells with nuclei approximately 4  $\mu\text{m}$  in di-

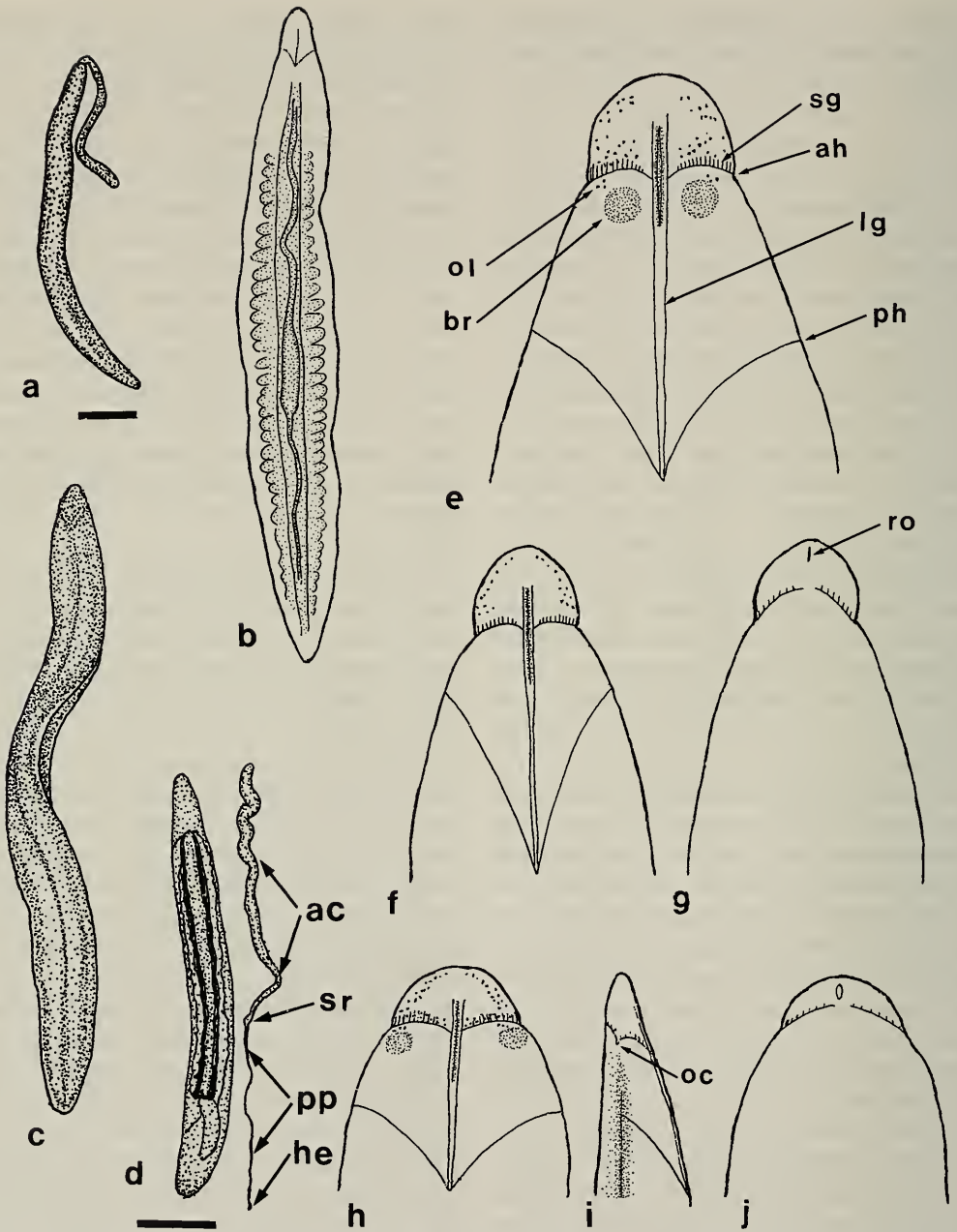


Fig. 1. *Nipponnemertes fernaldi*, new species, external features. (a) holotype, dorsal view; (b) sketch of holotype, dorsal view; (c) paratype 1; (d) paratype 1, and proboscis apparatus; (e) sketch of head of holotype, dorsal view; (f, g) sketches of head of paratype 1 in dorsal and ventral views; (h-j), sketches of head of paratype 3 in dorsal, lateral, and ventral views. Scale = 1 cm (a, d). ac, anterior chamber of proboscis; ah, anterior oblique cephalic groove; br, brain; he, hind end of proboscis; lg, longitudinal cephalic groove; oc, opening of cerebral organ; ol, ocelli behind anterior oblique cephalic groove; ph, posterior oblique cephalic groove; pp, posterior portion of proboscis; ro, rhynchodeal opening; sg, secondary groove; sr, stylet region of proboscis.

ameter (Fig. 2c). Small nerves are found in the dermis.

The body-wall musculature consists of an outer circular layer, inner longitudinal layer, and a recognizable diagonal muscle layer between them (Fig. 2d) (cf. Crandall 1993a). The circular and longitudinal muscle layers extend to the tip of the head, but decrease in thickness precerebrally. The circular layer posterior to the brain region has a fairly uniform thickness of 60  $\mu\text{m}$ . The longitudinal muscle layer consists of bundles arranged perpendicular to the body surface; the dorsal and ventral bundles become thicker (up to 550  $\mu\text{m}$  thick) in the stomach region (Fig. 2e). Longitudinal muscle fibers embedded in the parenchyma of the precerebral region originate from the inner portion of the longitudinal body-wall musculature and extend to the tip of the head. In the precerebral and cerebral region, dorsoventral and radial muscle fibers are not present. Behind the cerebral sensory organs, dorsoventral muscle fibers appear in the parenchyma between the proboscis sheath and the lateral longitudinal body-wall musculature. In the midgut region, well-developed dorsoventral musculature, consisting of crowded fibers, is found between the intestinal diverticula (Fig. 2f). Parenchyma is clearly evident along the lateral sides of the body in the intestinal region.

*Rhynchodeum, rhynchocoel, and proboscis.*—The precerebral region, anterior to the opening of the rhynchodeum, forms a short snout, which is flattened dorsoventrally and contains the ocelli and frontal glands associated with the frontal organ (Fig. 2g). A midventral epidermal groove leads from the rhynchodeal opening to the tip of the snout (Fig. 2g, h). The lining of the groove, forming a narrow median depression, does not differ from the epidermis of the head region, except for a boundary area around the opening of the rhynchodeum, where an epithelium with cilia but without glands is present. The dermis and musculature dorsal to the groove are continuous with those of the remainder of the body wall but are thin-

ner. The longitudinal musculature, however, is displaced by the cephalic glands (Fig. 3a, b).

In paratype 1, the precerebral region does not form a short flattened snout and the mid-ventral groove runs from the tip of the head to the rhynchodeal opening.

The rhynchodeum is lined entirely with a ciliated epithelium without a glandular content. The epithelium rests on a layer of circular musculature 10–50  $\mu\text{m}$  thick in the holotype, 15–150  $\mu\text{m}$  thick in paratype 1; the thickness of the the layer of circular musculature gradually increases toward the posterior end of the rhynchodeum. In the holotype, whose proboscis was extruded, the rhynchodeum is cylindrical and has a length of about 500  $\mu\text{m}$ . Its diameter at the opening measures 350  $\mu\text{m}$ ; at the posterior end it measures 450  $\mu\text{m}$ . At the posterior end of the rhynchodeum, the circular muscle layer around this cavity, properly called the rhynchodeal sphincter, is 50  $\mu\text{m}$  thick; the inner circular muscle layer of the proboscis fuses with it, resulting in compression of the space of the rhynchodeum (Fig. 3b). Part of the fused circular muscle layer measures 120  $\mu\text{m}$  thick, but the thickness decreases posteriorly for about 200  $\mu\text{m}$ , where the fused layer extends transversely to join the circular muscle layer of the body wall (Fig. 3c, d). The inner longitudinal muscle layer of the proboscis, within which the proboscis nerves are situated, becomes thicker posteriorly and forms the precerebral septum of the proboscis apparatus (Fig. 3d, e). Thus the proboscis insertion and the precerebral septum are distinct.

In paratype 1, in which the proboscis was not extruded, the precerebral septum of the proboscis apparatus consists of about 20 loosely arranged bundles of longitudinal muscle. Farther posteriorly, the longitudinal muscles closely surround the thick circular muscle layer around the rhynchodeum.

Posterior to the precerebral septum, a layer about 20  $\mu\text{m}$  thick (Figs. 3e, f, 4c, 7e), in which circular and longitudinal muscu-

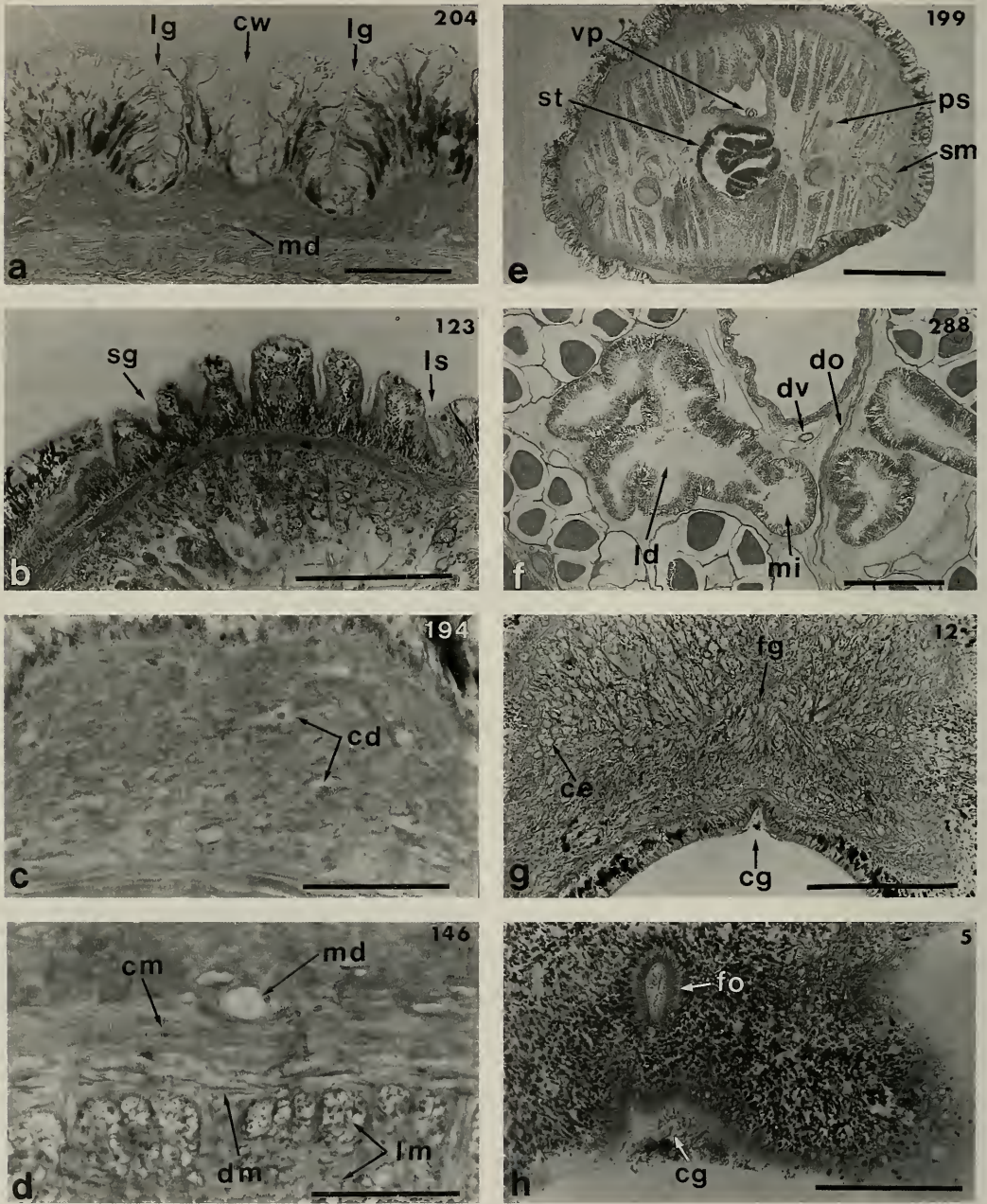


Fig. 2. *Nipponnemerytes fernaldi*, new species. Transverse sections of anterior and middle portions of body, showing (a) two epidermal folds (separated by a central depression) between longitudinal cephalic grooves and a central depression, (b) secondary grooves of anterior oblique cephalic groove (right side), (c) dermis, (d) middorsal nerve and diagonal muscle layer, (e) stomach, (f) midgut and lateral diverticula of midgut, (g) epidermal ciliated groove leading to rhynchodeum, and (h) pit of frontal organ. Scale = 0.5 mm (e, f), 200  $\mu$ m (b, g), 100  $\mu$ m (a), 50  $\mu$ m (c, d). Sections 5–204 from anterior end of body (a–e, g, h); section 288 from anterior end of middle portion of body (f). cd, cell in dermis; ce, cephalic glands; cg, ciliated groove; cm, circular muscle layer of body wall; cw, central depression between mediodorsal longitudinal cephalic grooves; dm, diagonal muscle layer; do, dorsoventral muscle; dv, dorsal blood vessel; fg, frontal gland; fo, frontal organ; ld, lateral diverticulum of midgut; lg, longitudinal cephalic grooves; lm, longitudinal



lature are interwoven, underlies the epithelium of the proboscis sheath.

In paratype 1, the rhynchodeum and esophagus, situated below the cephalic glands, are surrounded by thick bundles of longitudinal musculature and a thin layer of circular muscles.

In the area in which the circular muscle layer of the rhynchodeum and that of the proboscis are united into a thick layer, a coagulated mass of protein-rich rhynchocoel fluid, about 120  $\mu\text{m}$  thick, appears within the proboscis (Fig. 3b, c). The posterior part of this coagulated mass is hollowed out; the space marks the beginning of the rhynchocoel (Fig. 3d, e). The wall of the mass around the space becomes narrower and comes close to the epithelium of the proboscis sheath (Fig. 3g). In paratypes 1 and 2, a mass of coagulated rhynchocoel fluid was not observed (the proboscis was inside the body at the time of preservation).

The rhynchocoel within the proboscis sheath ends a little anterior to the posterior nerve anastomosis. It is narrow in the foregut region, where the longitudinal musculature of the body wall is well developed. The pressure of peripheral tissues causes the rhynchocoel walls to buckle inward into various folds that protrude into the lumen of the rhynchocoel, forming a pair of dorsal and ventral ridges (Figs. 3g, h, 4a, b). In the intestinal region, the rhynchocoel widens and becomes cylindrical (Fig. 4c).

In paratype 1, a pair of small dorsal ridges of the rhynchocoel are present in the cerebral and stomach regions, and a pair of deep ventral ridges also are present at the lateroventral corners of the rhynchocoel.

The structures associated with the central stylet form an unusual complex, as yet not reported for any monostiliferan hoploneurtean. The following observations are

based on sections of the holotype (Fig. 5a–o). The stylet itself, about 10  $\mu\text{m}$  long, is attached to an ovoid structure in which many small cellular or granular bodies are embedded (Figs. 4d, 5c–e, 6a). This structure, about 25  $\mu\text{m}$  long and 17  $\mu\text{m}$  wide, has a thick, slightly irregular wall. Posterodorsal to it is a nearly columnar, eosinophilous stalk bearing a projection that is oriented obliquely; this has a darkened edge on one side (Figs. 4f, 5g, h, 6a). The stalk is essentially a prolongation of the more massive posterior portion of the basis, about 110  $\mu\text{m}$  long by 80  $\mu\text{m}$  wide. Most of this is stained pale purple, but the nearly conical anterior half of it has a thick coating that is deeply stained purple and has sharp or blunt protuberances, as well as a collar-like ridge that encircles the base of the columnar stalk (Figs. 4f, 5h). The conical portion is free from the tissue surrounding it, but the posterior bulbous part is tightly bound to tissue (Fig. 5f–n).

In paratype 1, the tip of the basis is curved downward and the anterior portion of the central stylet, 17  $\mu\text{m}$  long, is damaged (Fig. 4g). Several large cellular bodies and a few deformed cyanophilous structures are present between the central stylet and the basis. The basis is conical, and its lateral surfaces, stained purplish, have several small and irregular protuberances. One side of the basis faces the ductus ejaculatorius (Stricker & Cloney 1981). In paratype 2, however, the tip of the basis is not curved, and a rectangular body containing a mass of small cyanophilous spheres rests on the tip of the conical portion of the basis (Fig. 4h). The rectangular body, with a wall 5  $\mu\text{m}$  thick, measures 32  $\mu\text{m}$  wide and 37  $\mu\text{m}$  high. The basis is conical, as in the holotype; the free portion of its dorsal side has

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muscle layer of body wall; ls, most lateral groove on lateral side of head; md, middorsal nerve; mi, midgut; ps, posterior end of cerebral sensory organ; sg, secondary groove; sm, submuscular gland; st, stomach; vp, vascular plug inside proboscis sheath.

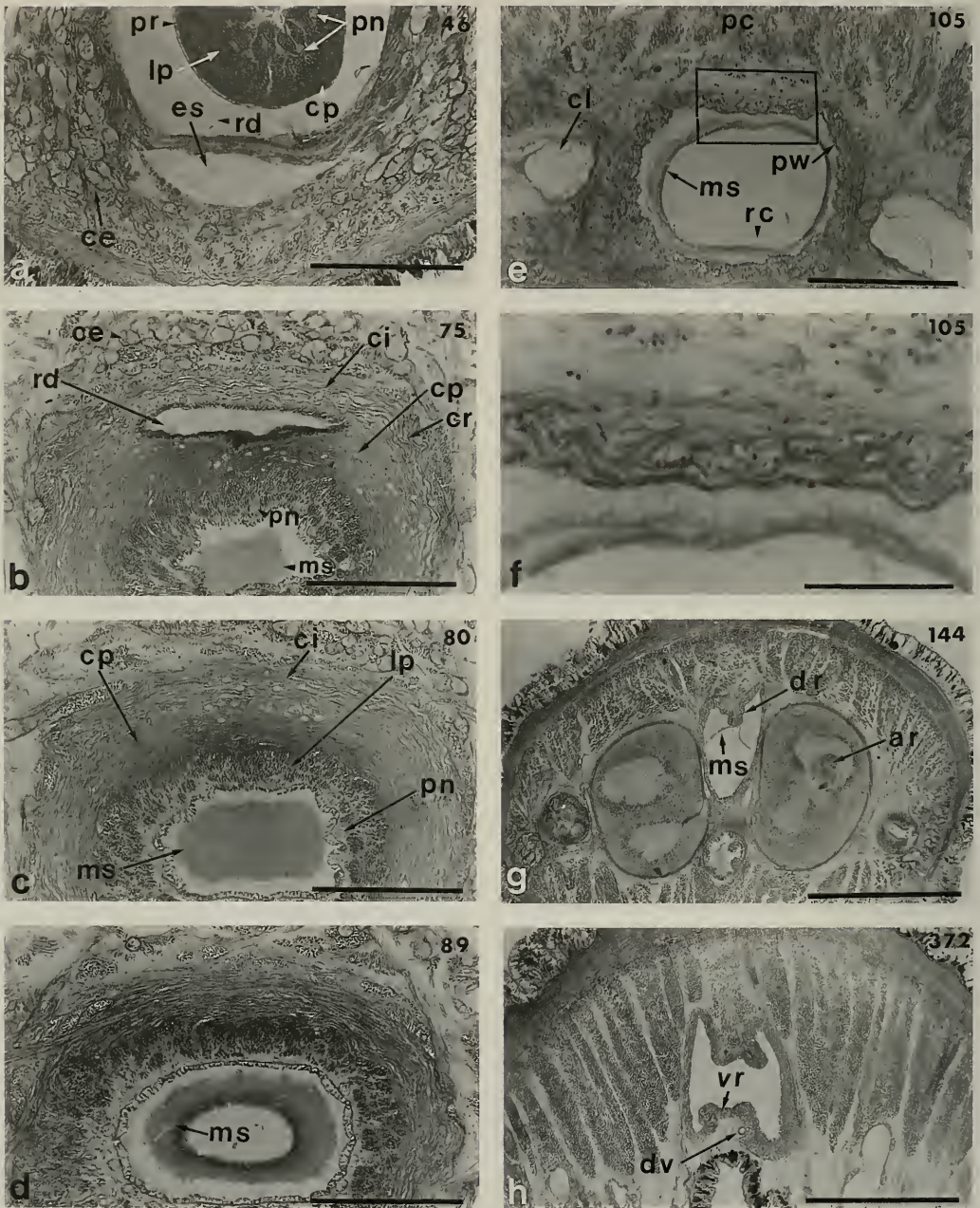


Fig. 3. *Nipponnemertes fernaldi*, new species. Transverse sections of anterior portion of body, showing (a) flattened portion of esophagus under rhynchodeum, (b) tight connection of circular muscle layer of rhynchodeum to that of proboscis, (c) united circular muscle layers of rhynchodeum and proboscis, (d) reduction of thickness of united circular muscle layers running laterally to circular muscle layer of body wall, (e) formation of pre-cerebral septum from longitudinal muscle layer of proboscis, (f) enlarged proboscis sheath formed from epithelium of proboscis, and (g, h) successive changes in shape of rhynchocoel. Scale = 0.5 mm (g, h), 200  $\mu$ m (a–e) and 50  $\mu$ m (f). 46–372, numbers of sections from anterior end of body. ar, artifact; ce, cephalic glands; ci, circular muscle layer of rhynchodeum; cl, cephalic blood lacuna; cp, circular muscle layer of proboscis; cr, circular muscle layer of rhynchodeum united to that of proboscis; dr, dorsal ridge of proboscis sheath; dv, dorsal blood vessel; es, esophagus; lp, longitudinal muscle layer of proboscis; ms, membranous sheath of coagulated

purplish edges, but lacks protuberances. In paratype 2, the central stylet is lacking.

The basis rests on a large bolster consisting of interwoven circular and longitudinal muscle (Fig. 4e). It is 110  $\mu\text{m}$  long medially, 150  $\mu\text{m}$  long laterally, and 370  $\mu\text{m}$  wide. The basis is surrounded by circular and longitudinal muscle bundles extending dorsally from the bolster. This muscular arrangement continues beyond the basis to the middle area of the stylet column, which extends from the tip of the proboscis to the central stylet of the proboscis apparatus (Fig. 4e). Posterior to the basis, the bolster is divided into two parts, with a space between. The bolster, basis, and muscular wall are continuous with the wall of the middle part of the proboscis. The clusters of eosinophilous glands of the proboscis epithelium are evident at the anterior end of this organ (Fig. 4e).

Posterior to the bolster, there is a large bulb-like structure called the dilated ampulla or stylet bulb (Stricker 1985) (Fig. 4e); its wall is about 50  $\mu\text{m}$  thick, and consists of interlacing circular muscles, thick connective tissue, a plate-like muscular wall on its anterior side, and a thick layer of glandular cells. In *Nipponnemertes punctatulus* and *N. bimaculatus* (reported by Iwata 1951, 1954), the platelike muscular wall and the thick layer of glandular cells were not found. In the area where a space is formed between the two halves of the divided bolster, the muscular anterior plate of the bulb is extended forward, and a narrow duct called the ductus ejaculatorius connects the interior of the stylet bulb with the space. On the posterior side of the bulb, a narrow canal leads to the posterior chamber of the proboscis (Fig. 7a).

In the holotype and paratype 1, two large pouches of accessory stylets are situated an-

terior to the central stylet, between the outer epithelium and the muscular wall of the bolster (Figs. 4e, 5a). Through a narrow curved duct, each pouch, measuring 265  $\mu\text{m}$  dorsoventrally, 230  $\mu\text{m}$  long, and 170  $\mu\text{m}$  wide, opens into the lumen of a canal that is directed upward from the basis. In each pouch, there are four accessory stylets, about 10  $\mu\text{m}$  long; they lie in vesicles about 30  $\mu\text{m}$  by 20  $\mu\text{m}$  (Figs. 4e, 5a). In paratype 2, there are three pouches of accessory stylets, and the number of stylets is 6, 8, and 8, respectively.

The proboscis has an outer circular and inner longitudinal muscle layer (Fig. 3a, c); there are 14 nerves within the proboscis in the holotype and paratype 1.

*Alimentary canal.*—The alimentary canal has five major divisions: esophagus, stomach, pylorus, midgut (with anteriorly directed caecum and lateral diverticula), and hindgut. The mouth is small and on the ventral side of the head close to the rhynchodeal opening (Fig. 7b). The distance between the rhynchodeal opening and the mouth is 150  $\mu\text{m}$  in the holotype, 200  $\mu\text{m}$  in paratype 1. Neither the esophagus nor the stomach has longitudinal or circular musculature; the shape of the esophagus is influenced by the longitudinal musculature of the body wall, situated on its dorsal and lateral sides. The esophagus soon flattens dorsoventrally (Fig. 3a). At first its epithelium is very thin but then thickens. It is not ciliated, but middorsally it has a mass of gland cells projecting inward. Near the level of the midventral portion of the brain, the esophagus widens and develops two folds; these mark the transition into the stomach. The first fold incorporates some of the glandular cells. The stomach epithelium, in which eosinophilous gland cells begin to predominate, has two folds that are contin-

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fluid; pc, precerebral septum of proboscis apparatus; pn, proboscis nerves; pr, proboscis in rhynchodeum; pw, proboscis sheath, consisting of interwoven circular and longitudinal muscles; rc, rhynchocoel; rd, rhynchodeum; vr, ventral ridge of proboscis sheath.

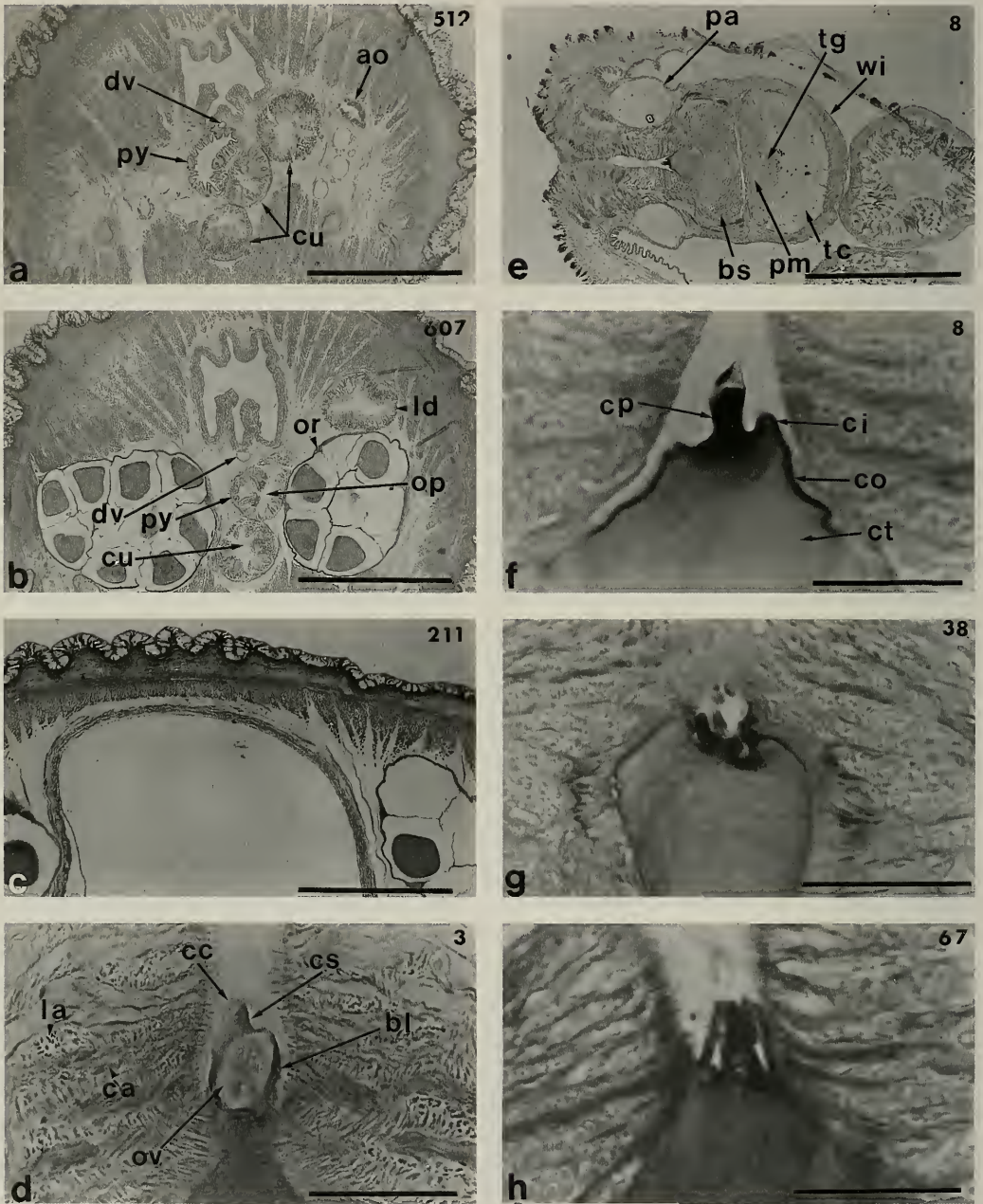


Fig. 4. *Nipponnemertes fernaldi*, new species. Transverse sections of anterior and middle portions of body, showing (a-c) successive changes in shape of rhynchoeol, (d) central stylet on ovoid anterior portion of basis in the holotype specimen, (e) columnar portion of basis in the holotype specimen, (f) central stylet damaged in shape in the specimen of paratype 1, (g) rectangular anterior portion of basis in the specimen of paratype 2, (h) anterior end of proboscis extruded outside, showing proboscis apparatus in the holotype specimen. Scale = 0.5 mm (a-c, e), 200  $\mu$ m (f, g) and 50  $\mu$ m (d, f-h). 3, 8, 38, and 67, number of sections of proboscis apparatus (d-h); 512 and 607, numbers of sections from anterior end of body (a, b); 211, section from middle portion of body (c). ao, anterior end of ovaries; bl, bulb-like basis of central stylet; bs, bolster; ca, circular muscle bundle of proboscis sheath; cc, cover of stylet; ci, collar-like ridge of massive posterior portion of basis (the ridge encircles the columnar portion of the basis); co, nearly conical part of posterior portion of basis, free of sur-

uous with those of the esophagus, as in most species of *Nipponnemertes*. At the level of the posterior end of the cerebral sensory organs, the stomach enlarges and develops a third fold (Fig. 2e). Over most of its length, the stomach is more than twice as wide as it is where it joins the esophagus (Fig. 2e). Beneath the stomach is a substantial mass of longitudinal body-wall muscle (Fig. 2e). Measured from the anterodorsal to posteroventral limits of the gastric folds, the stomach is about three times as long as the brain.

In the holotype, the pylorus, which follows the stomach, is about 1.5 mm long and about two and one-half times as long as the stomach. It originates from the right side of the stomach, between its lateral wall and its principal fold. The left side of the stomach continues posteriorly into a diverticulum formed as an artifact of contraction (Fig. 7c). The pylorus is oval in transverse section; it is about 0.25 mm wide at its junction with the stomach, and narrows to 0.15 mm at the point where it opens into the midgut (Fig. 4b). Its ciliated epithelium contains cyanophilous gland cells and is thus different from the lining of the postero-dorsal area of the gastric cavity (Fig. 7d).

In paratype 1, the pylorus is about 4 mm long and about three times as long as the stomach. The diverticulum of the stomach, about 0.6 mm long, has three caecal folds in its outer portion.

In the holotype, the intestinal caecum has four anterior tubular branches, of which three arise from the main caecum (Fig. 6b). Posteriorly, it has two pairs of lateral diverticula; those of the anterior pair are of unequal length and are parallel to the main caecum. Those of the posterior pair form a tube connected by a short duct to the main

caecum; this tube extends posteriorly beyond the pylorus. The intestinal caecum and anterior branches extend anteriorly for about half the length of the pylorus.

In paratype 1, the intestinal caecum has four anterior pouches that originate from the main caecum just anterior to where the first pair of lateral diverticula branch off; the main caecum does not extend any farther anteriorly. The intestinal caecum, about 1.5 mm long, extends anteriorly above the posterior portion of the pylorus for less than half its length.

Most of the lateral diverticula of the anterior part of the intestine are divided into dorsal and ventral lobes (Fig. 2f); the lobes are unequal and variable in number and length. The epithelium of the intestine contains eosinophilous gland cells. In the holotype, this part of the digestive tract, circular in transverse sections, does not have its own musculature, but in paratype 1, there are a few circular muscles in the wall of the intestine.

In paratype 2, the anus opens ventrally near the posterior end of the body. It is a slit about 100  $\mu\text{m}$  long, and has an inside diameter of 30  $\mu\text{m}$  transversely and 15  $\mu\text{m}$  dorsoventrally. The wall is 40  $\mu\text{m}$  thick. The rectum is 140  $\mu\text{m}$  long and is surrounded by a circular muscle layer 50  $\mu\text{m}$  thick. In paratype 1, the rectum has the same structure as in paratype 2. In the holotype, the series of sections of the posterior portion of the body is not complete.

*Blood-vascular system.*—The blood vascular system has three longitudinal vessels. The two cephalic blood vessels lateral to the rhynchodeum anastomose above the rhynchodeum near the tip of the head to form the cephalic loop. Farther posteriorly, however, the cephalic vessels become large

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rounding tissue; cp, columnar portion of basis; cs, central stylet; ct, bulbous part of posterior portion of basis, tightly bound to tissue; cu, intestinal caecum; dv, dorsal blood vessel; la, longitudinal muscle bundle of proboscis sheath; ld, lateral diverticula of midgut; op, opening of pylorus; or, ovary; ov, ovoid anterior portion of basis; pa, pouch of accessory stylet; pm, platelike muscular wall; py, pylorus; tc, dense connective tissue; tg, dense layer of glandular cells; wi, stylet bulb-wall consisting of circular muscle.

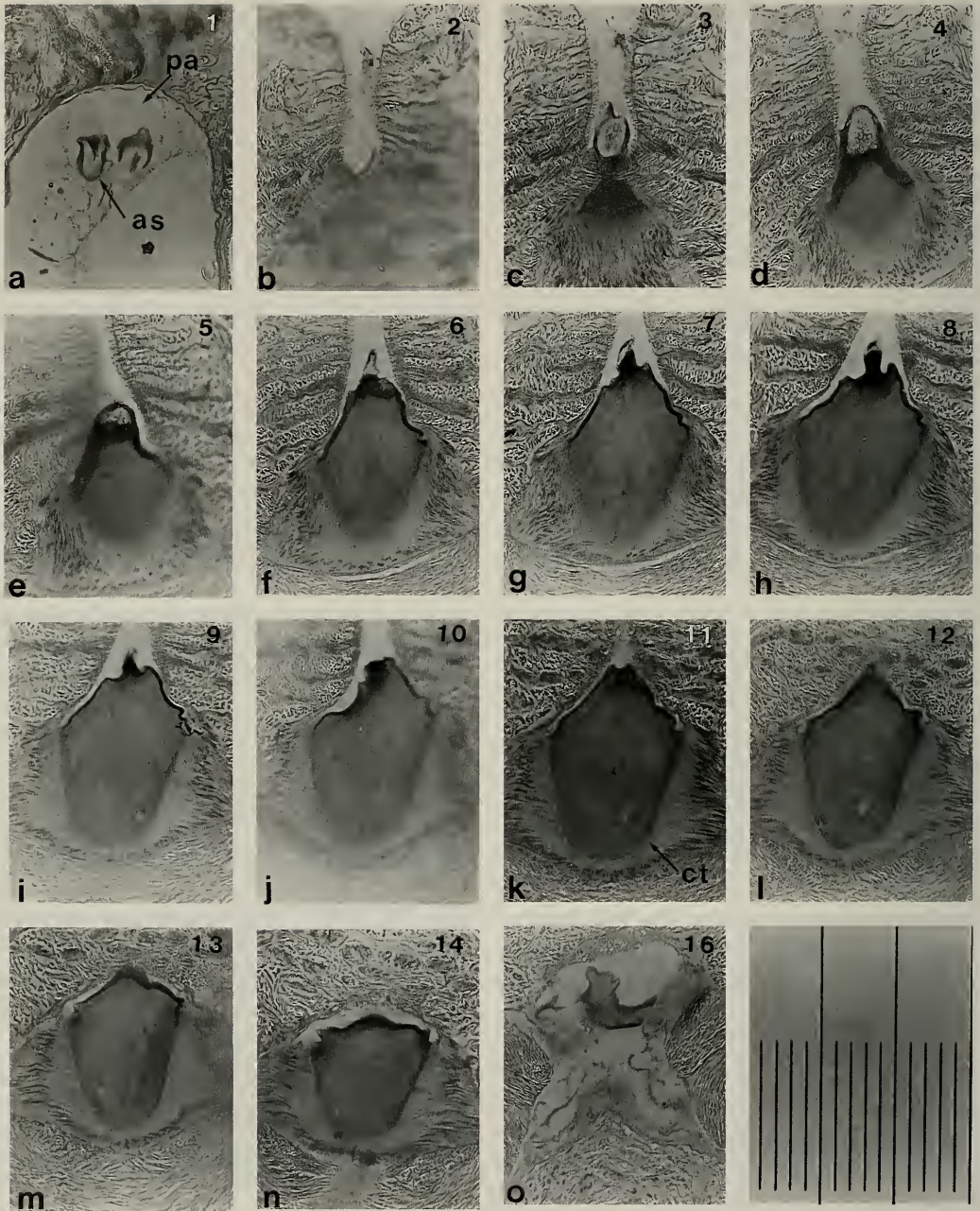


Fig. 5. *Nipponnemertes fernaldi*, new species. Successive transverse sections of proboscis apparatus in the holotype specimen (a-o), showing especially accessory stylet (a), bulbous proboscis vesicle (c-e), and obliquely oriented projection of columnar portion of basis (f-i). Scale = 150  $\mu$ m, 1-16, numbers of sections of proboscis apparatus. as, accessory stylet; ct, bulbous part of posterior portion of basis; pa, pouch of accessory stylets.

lacunae that turn medially in front of the brain. At the level of the anterior end of the ventral ganglia, they become narrowed into vessels that enter the brain ring without giving off cerebral vessels and then run alongside the rhynchocoel (Fig. 3g). In the holotype, the right vessel soon communicates with the dorsal vessel, which then enters the proboscis sheath, at the level of the posterior end of the brain, as a single median vascular plug, and extends medioventrally in the sheath as far as the anterior pyloric region, a distance of about 1.4 mm (Figs. 2e, 7c–e, g, 8e). This portion of the vascular plug seems to form a specialized communication with the rhynchocoel (Fig. 7e). After passing ventrally out of the rhynchocoel, the dorsal vessel continues posteriorly under the proboscis sheath between the rhynchocoel and the alimentary canal (Figs. 2f, 3h, 4a, b). In paratype 1, however, it is the left vessel that communicates with the dorsal vessel at the level of the posterior portion of the cerebral sensory organs or behind the brain, and the single median vascular plug extends as far as the middle pyloric region, a distance of about 3.1 mm.

Behind the cerebral organs, the lateral vessels enter the nephridial region, which extends from the posterior end of the cerebral organs to the level of the anterior portion of the pylorus (in the holotype) or to the level of the anterior portion of the intestine (in paratype 1) (Figs. 4a, 7c, d, f); there the vessels are dorsal to the lateral nerve cords.

Transverse anastomoses of the lateral vessels in the intestinal region were not observed.

In both paratype 1 and 2, the dorsal and lateral vessels anastomose just above the posterior end of the rectum, where a commissure of the lateral nerves and the end of the rhynchocoel come together at the same transverse level.

*Nervous system.*—The brain is situated immediately behind the large cephalic lacunae. The right lacuna is 340  $\mu\text{m}$  wide and 100  $\mu\text{m}$  high. The dorsal and ventral gan-

glia are not demarcated externally. The ventral commissure of the brain is situated near the anterior end of the brain and the ventral ganglia are not distinctly separated from the dorsal ganglia, except posteriorly. They become completely separated for a distance of 30  $\mu\text{m}$ . (Figs. 6c, 7g). The dorsal and ventral fiber cores are not divided anterior to the middle portion of the brain; the dorsal cores are more voluminous than the ventral cores. The dorsal ganglia do not extend as far posteriorly as the ventral ganglia, and dorsal and ventral lobes are lacking (Fig. 6c). A thick nerve cord from the posterior end of each dorsal ganglion enters the corresponding cerebral sensory organ (Figs. 6c, 7g). A long, thin dorsal commissure (40  $\mu\text{m}$  thick), and a short, much thicker ventral commissure (110  $\mu\text{m}$  thick), connect the right and left ganglia at about the same transverse level (Fig. 6c). In paratype 1, however, the dorsal commissure (70  $\mu\text{m}$  thick) is situated a short distance (30  $\mu\text{m}$ ) farther anterior than the ventral one (130  $\mu\text{m}$ ). The dorsal commissure curves upward to lie above the dorsal ridge of the proboscis sheath. On both sides, the brain is in contact with the dorsolateral wall of the esophagus, which is spanned dorsally by the ventral commissure. The brain and lateral nerves are covered by a thin neurilemma and a thick layer of fibrous connective tissue (Fig. 7h). In the intestinal region, however, the neurilemma of the lateral nerves is not evident. In the cerebral fiber core of each dorsal ganglion, there are numerous large cellular bodies (Fig. 8a, b), similar to those in *Nipponnemertes punctatulus* (reported by Iwata 1951) (Fig. 9c, d) and the reptant polystyliferan *Kameginemertes parmiornatus* (Iwata 1998). The structure of these cellular bodies is not clearly defined.

In the mass formed by the dorsal and ventral ganglia, there is, in the outer part of the right side of the brain, a large ganglion cell 20  $\mu\text{m}$  long; its nucleus measures 6  $\mu\text{m}$ . It is situated immediately behind the ventral commissure (Fig. 8c). A large gan-

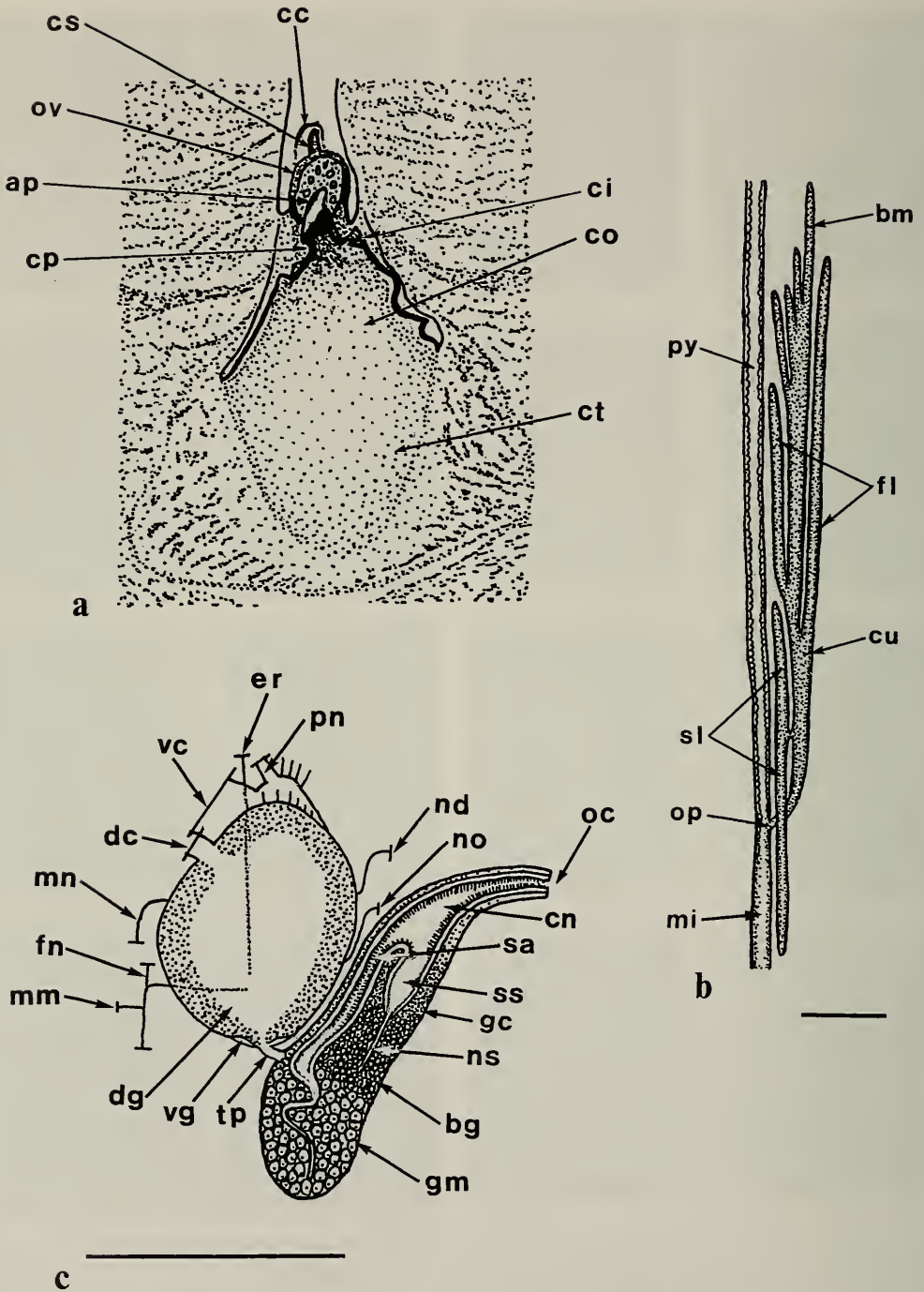


Fig. 6. *Nipponnemertes fernaldi*, new species. (a) Drawing of frontal sections of central stylet-basis complex of proboscis, (b) Drawing of dorsal view of caecum of midgut and pylorus, arranged laterally to the caecum of midgut, showing four branches and two pairs of tubular lateral diverticula, and (c) Drawing of dorsal view of brain and cerebral sensory organ (right side) showing relationships of these structure. Scale = 200  $\mu$ m (b) and 0.5 mm (c). ap, obliquely oriented projection of columnar portion of basis; bg, cyanophilous glandular mass of saclike canal; bm, branch of midgut caecum; cc, cover of central stylet; ci, collar-like ridge of massive posterior



gion cell on the left side was not observed. In paratype 1, large ganglion cells, 20  $\mu\text{m}$  long and containing nuclei measuring 10  $\mu\text{m}$ , lie medially in the brain, in the region of the ventral commissure (left) or behind it (right). It appears that the ganglion cells in this species are identical to Bürger type-3 ganglion cells, which are found in several cratenemertids (Bürger 1895). In the heteronemertean *Micrura leidyi*, Riser (1998) demonstrated a neurochord cell in the ganglionic layer of each ventral lobe of the brain and additional neurochord cells in the lateral nerve cords. His photomicrograph shows features similar to those of the large ganglion cell of *N. fernaldi*, but neurochords are lacking in both the brain and lateral nerve cords of this species.

In the intestinal region, the lateral nerve cords, ventrolateral in position, lie above the longitudinal musculature of the body wall, and they give off dorsal or dorsoventral peripheral nerves that extend toward the dorsal and ventral sides of the body (Fig. 8d).

Several slender but conspicuous nerves originate from the brain (Fig. 6c). They branch out pre- and post-cerebrally to supply various structures. A proboscis nerve trunk arises from the anterior side of each ventral ganglion and immediately extends to the proboscis sheath. Both proboscis nerves soon branch into seven nerves that lie on the lateral side of the sheath. Three small cephalic nerves, arranged one above the other and parallel to the proboscis nerve trunks, emerge from the anterior face of each ventral ganglion and proceed anteriorly

only on the ventral side of the cephalic region. Six small cephalic nerves originate from the dorsal ganglion a little farther posteriorly than the cephalic nerves on the ventral side, and they extend precerebrally to supply the eyes. A small nerve from each ventral ganglion extends anteriorly and then turns toward the outer side of the head, entering the dermis after passing the ventral side of the cerebral organ canal. A conspicuous nerve originates from the lateral surface of each ventral ganglion and runs anteriorly; its branches supply the oblique cephalic grooves. A small nerve from the lateral side of each dorsal ganglion extends anteriorly for a short distance and turns toward the lateral side of the head, innervating the ocelli of the most posterior group.

The midgut nerves originating from the medial side of each ventral ganglion run between the ventral ganglia and the foregut, extending posteriorly along the dorsolateral portion of the foregut (Figs. 6c, 8e). The foregut nerves are a conspicuous feature of this species. They emerge on the ventral wall of the ventral ganglion, continue along the lateral side of the foregut, and have a commissure under the esophagus (Fig. 8e). The esophagus nerves, under the rhynchodeum, emanate from the ventral surface of the ventral ganglia and extend anteriorly along the lateral sides of the esophagus, reaching beyond the brain.

Three nerves, originating from the ventral side of each ventral ganglion, separately control different regions of the gut. One runs beneath the rhynchodeum and the anterior part of the esophagus; one innervates

←

portion of basis (the ridge encircles the columnar portion of the basis); cn, cerebral organ canal; co, conical part of posterior portion of basis, free of surrounding tissue; cp, columnar portion of basis; cs, central stylet; ct, bulbous part of posterior portion of basis, tightly bound to tissue; cu, caecum of midgut; dc, dorsal commissure of brain; dg, dorsal ganglion; er, esophagus nerve; fl, first pair of lateral diverticula of midgut caecum; fn, foregut nerve; gc, ganglionic mass of cerebral ganglion; gm, eosinophilous glandular mass of sensory canal; mi, midgut; mm, commissure of foregut nerve; mn, midgut nerve; nd, nerve to dermis; no, nerve to ocelli; ns, narrow duct of sa-like canal; oc, opening of cerebral organ; op, opening of pylorus; ov, ovoid anterior portion of basis; pn, proboscis nerve; py, pylorus; sa, sensory canal; sl, secondary pair of lateral diverticula of midgut-caecum; ss, sac-type canal; tp, thick nerve from dorsal ganglion; vc, ventral commissure of brain; vg, ventral ganglion.

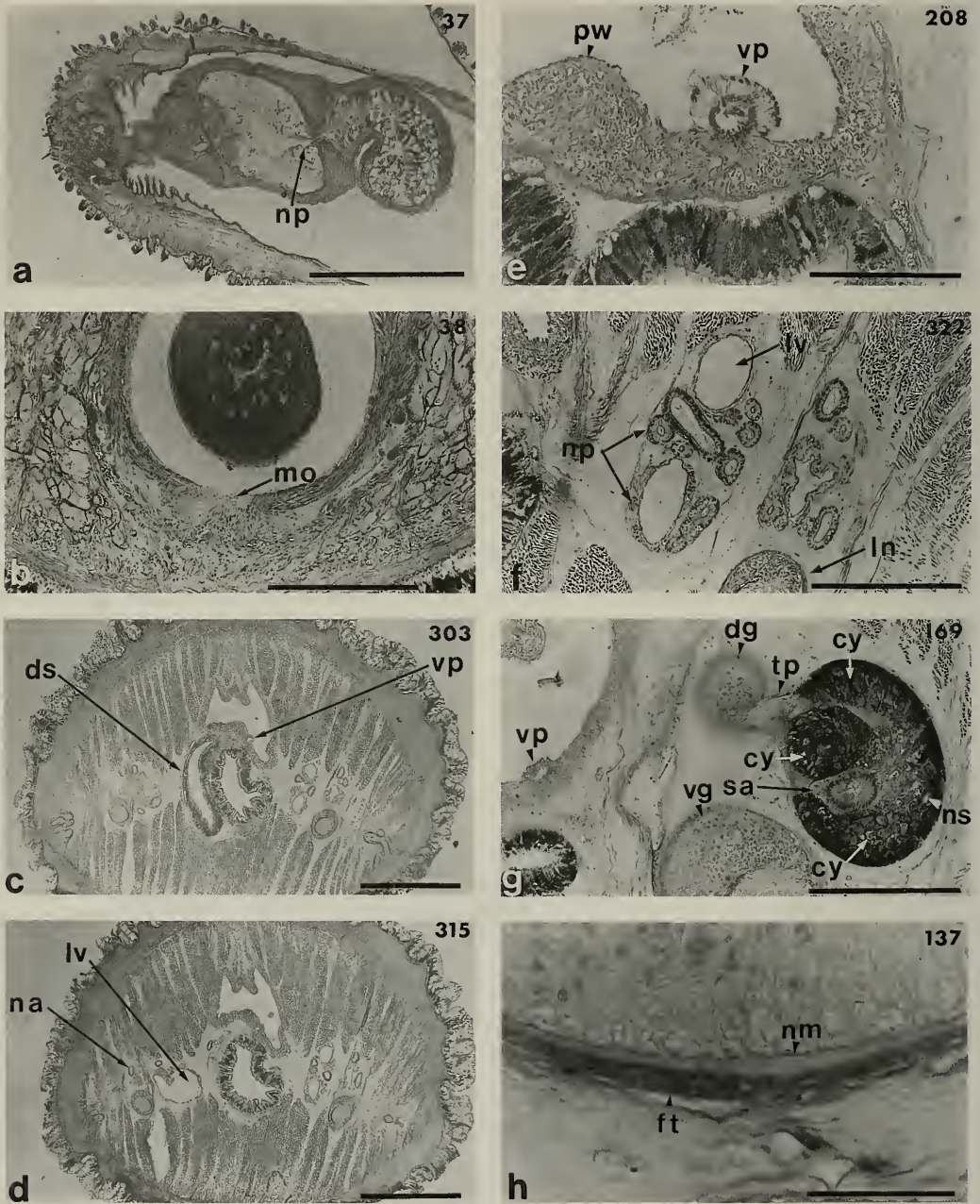


Fig. 7. *Nipponnemertes fernaldi*, new species. Transverse section of proboscis apparatus in the holotype specimen (a), showing narrow canal in thick connective tissue of stylet bulb. Transverse sections of anterior portion of body, showing (b) mouth opening to rhynchodeum, (c) diverticulum of stomach, (d) pylorus, (e) vascular plug inside proboscis sheath, (f) nephridium, (g) thick nerve from dorsal ganglion to cerebral sensory organ, and (h) neurilemma and fibrous connective tissue of brain. Scale = 0.5 mm (a, c, d, h), 200  $\mu$ m (b, f, g), 100  $\mu$ m (e) and 50  $\mu$ m (h). 37, number of section of proboscis apparatus (a) and 38–315; numbers of sections from anterior end of body (b–h). dg, dorsal ganglion; ds, diverticulum of stomach; ft, fibrous connective tissue; ln, lateral nerve; lv, lateral blood vessel; mo, mouth; na, nephridium; nm, neurilemma; np, narrow canal in thick connective tissue and muscular wall of stylet bulb; ns, narrow duct of sac-type canal; pw, proboscis sheath, consisting of interwoven circular and longitudinal muscles; tp, thick nerve from dorsal ganglion; vg, ventral ganglion; vp, vascular plug inside proboscis sheath.

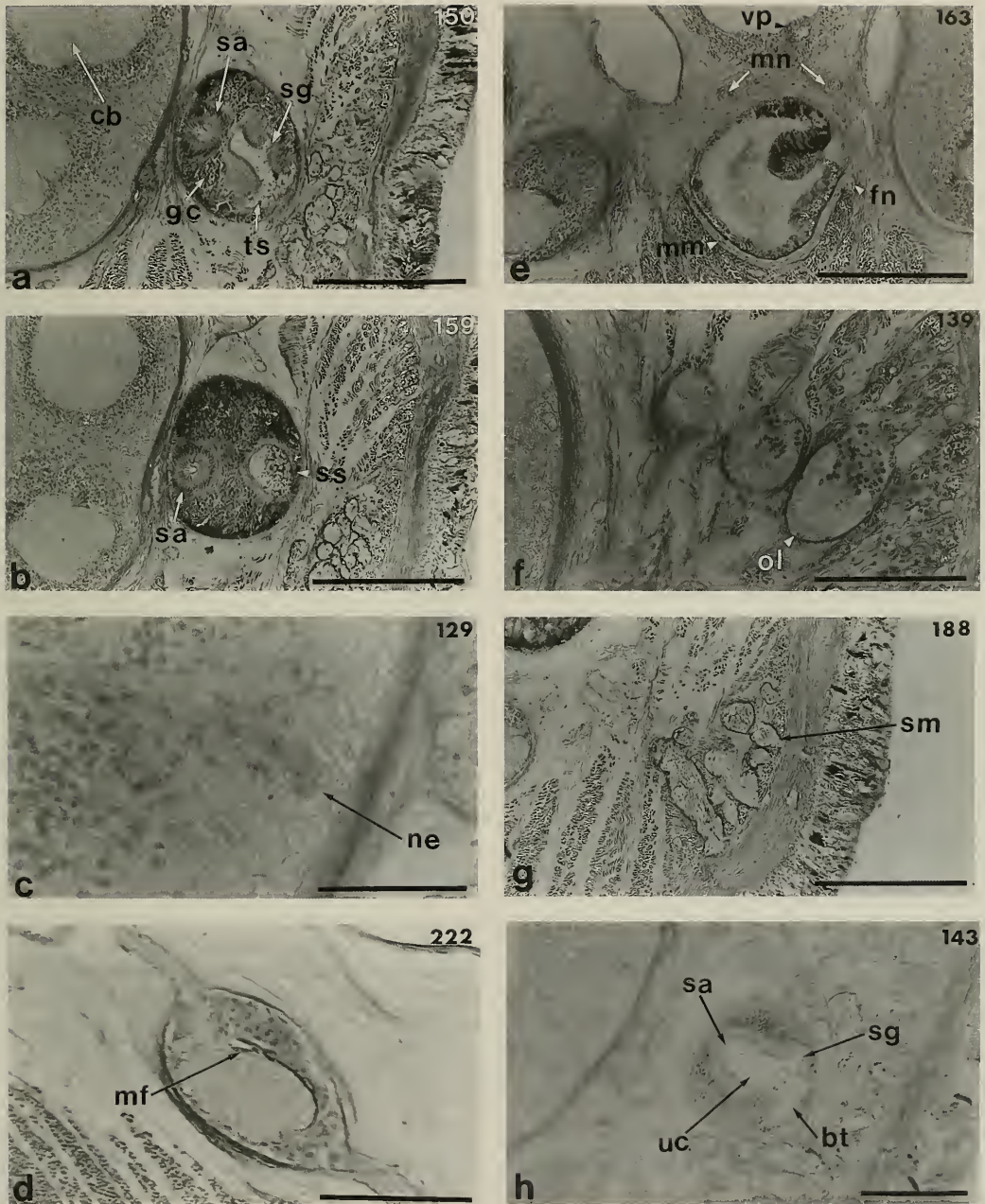


Fig. 8. *Nipponnemertes fernaldi*, new species. Transverse sections of anterior portion of body, showing (a, b) sensory canal and saclike canal after separation from cerebral organ canal, (c) large ganglion cell, (d) lateral nerve cord, (e) nephridium, (f) ocelli, (g) submuscular gland, and (h) posterior end of cerebral organ canal. Scale = 200  $\mu\text{m}$  (a, b, e, g), 100  $\mu\text{m}$  (d, f, h) and 50  $\mu\text{m}$  (c). 129–188, numbers of sections from anterior end of body (a–c, e–h); 222, number of section from anterior end of middle portion of body (d). bt, beginning of T-shaped canal; cb, cellular body in dorsal ganglion; fn, foregut nerve; gc, ganglionic mass of cerebral sensory organ; mf, myofibril; mm, commissure of foregut nerve; mn, midgut nerve; ne, large ganglion cell; ol, ocelli; sa, sensory canal; sg, shallow lateral groove; sm, submuscular gland; ss, sac-like canal; ts, sac epithelium; uc, U-shaped ciliated sensory portion; vp, vascular plug inside proboscis sheath.

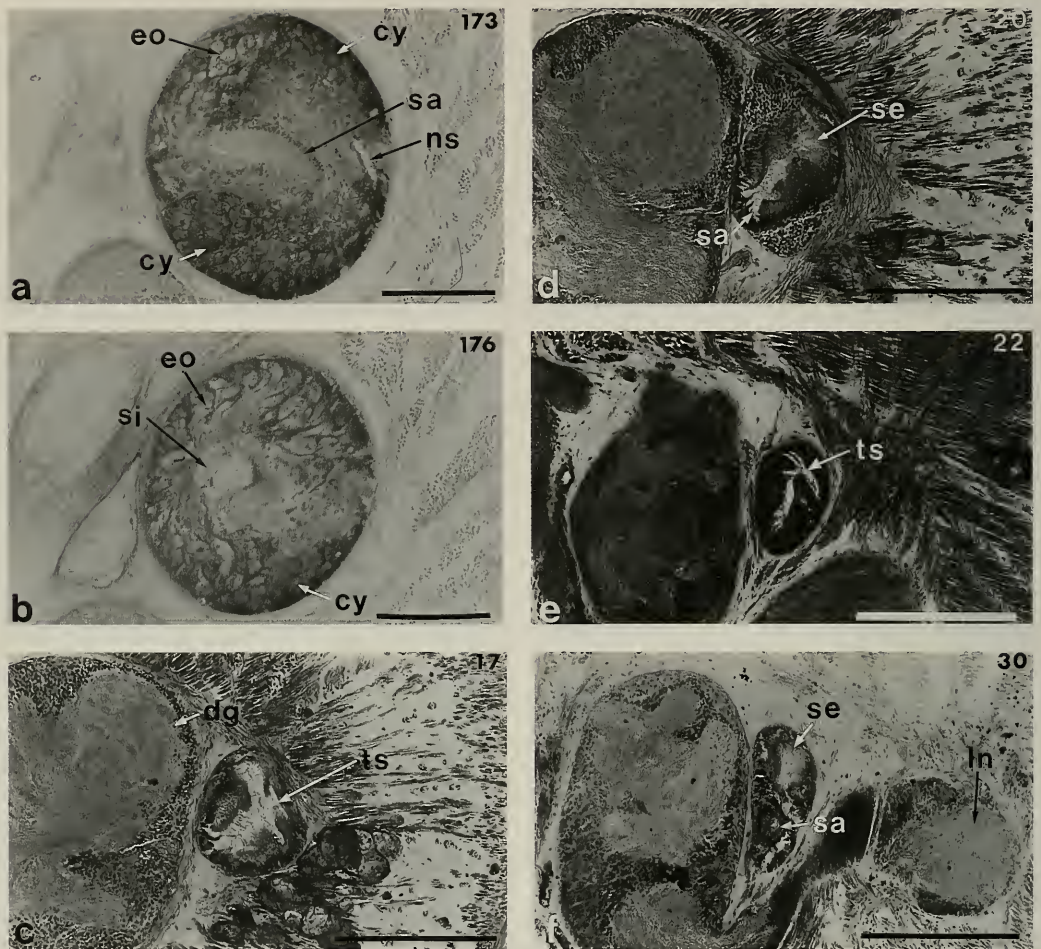


Fig. 9. *Nipponnemertes fernaldi*, new species. Transverse sections of posterior portion of cerebral sensory organ. *Nipponnemertes bimaculatus*, transverse sections showing (c) sensory canal and sac (lumen T-shaped) and (d) sensory canal and sac without epithelium. *Nipponnemertes punctatulus*, transverse sections showing (e) sensory canal and sac (lumen T-shaped) and (f) sensory canal and sac without epithelium. Scale = 200  $\mu\text{m}$  (d–f) and 50  $\mu\text{m}$  (a, b). 173 and 176, numbers of sections from anterior end of body; 17, 20 and 22, 30, numbers of sections of proboscis apparatus (c–f). cy, cyanophilous glandular mass; dg, dorsal ganglion; eo, eosinophilous glandular mass; ln, lateral nerve; ns, narrow duct of sac-like canal; sa, sensory canal; se, sac; si, sensory canal in eosinophilous glandular mass; ts, sac epithelium with T-shaped lumen.

the posterior part of the esophagus, as well as the stomach and pylorus; the last innervates the midgut.

The middorsal nerve lies in the dermis just above the circular muscle layer of the body wall and extends beyond the brain anteriorly, below the dorsomedial longitudinal grooves (Fig. 2d). Its origin from the dorsal commissure of the brain was observed in paratype 1 but was not clear in the holotype. The lateral nerves, with myofibrillae,

give off peripheral nerves and are posteriorly connected to each other by a commissure on the dorsal side of the rectum (Fig. 8d). Myofibrillae in the lateral nerves are situated on the dorsal side between the outer ganglion mass and the inner fibrous core. Myofibrillae have been described for some members of the Cratenemertidae (Crandall 1993a, b; Crandall & Gibson 1998; Riser 1998).

*Special sensory organs and frontal or-*

*gan.*—In the holotype, the ocelli, counted in transverse sections of the head, number 76. They are large and confined to the area between the flattened anterior end of the head and the middle region of the brain. There are 34 ocelli on the right side of the head and 35 on the left. Two groups on each side are recognizable; one consists of 23 (right) and 24 (left) ocelli lateral to the rhynchodeum, and the second consists of 11 (right and left) ocelli; three (right) and four (left) near the middle region of the brain are arranged dorsoventrally along the lateral sides of the head (Fig. 8f).

In paratype 1, there are 78 ocelli, 39 on both sides. Of the two groups on the right side; one consists of 22 ocelli, and the other consists of 14; of the two groups on the left side, one consists of 25 ocelli, the other consists of 11. Three ocelli (right and left) near the middle region of the brain are arranged as in the holotype specimen. In paratype 3 (Fig. 1h), there are 52 ocelli, 26 on both sides. 13 are marginal, 10 are on the anterior oblique cephalic grooves, and 3 are behind it. The arrangement of ocelli in paratype 2 was not studied.

The ocelli are of the inverted pigment-cup type and have dimensions of up to 90  $\mu\text{m}$  wide and 110  $\mu\text{m}$  high (Fig. 8f).

The cluster of frontal gland cells, which fan out into separate strands in the dorsal side of the head, is not large. In both the holotype and paratype 1 the cluster extends to the region of the proboscis insertion without reaching posteriorly to the cerebral ganglia (Figs. 3a–c, 7b). The frontal glands deliver their secretions to a pit at the anterior tip of the snout (Fig. 2g, h). The pit represents a frontal organ.

The cephalic glands, confined to the lateral sides of the head, are found close to the frontal glands. The lateral bands of mucoid glands are posterior extensions of the cephalic glands. Below the frontal organ, there is a narrow and short ciliated groove running posteriorly to the dorsal side of the rhynchodeal opening (Fig. 2g, h). In para-

type 1, this groove continues to the opening of the rhynchodeum.

The posterior extensions of the mucoid cephalic glands, namely the submuscular glands, are situated laterally in the foregut region, beginning at the level of the anterior end of the cerebral organs (Fig. 8g).

The cerebral organs, 510  $\mu\text{m}$  long, are very large and extend behind the cerebral ganglia (Fig. 6c). For about 180  $\mu\text{m}$  of its length, each is closely adjacent to the brain, which has a length of 460  $\mu\text{m}$ . Anteriorly, the organ is circular in transverse section, but it becomes oval farther posteriorly (Fig. 7g), and its posterior glandular portion is circular (Fig. 9b). The cerebral organ canal, ciliated and 220  $\mu\text{m}$  long, begins at one of the secondary grooves of the anterior oblique cephalic grooves on the midlateral portion of the head, and is directed posteromedially. It widens just before entering the cerebral organ and forms a U-shaped, ciliated sensory portion (Fig. 8h). The epithelium of this is 20  $\mu\text{m}$  thick. The canal has a widened lateral portion with a dorsally directed small groove lined with unciliated epithelium 8  $\mu\text{m}$  thick (Fig. 8h). Farther posteriorly, the canal divides into a narrow sensory canal and a short, sac-like canal that has a T-shaped configuration when seen in transverse sections (Fig. 8a), and the dorsally directed groove disappears (Fig. 8a, b).

The sensory canal, 20  $\mu\text{m}$  thick, lies on the side closest to the brain (Figs. 7g, 8a, b). It consists of a ciliated wall in which the sensory cells containing eosinophilous cytoplasm are arranged in a row. Farther posteriorly, the ciliation disappears and the canal enters a mass of eosinophilous glands about 40  $\mu\text{m}$  long and 20  $\mu\text{m}$  wide (Figs. 6c, 9a, b). The total length of the canal is about 260  $\mu\text{m}$ .

The anterior portion of the sac-like canal (Fig. 6c), 80  $\mu\text{m}$  by 60  $\mu\text{m}$  in diameter and about 110  $\mu\text{m}$  long, has a wall 10  $\mu\text{m}$  thick. Its unciliated epithelium consists of slightly eosinophilic cells 6  $\mu\text{m}$  wide; these are arranged in one or two layers (Fig. 8b). Its

Table 1.—Summary of the main morphological characters of eleven marine nemerteans related to the genus *Nipponemertes* including *N. fernaldi*, new species.

Character	Character states	Coding
1. Body color	With pattern	0
	Without pattern	1
2. Cephalic grooves	Two pairs of oblique cephalic grooves and dorsomedial longitudinal grooves	0
	Two pairs of fluted cephalic grooves and inconspicuous oblique grooves	1
	A pair of shallow oblique fluted grooves	2
	A pair of lateral transverse grooves	3
	No record	4
3. Cephalic grooves	Anterior oblique cephalic groove subdivided by 14 secondary grooves, ventrolateral surface of head with 7 secondary grooves, posterior oblique cephalic grooves originating at the end of dorsomedial longitudinal grooves, and dorsomedial longitudinal grooves forming anteriorly a pair of epidermal folds	0
	No record	1
4. Ocelli	Numerous large ocelli in four groups	0
	In lateral rows	1
5. Body wall	Longitudinal muscle layer well developed	0
	No record	1
6. Diagonal muscles	Present between circular and longitudinal muscle layers	0
	No record	1
7. Dermis	Thick	0
	No record	1
8. Rhynchocoel	Nearly equal to body length	0
	No record	1
9. Proboscis sheath	Composed of interwoven circular and longitudinal muscles	0
	No record	1
10. Rhynchodeum	Provided with a circular muscle layer	0
	No record	1
11. Precerebral septum	Composed of muscular septum surrounding rhynchodeum	0
	Composed of muscular bundle	1
	No record	2
12. Proboscis diaphragm	Provided with central stylet-basis complex	0
	Provided with a single central stylet and a barrel-, bell-, drop-shaped or conical basis	1
	No record	2
13. Basis of central armature	With posteriorly-inserted accessory stylet	0
	No record	1
14. Stylet bulb	With a plate-like muscular wall and a thick layer of glandular cells	0
	No record	1
15. Accessory stylet pouches	2	0
	2 or more	1
	No record	2
16. Proboscis nerves	11	0
	12–14	1
	14	2
	14–16	3
	15	4
	20	5
17. Mouth	No record	6
	Opening into rhynchodeum	0
18. Esophagus	Anterior to brain surrounded by longitudinal muscle	0
	No record	1
19. Foregut caecum	Esophageal caecum present	0
	Stomach caecum present	1
	No record	2

Table 1.—Continued.

Character	Character states	Coding
20. Intestinal caecum	Without anterior diverticula but with lateral ones	0
	With a pair of anterior diverticula sending off numerous branches	1
	No record	2
21. Intestinal caecum and diverticula	Intestinal caecum with anterior branches or pouches and two pairs of lateral diverticula, and intestinal diverticula branched	0
	No record	1
22. Blood vascular system	With three longitudinal vessels, middorsal vessel with single vascular plug	0
	No record	1
23. Nervous system	Brain and lateral nerves covered by a thin neurilemma and a thick layer of fibrous connective tissue, nervous system without neurochord cells, and accessory lateral nerves, middorsal nerve extending anteriorly beyond brain, and lateral nerve cords with myofibrillae and peripheral nerves	0
	No record	1
	No record	1
24. Ventral ganglia	Not distinctly separated from dorsal ganglia	0
	Posteriorly separated	1
	No record	2
25. Dorsal ganglia	Without bifurcated fiber core	0
	No record	1
26. Nerve cords	Paired midgut, foregut, and esophagus nerves originating from ventral brain	0
	No record	1
27. Frontal organ	Present	0
	No record	1
28. Cephalic glands	Well developed and reaching posteriorly to cerebral ganglia	0
	Prominent but reaching posteriorly to cerebral ganglia	1
	Moderately developed	2
	Small	3
29. Submuscular glands	Abundant in brain region	0
	Limited to a narrow area	1
	Absent	2
	No record	3
30. Cerebral sensory organ	Large and extending behind cerebral ganglia	0
31. Cerebral sensory organ	With neurilemma and cerebral organ canal branching into medial sensory canal and lateral sac-like canal with two kinds of glandular masses	0
	No record	1
32. Cerebral organ canal	Open laterally in front of brain	0
	Far anterior to brain	1
	No record	2
33. Excretory system	Pair of excretory pores lateral to nerve cords and situated in posterior portion of nephridial region	0
	Situated at middle of nephridial region	1
	Situated behind cerebral sensory organs	2
	No record	3
34. Sexes	Separated	0
	No record	1

very first part is still T-shaped in transverse section, and still has a shallow, dorsally directed lateral groove (Fig. 8a). The sac-like canal is succeeded by a narrow duct, 180  $\mu\text{m}$  long, surrounded by cyanophilous

glands about 20  $\mu\text{m}$  long and 15  $\mu\text{m}$  wide (Figs. 6c, 7g, 9a).

The internal configuration of the sensory canal and the sac-like canal can be understood by studying transverse sections at

their proper levels in Figures 6c, 7g, 8a, b, 9a, b. The term "sac-like canal" is used here because this structure has a thick epithelium and also because it has cyanophilous glands (cf. Crandall 1993a).

The ganglionic mass of the cerebral organ is mostly confined to the anterior portion of the organ, where it surrounds the sensory canal and sac-like canal. Glands are not present at the bifurcation of the cerebral organ canal (Fig. 8h). All of the organs are covered with connective tissue from the neurilemma of the cerebral nerve. The thick nerve from the posterior end of the dorsal ganglion enters the posterior portion of the glandular mass of the sac-like canal (Figs. 6c, 7g).

*Excretory and reproductive systems.*—The excretory tubules wind around and along the lateral blood vessels (Figs. 4a, 7c, d, f). In the holotype, they extend from the level of the posterior portions of the cerebral sensory organs to the level of the posterior part of the pylorus; the region they occupy is 3.6 mm long. The efferent duct, beginning in the middle portion of the nephridial region, is conspicuous and extends above and lateral to the lateral nerve cord, reaching the excretory pore on the lateroventral side of the body. The pore is ventral to the lateral nerve cord, and is at the level of the mid-pyloric region. The efferent duct of the left side, about 120  $\mu\text{m}$  long, is much longer than that of the right side. The left excretory pore is located about 810  $\mu\text{m}$  farther posterior than the right pore.

In paratype 1, the excretory tubules extend from the level of the posterior end of the cerebral sensory organs to a short distance behind the pylorus; the region they occupy is 5.4 mm long. The efferent ducts, beginning in the posterior portion of the nephridial region, are 200  $\mu\text{m}$  long; the excretory pores are situated at their anterior ends.

The ovaries of the fully mature holotype specimen are located near the beginning of the intestinal caecum, and are arranged irregularly between the intestinal diverticula

(Figs. 2f, 4a, b). Gonoducts open at gonopores on the lateral sides of the body. In the other two sectioned paratypes, both males, the gonads are undifferentiated and lack gonoducts.

*Swimming.*—The specimens were observed to swim vigorously in the laboratory when the container was shaken. During swimming the body became more flattened and the swimming pattern was anguilliform, resembling that of a *Cerebratulus*. Swimming has been described for the hoplonemertean *Nipponnemertes punctatulus* (Coe 1905) and *N. pulcher* (McIntosh 1873, Brunberg 1964, Berg 1972).

#### Discussion of Systematics\*

The species described here is a member of the suborder Monostilifera (sensu Gibson 1995), owing to the morphology of the armature of the proboscis and the location of the mouth opening. It fits in the family Cratenemertidae (Friedrich, 1968) with respect to the following characteristics: rhynchoel wall with interwoven muscle layers of the proboscidial sheath; rhynchoel extending nearly to the posterior tip of the body; cerebral organs large, extending behind the cerebral ganglia (Berg 1985, Gibson & Crandall 1989, Crandall & Gibson 1998).

The cratenemertid genus *Nipponnemertes* (type species: *Nipponnemertes punctatulus* (Coe, 1905), recently designated by Crandall (2001), is closest to the present species, especially with regard to the features cited in the generic diagnosis. Comparisons with other related species are found in Tables 1 and 2.

The arrangement of ocelli in *N. fernaldi* is virtually the same as that of all other Pacific *Nipponnemertes*, and the close juxtaposition of the end of the rhynchoel and the two posterior anastomoses also occurs in a few species of *Nipponnemertes*. In most cratenemertids, the anastomoses of blood vessels and lateral nerves are decid-



Table 2.—Character matrix for species of *Nipponnemertes*. Character numbers refer to Table 1.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
<i>N. drepanophoroides</i>	0	4	1	1	1	1	1	1	0	1	2	2	1	1	2	6	0	1	2	2	1	1	1	1	2	1	1	1	0	1	0	3	1		
<i>N. pacificus</i>	0	3	1	1	1	1	1	0	0	2	2	1	1	1	2	0	1	2	2	0	1	0	1	2	2	1	1	1	0	1	0	2	0		
<i>N. occidentalis</i>	1	3	1	1	1	1	0	1	0	2	2	2	1	1	0	6	0	1	0+1	1	1	1	1	2	2	1	1	1	2	0	1	2	0		
<i>N. punctatulus</i>	1	2	1	0	0	1	0	0	0	2	2	1	1	1	0	1	0	1	2	0	1	0	1	0	0	0	1	1	0	1	0	0	0		
<i>N. bimaculatus</i>	0	1	1	0	0	1	0	0	0	2	2	1	1	1	3	0	1	0	0	0	1	1	1	0	0	0	1	1	2	1	0	0	2	0	
<i>N. pulcher</i>	0	0	1	1	0	1	0	0	1	0	1	1	0	1	0	1	0	1	2	0	1	0	1	0	0	0	1	0	0	1	0	2	0	0	
<i>N. africanus</i>	1	4	1	1	1	1	0	0	1	2	2	2	1	1	0	0	1	2	2	2	1	1	1	2	2	1	1	0	1	3	0	1	0	2	0
<i>N. magnus</i>	0	4	1	0	1	0	0	0	1	2	2	2	1	1	2	5	0	1	2	2	1	1	1	2	2	1	1	1	3	3	0	1	0	1	0
<i>N. marioni</i>	0	4	1	0	0	1	0	0	1	2	2	2	1	1	0	4	0	1	2	0	1	1	1	2	2	1	1	0	0	3	0	1	0	0	0
<i>N. schollaerti</i>	0	3	1	1	0	1	0	0	1	2	2	2	1	1	0	2	0	1	2	0	1	1	1	2	2	1	1	0	0	0	1	0	0	0	0
<i>N. fernaldi</i>	0	2	0	0	0	0	0	0	0	0+1	0	0	1	0	1	2	0	0	2	0	0	0	0	0+1	0	0	0	2	1	0	0	0	0	0	0

edly posterior to the end of the rhyncho-coel.

Concerning the structure of the cerebral organs, Gibson (1988) stated that the cerebral organs of Antarctic species of *Nipponnemertes* resemble those of inaequifurcate Eurentantia in being large and elaborate structures, close to and reaching behind the cerebral ganglia; furthermore, their cerebral canals are divided. Gibson (1988) also pointed out that the cerebral organs of *Nipponnemertes* appear much more highly evolved than those of almost all Monostilifera, and that their organization and position may be indicative of a closer evolutionary relationship to Reptantia than has previously been appreciated. On the basis of these features, Gibson (1988) pointed out that there are similarities between *Nipponnemertes* and Reptantia (Inaequifurcata). Crandall (1993a) wrote that *N. bimaculatus* (*Amphiporus bimaculatus*), now known to be a cratenemertid, possesses a canal that divides, just after entering the cerebral organ, into two branches: a sensory branch having a uniform elliptical cross-section throughout its length, and a shorter branch of similar size but complex shape, lined with characteristic ‘sac-like’ epithelium.

*Nipponnemertes bimaculatus* from Rishiri Island in Hokkaido, Japan (Iwata 1954) has large cerebral organs situated at the lateral side of the brain and extending posteriorly behind the brain. In addition, the muscle layer of the proboscis sheath is interwoven, a feature clearly evident in my slides. The cerebral organs are like those in the present species (Fig. 9c, d). *Nipponnemertes punctatulus* from Onomichi (Iwata 1951) has several characters of the genus: large cerebral organs situated at the lateral side of the brain and extending posteriorly behind the brain; the interwoven muscle layer of the proboscis sheath; similarity of the cerebral organs to those of *N. bimaculatus* (Fig. 9e, f); and a distinct rectum with circular muscle sphincter.

*Nipponnemertes fernaldi* is distinctive because of the following features: a central

stylet-basis complex of unique structure; a bulblike stylet bulb with a platelike muscular wall and a thick layer of glandular cells; an intestinal caecum with four branches or pouches and two pairs of lateral diverticula; a pair of dorsomedial longitudinal epidermal folds in the anterior region. These features have not been reported for cratenemertids of the genus *Nipponnemertes* until now. The combination of characters found in *N. fernaldi* decidedly excludes it from the existing species of *Nipponnemertes* (Griffin 1898, Coe 1901, 1905; Punnett 1903, Wheeler 1934, 1940; Iwata 1951, 1954; Friedrich 1968, Berg 1972, 1985; Gibson 1995, Crandall & Gibson 1998). Because of this, a new species is proposed to accommodate it.

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\* Editor's note: The author mentioned the taxon as *Nipponnemertes fernaldi* nov. sp. in an abstract published in the Japanese journal *Taxa* (no. 11, 2001) in September 2001. However, this publication of it did not make the name 'available', since no type specimen was designated therein as required by Article 72.3 of the International Code of Zoological Nomenclature (4th Ed., 1999). The full description and designation of type specimens in this issue of the *Proceedings of the Biological Society of Washington* 114(4):833–857, make the name available for the first time, and it is correctly used therein as *Nipponnemertes fernaldi* n. sp.

***Dhondtichlamys*, a new name for *Microchlamys* Sobetski, 1977  
(Mollusca: Bivalvia: Pectinidae), preoccupied by *Microchlamys*  
Cockerell, 1911 (Rhizopoda: Arcellinida)**

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*Abstract.*—The Cretaceous pectinid subgenus name *Chlamys* (*Microchlamys*) Sobetski, 1977, is preoccupied by *Microchlamys* Cockerell, 1911, a protozoan. The new name *Dhondtichlamys* is introduced to replace the junior homonym.

Sobetski (1977:56) introduced a new subgenus, *Chlamys* (*Microchlamys*), for a group of Eurasian Upper Cretaceous bivalves of the family Pectinidae. The type species designated by Sobetski is *Pecten pulchellus* Nilsson, 1827, the type stratum and locality of which are the Campanian greensands at Köpingemölla, Sweden (Dhondt 1972:19). These Cretaceous glauconitic sandstones occur in the Köpings district, which includes Köpingemölla, and are now referred to by the informal name "Köpings sandstone." Christensen (1986) described two belemnite assemblages from it, the older indicating a latest Early Campanian age and the younger a middle Late Campanian age. Kennedy and Christensen (1997) recorded ammonites from this sandstone that indicated an age compatible with the younger belemnite assemblage. Nilsson's material likely came from that part of the Köpings sandstone that yielded the ammonites and therefore is probably of middle Late Campanian age (W. K. Christensen, in litt.).

Vokes (1980:229) reported that Sobetski's subgenus name is preoccupied by *Microchlamys* Cockerell, 1911 (a rhizopodan protozoan of the order Arcellinida), but Sobetski did not rename the taxon before his death in 1988. As required by the International Code of Zoological Nomenclature

(Fourth Edition, Article 60.3), I replace *Microchlamys* Sobetski, 1977, with *Dhondtichlamys*, new name, based on the same type species, *Pecten pulchellus* (ICZN Recommendation 60A). The name honors Dr. Annie V. Dhondt, Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels, for her many contributions to our knowledge of Cretaceous Pectinidae. She was the first (Dhondt 1972) to recognize the taxonomic significance of the group of species that Sobetski later named.

In addition to the type species, *Dhondtichlamys* includes eight of the nine species that Sobetski (1977) included in *Microchlamys*: *Pecten acuteplicatus* Alth, 1850; *P. arlesiensis* Woods, 1902; *P. campaniensis* d'Orbigny, 1847; *P. inflexus* Hagenow, 1842; *P. puggaardi* Ravn, 1908; *Chlamys* (*Microchlamys*) *subacutiformis* Sobetski, 1977; *P. subaratus* Nilsson, 1827; and *Chlamys* (*Aequipecten*) *wisniowskii* Pasternak, 1961. He originally also included *P. trisulcus* Hagenow, 1842, but later (Sobetski in Sobetski et al. 1982) moved this species to *Chlamys* (*Chlamys*). Dhondt (1972) had earlier included essentially the same assemblage, with the addition of *Pecten sarumensis* Woods, 1902, under the now obsolete combination "*Lyropecten* (*Aequipecten*)." She determined that *P. inflexus* is a junior homonym, which she renamed *Lyr-*

*opecten (Aequipecten) subinflexus* Dhondt, 1972. She also regarded *Pecten puggaardi* and probably also *P. wisniowskii* as junior synonyms of *Pecten campaniensis*. Sobetski et al. (1982) added three new species, *Chlamys (Microchlamys) acuticostata* Sobetski, 1982, *C. (M.) plestshejevi* Sobetski, 1982, and *C. (M.) entis* Sobetski, 1982.

Collectively, the above assemblage of species ranges in age from Albian to Maastrichtian and occurs in Great Britain, Eurasia, and Egypt. As noted by Dhondt (1972: 13, 40), the genus also includes a species from the Upper Cretaceous of eastern North America, *Pecten venustus* Morton, 1833. Darragh & Kendrick (1991:55) described a new species, *Chlamys (Microchlamys) propealebroa*, from the Maastrichtian of northwestern Australia, this being the first record of the genus in the Southern Hemisphere. Stilwell (1998:44), however, questioned this generic placement. It is likely that *Dhondtichlamys* survived the end-Cretaceous mass extinction (Waller 1991, Waller & Marinovich 1992), but Paleocene or Eocene specimens remain poorly documented (for example, *Pecten farafrensis* Zittel, 1883, a nomen nudum discussed by Dhondt 1972:28). Waller (1991) and Waller & Marinovich (1992) used *Microchlamys* at the genus rather than the subgenus level for phylogenetic reasons, a usage that was followed by Dhondt et al. (1996:57) and Dhondt & Jagt (1997:44).

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## Sipuncula from Antarctic waters

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*Abstract.*—A collection of 3156 Sipuncula from water south of 53° S latitude collected by several American expeditions during 1948–1986, at depths from 1–5790 m yielded 11 species. Only *Apionsoma murinae* (both subspecies) are new to this region but the known longitudinal ranges of the others are expanded. There is one numerically dominant species in each of the other three genera: *Golfingia margaritacea*, *Phascolion lutense* and *Nephasoma diaphanes*. Comments on the morphology of each taxon are presented plus a general observation about the deciduous nature of introvert hooks across these four genera. An illustrated key and distribution maps are provided.

*Resumen.*—Se estudia una colección de 3156 ejemplares de sipuncúlidos procedentes de los mares antárticos situados por debajo de los 53° latitud sur, siendo encontrándose un total de 11 especies. *Apionsoma murinae* (ambas subespecies) representan citas nuevas para la zona investigada, mientras que se amplían los rangos de distribución longitudinal de las otras especies identificadas. Una de las especies de cada uno de los géneros restantes: *Golfingia margaritacea*, *Phascolion lutense* y *Nephasoma diaphanes*, siempre es particularmente abundante en la colección. Asimismo se presentan comentarios sobre la morfología de cada taxon identificado, destacándose la naturaleza caediza de los ganchos de la trompa en los 4 géneros investigados. Finalmente se incluyen claves de identificación y mapas de distribución de todas las especies tratadas.

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This report is based on 3156 specimens collected at 456 stations over 38 years (1948–1986) by several American research vessels, Operation Deepfreeze contributed a few in 1948, then no more until 1956. Most of the collecting was done over the next two decades, with less intensity from the mid 1970's through the mid 1980's. Among the ships making the largest contribution are the R/V *Eltanin*, *Hero*, *Glacier*, and *Islas Orcadas*, but there were several others as well as a few land based operations.

Initial processing was by the Smithsonian Oceanographic Sorting Center (SOSC). The samples came from depths of 1–5790 m and latitudes of 53–78.5° S. This is an arbitrary

northern boundary since there are specimens scattered throughout the oceans of the world, including some from the Arctic Ocean. These will be treated in other reports. Several dozen Antarctic specimens were omitted from this report due to their damaged or incomplete nature. The nomenclature used here follows that of Cutler (1994).

### Materials and Methods

Specimens were collected using a wide range of trawls, dredges and grabs. The location and number of specimens are listed in the text if there were five or fewer stations. For more commonly collected species

this is summarized in the text and the detailed data can be found in Appendix I. For identification, standard dissecting techniques and both binocular dissecting and compound microscopes were used as required. The specimens are housed in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Results

Key to the species in this report (see Fig. 1).

- 1. Single nephridium ... (genus *Phascolion*) ..... 2
  - Two nephridia ..... 4
- 2. Introvert retractor muscles appear as two separate units and of nearly equal size ..... *Phascolion (Isomya) hedraeum*
  - Introvert retractor muscles fused into single column with very short distinct origins ..... (subgenus *Montuga*)
- 3. Trunk smooth, without apparent holdfast papillae, lives in clay tubes ....
  - ..... *Phascolion lutense*
  - Trunk with thin but distinct holdfast papillae ..... *P. pacificum*
- 4. One pair introvert retractor muscles ..
  - ..... (genus *Nephasoma*) ..... 5
  - Two pair introvert retractor muscles .. 7
- 5. Elongate very slender trunk, sometimes threadlike (width usually <0.1 the length); gut with separated coils .....
  - ..... *Nephasoma capilleforme*
  - Cylindrical trunk (width rarely <0.1 the length); gut coils close together ..... 6
- 6. Introvert hooks spine-like (one edge shorter than others) <50 μm tall ....
  - ..... *Nephasoma diaphanes*
  - Hooks pyramidal, >50 μm tall .....
    - ..... *Nephasoma abyssorum benhami*
- 7. Introvert more than twice length of trunk .... (*Apionsoma murinae*) ..... 8
  - Introvert less than twice trunk length (*Golfingia*) ..... 9
- 8. Nephridia single-lobed .....
  - ..... *Apionsoma murinae murinae*
  - Nephridia with secondary lobe .....
    - ..... *Apionsoma murinae bilobatae*
- 9. Posterior trunk without caudal appendage ..... *Golfingia margaritacea*

- Posterior trunk with caudal appendage ..... 10
- 10. Large bladder-like papillae at base of tail ..... *Golfingia anderssoni*
  - Base of tail without large bladder-like papillae ..... *G. muricaudata*

Note: If one has worms less than 2 or 3 mm long, one must use more comprehensive sources to go beyond the generic level.

Genus *Golfingia* Lankester, 1885  
*Golfingia anderssoni* (Théel, 1911)

*Material examined.*—48 specimens from 60 stations at latitudes 53–78° S, longitudes from 26–64° W, then skip to 160° W–165° E. The total depth range was 22–3413 m, but 70% of the samples from 100–1200 m (Fig. 5a).

*Description.*—The trunks range from 2–133 mm in length; most from depths >1000 m are >35 mm long, while those from shallower water are mostly <10 mm long. Unlike data published prior to Saiz (1995) (he had specimens up to 110 mm from the Antarctic) that records no specimen longer than 35 mm, this collection has 44 worms (30%) that exceed this length. A surprising number of specimens were unusually elongated and thin reflecting the highly plastic nature of this body and perhaps a distortion of their living state.

The posterior end of most specimens exhibits the characteristic large, bladder-like papillae on the posterior quarter of the trunk and thin, rat-like caudal appendage (tail, Fig. 2a). In worms less than 8 mm long these attributes may be under-developed (Fig. 2b) and inspection under a compound microscope may be necessary to differentiate this from small *G. muricaudata*. Occasionally, these papillae resembled bladders that had been drained, thus looking more like flattened scales. Tails can be broken during collection, but in a sample of 24 worms 11–133 mm long, the tails are 4–16% of the trunk plus one each at 22 and 33%.

While earlier observers did not see intro-



vert hooks on this species, we observed small (30–35  $\mu\text{m}$ ), triangular, pale, scattered hooks on a number of specimens (Fig. 2c). These could not be seen with the dissecting microscope but required examination under the compound scope. However, as predicted in Cutler (1994), these hooks are numerous on 2–6 mm worms. They are still present but few on 9–12 mm worms and absent in 17 and 30 mm worms from the same station.

A single worm from the most southerly station (USNM 170138) displayed what we interpret to be an anomalous condition in that the dorsal pair of introvert retractor muscles is absent. If this worm were collected from another part of the world it would very likely be identified as *Nephasoma flagriferum*. The occasional absence of one or two retractor muscles in *Golfingia* species has been commented previously (Gibbs 1973).

**Distribution.**—Of the 14 previous reports between 1911–1996, all but three are from the far southern latitudes at depths of 75–1880 m. One is from the equatorial Atlantic Ocean (4 worms near 18° S, 9° E) at 4300–4600 m. This might be a case of equatorial submergence or a mistake (Cutler & Cutler 1987). Two northern Pacific Ocean reports of single worms (28 and 44° N) from deep water (3150 and 6135 m), are difficult to reconcile with what seems to be a southern ocean taxon (Murina 1964, 1971). The present data strengthens the concept of this as a circum-Antarctic bathyal species.

*Golfingia margaritacea* (Sars, 1851)

**Material examined.**—These 1442 specimens came from 305 stations at depths from 1–4886 m. However, 90% came from 50–1200 m (9% <50, none between 1200–2273 and only 1% >2200 m). The full range of latitudes from 53–78.5° S is represented but the longitudinal coverage is discontinuous. Going westward from 0°, there are scattered records from 16 and 22°, then the bulk from 26–70°, then scattered

again at 110–115°, 158° and 166° W, then another heavy concentration between 173° W and 159° E. A final few came from 150°, 116–110°, 101°, and 93° E (Fig. 5b).

**Description.**—This most common Antarctic species (45% of the material) ranges in trunk length from 1–79 mm. Those worms exceeding 25 mm lived at depths >150 m, mostly >300 m. One exception is the two intertidal worms from the tip of South America (USNM 170049) measuring 23 and 34 mm. Small worms dominated this collection with 94% being <10 mm long, while 4% are 10–25 mm, and only 2% are >25 mm in trunk length.

While most specimens are cylindrical (length 4–8 times width) with rounded or bluntly pointed conical posterior ends (occasionally with a dimple or small depression), others are elongate and thin while some are short and fat. The color varies from pale through orange to dark brown and the skin which is usually thin and smooth can be quite thick and rugose. The more slender introvert in the smaller worms is about equal to the trunk in length, but due to allometric growth is only about half the trunk length in larger specimens. Also, in small worms (1.5–8 mm) small (20–35  $\mu\text{m}$ ) scattered hooks exist that are lost as the worm matures. Papillae are more dense near the extremities of the trunk, and are generally small digitiform structures, but their size is remarkably variable.

Internally, one can often observe vesicles or bubbles on the swollen contractile vessel. Two individuals had only 3 retractor muscles, one of the dorsals being absent, a phenomenon known in other populations (e.g., Gibbs 1973). Within the coelomic cavity of several worms maturing ova were seen. These worms were 6–17 mm long and had been collected between December and May, most during February and March.

**Note.**—When Cutler (1994:73) retained the sub-species *G. margaritacae ohlini* (Théel, 1911), it was with some hesitation since there were only two indistinct differences, i.e. hooks sometimes present and a

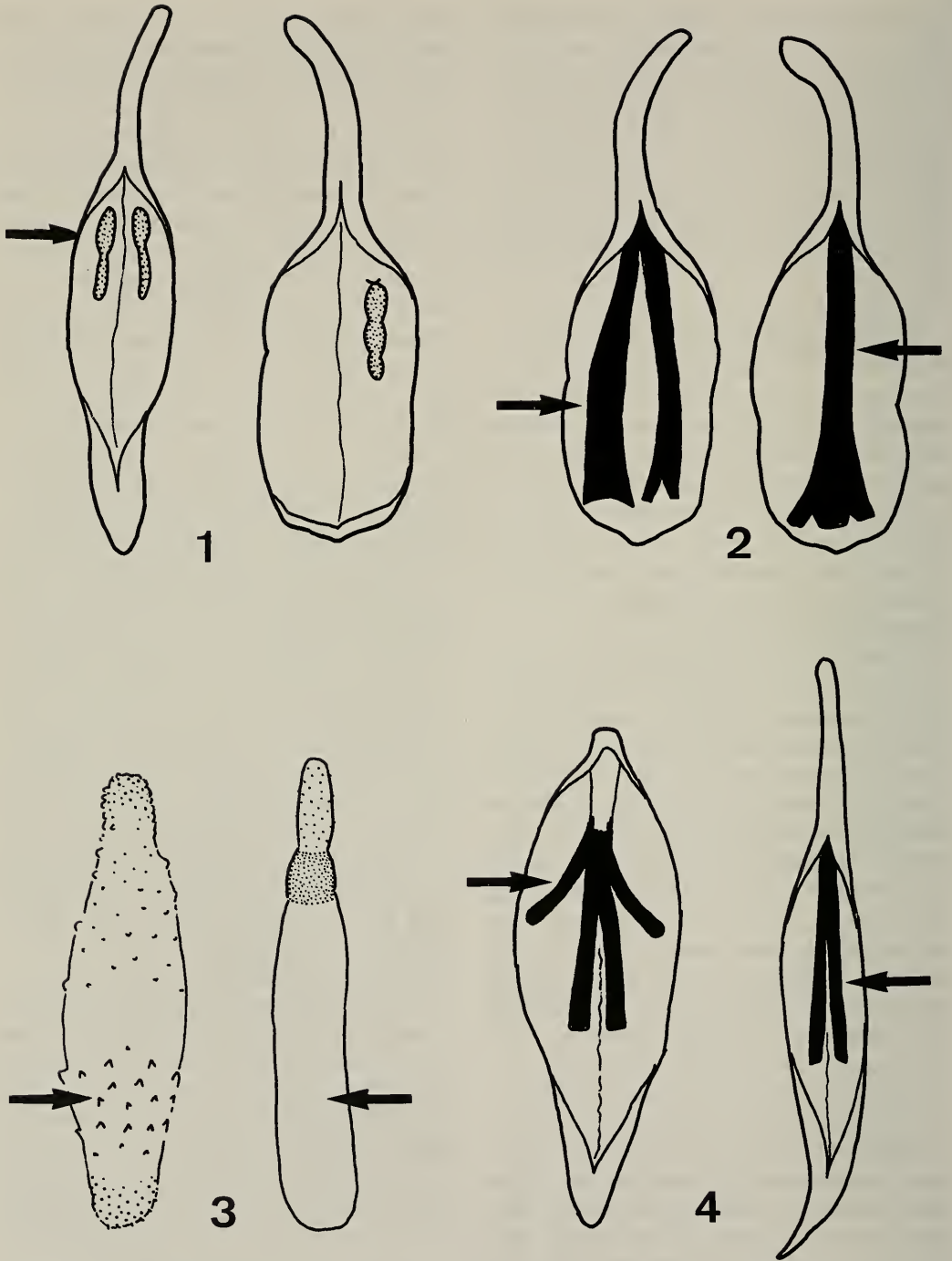


Fig. 1. Schematic drawings of the sipunculans to illustrate the identification key. Numbers are in accordance with the couplet numbers of the key.

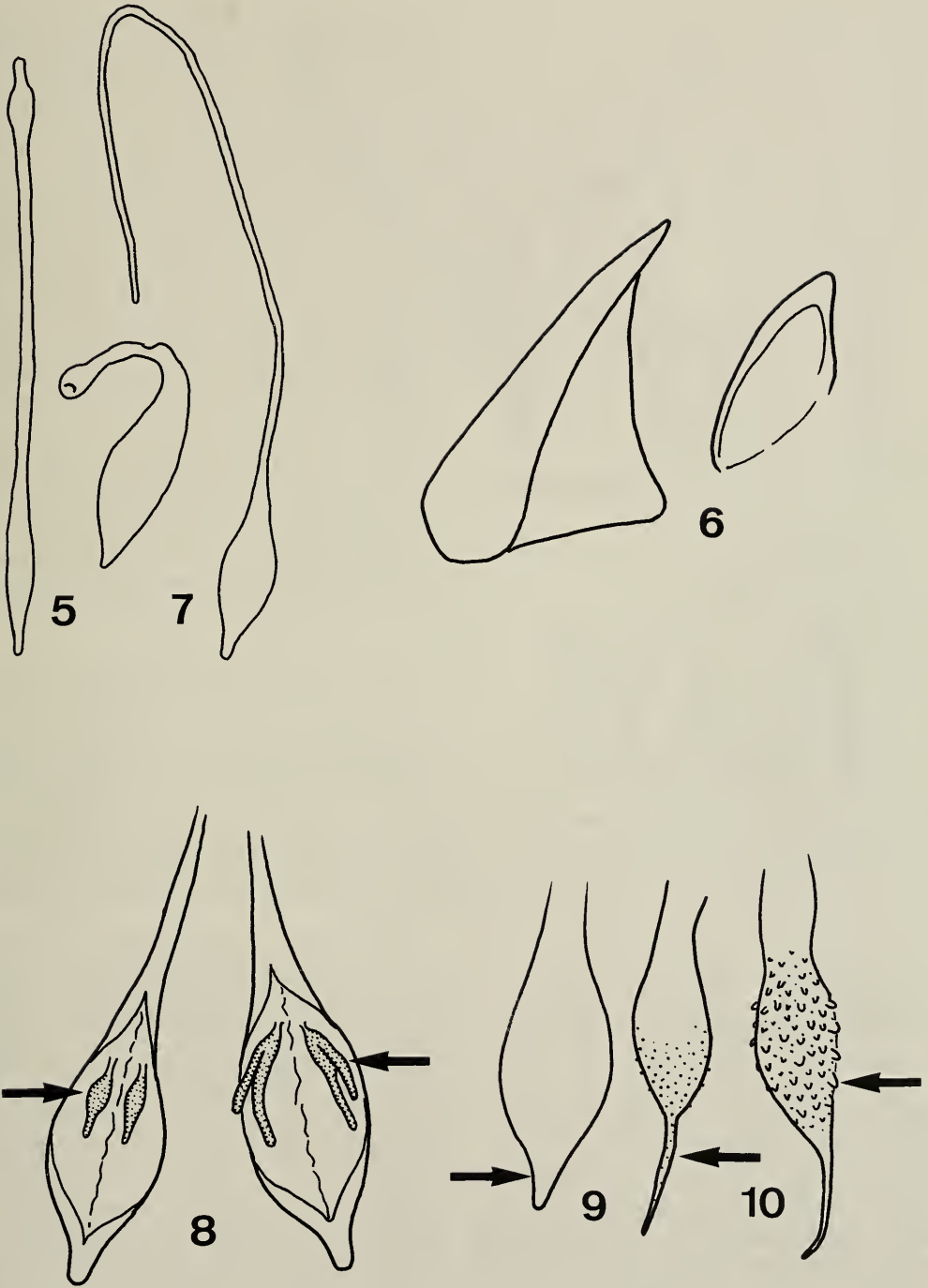


Fig. 1. Continued.

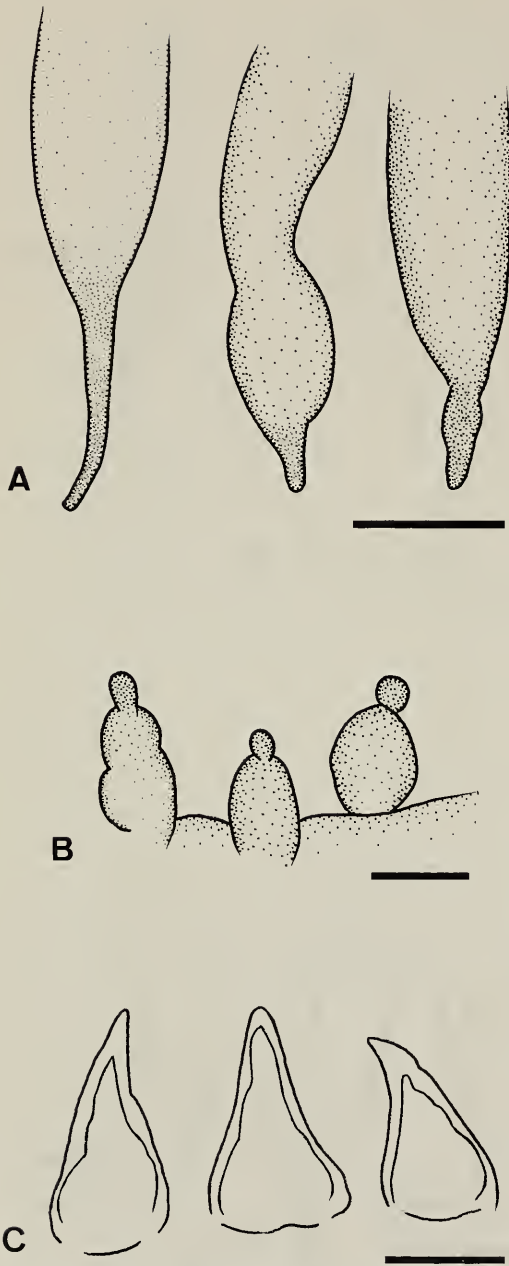


Fig. 2. Small specimens (less than 8 mm trunk length) of *Golfingia anderssoni*. A: Variation in caudal appendage development. B: Bladder-like papillae. C: Hooks. Scale bars: A = 2 mm; B = 50  $\mu$ m; C = 20  $\mu$ m.

variably pointed posterior end. When Saiz (1995) examined a large collection of Weddel Sea specimens, he concluded that any attempt to retain a distinction between these putative sub-species was an exercise in futility. We affirm that conclusion.

*Distribution.*—Very wide-spread in the Atlantic, Arctic, and Antarctic oceans ( $80^{\circ}$  N to  $78^{\circ}$  S). In the Pacific Ocean at higher latitudes ( $>30^{\circ}$  N & S) and on those occasions when reported from lower latitudes it is from depths  $>2000$  m. Recent Indian Ocean records are limited to sub-Antarctic latitudes ( $46$ – $50^{\circ}$  S) most from near the Kerguelen Islands. The reported depth range is 1–5300 m, but most specimens have been collected from depths less than 400 m. Eighty six percent of the specimens reported here were from that depth range, and while filling in some gaps in longitudinal distribution there are no surprises.

*Golfingia muricaudata* (Southern, 1913)

*Material examined.*—69 specimens from 30 stations at latitudes  $54$ – $77.8^{\circ}$  S, and the bulk between longitudes  $27.5$ – $65^{\circ}$  W, plus a few at  $166$ – $170^{\circ}$  E, and a single station at  $90.6^{\circ}$  E. Depths range from 20–892 m, but 80% of these stations were at 100–600 m (Fig. 5a).

*Description.*—The trunks in this collection range from 2–19 mm long, but only 5 (7%) are over 10 mm long, thus somewhat smaller than elsewhere. The characteristic caudal appendage easily seen in larger worms, may be only a small pointed bump in worms less than 5 mm long. These small worms are not easy to differentiate from *G. anderssoni* except for the papillae on the posterior trunk which are very small, thin, and hair-like, not large bladders (Fig. 3a). Scattered hooks, known to be deciduous, were observed on a few small (4–7 mm) worms (Fig. 3b).

Not included above are two worms from USNM 170708 that are much larger (32 & 60 mm) and collected from much greater depths (2975 m). While such depth and size

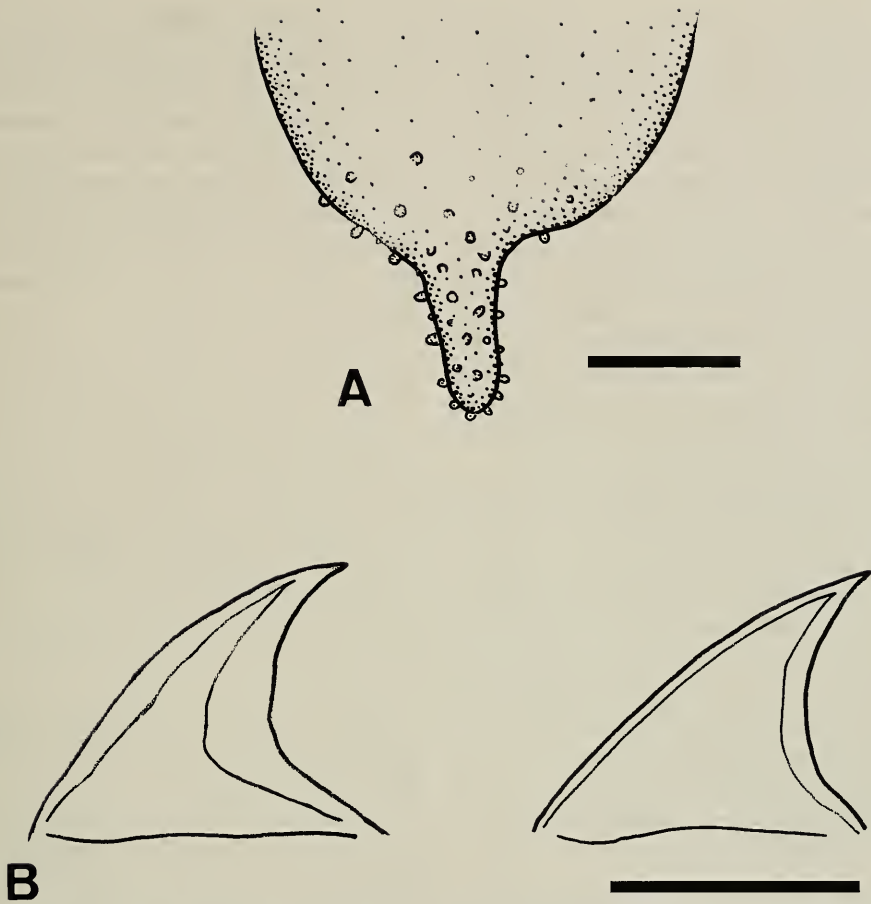


Fig. 3. Small specimens (less than 7 mm trunk length) of *Golfinigia muricaudata*. A: Caudal appendage showing thin papillae. B: Hooks. Scale bars: A = 200  $\mu\text{m}$ ; B = 15  $\mu\text{m}$ .

are not unusual for the species they are very striking in this collection. Their caudal appendages are 28 & 17%, respectively. Of particular interest is the fact that at this same station we found two examples of the very similar *G. anderssoni* of similar large size.

*Distribution*.—A widely distributed but low density cold water species in the higher latitudes of the Atlantic, Pacific, and Indian Oceans (e.g., Bering and Weddell Seas). The few records at lower latitudes (<35) are at bathyal or abyssal depths. The present data supplement those of Saiz (1995) showing this to be a well established inhabitant of the Antarctic Ocean.

Genus *Nephasoma* Pergament, 1940  
*Nephasoma abyssorum benhami* (Stephen, 1948)

*Material examined*.—56°51'S. 34°25'W, 3170 m, 13 ind., 6 Sep 1963, USNM 170243; 67°14'S, 70°12'W, 640 m, 3 ind., 26 Feb 1972, USNM 170420; 73°28'S, 30°27'W, 3111 m, 4 ind., 13 Mar 1969, USNM 170860; 77°32'S. 163°02'W, 624 m, 1 ind., 5 Feb 1968, USNM 170963; 78°24'S, 168°58'W, 565 m, 1 ind., 27 Jan 1968, USNM 170187 (Fig. 5c).

*Description*.—There are 21 specimens 2–13 mm long and only 3–6 times longer than wide with the smooth white trunks typical

of this species. The ends of the trunks have low skin bodies and may appear rough in a few individual, significant papillae are not present. The introvert seems to be from 50–150% of the trunk length and bears dark pyramidal hooks 40–100  $\mu\text{m}$  tall that are arranged in an irregular spiral manner, not random. The pair of retractor muscles originate at 50–65% of the distance towards the posterior end of the trunk, and the longitudinal muscle layer is fractured into partially separate bundles in the area around the anus in one 10 mm worm. Maturing ova are present in one 6 mm specimen that had been collected in September.

The most southerly specimen (USNM 170187) is quite different looking since it seems to have lost the outer layer of cuticle/epidermis such that the underlying papillae are now exposed looking like tall, thin, hair-like papillae. It is also much larger, the trunk being 48 by 7 mm so it is longer and thinner than the others. This has clearly experienced some post-collection stress.

*Distribution.*—The single previous report consisted of two worms taken at 66–67° S, 71 and 138° E, from 540 and 640 m. These new records are quite disjunct at 57–77.5° S and greatly increase the known range into the western longitudes and greater depths. One pair of stations is from 3100–3200 m at 30.5 and 34.5° W, while the other pair is from 600–650 m at 70 and 163° W (Fig. 5c).

*Nephasoma capilleforme* (Murina, 1973)

*Material examined.*—74°07'S, 39°38'W, 650 m, 4 ind., 6 Feb 1968, USNM 170838; 77°18'S, 37°43'W, 1025 m, 1 ind., 6 Mar 1969, USNM 170844 (Fig. 5c).

*Description.*—The five worms are 5–11 mm long and about 0.5 mm wide so that their trunks are 10–20 times longer than wide and the introverts are less than half the trunk length. The pair of retractor muscles originates in the middle of the trunk. All had been living in tubes of agglutinated sand grains and have scattered skin bodies

but no papillae on the posterior end. Scattered small hooks (25–50  $\mu\text{m}$ ) are present.

*Distribution.*—Widespread in the northern Atlantic and scattered reports in the southern hemisphere, including the Weddell Sea at 75° S, and the northern Pacific Ocean (to 56° N) at bathyal and abyssal depths (900–5000 m). These new records expand the southern boundary a small distance to 77.3° S.

*Nephasoma diaphanes* (Gerould, 1913)

*Material examined.*—There were 589 specimens from 46 stations (1 station yielded 472 worms, i.e. 80% of the total) from 53.2–78.5°S, but with a gap between 66–73.5° S. Longitudinally there are scattered stations from 27–56° W then a concentration at 66–71° W, and widely scattered stations to 180° and a small cluster at 170–175° E (Fig. 5c). Vertically the total range is from 1–5033 m, but 57% of the stations are between 100–1000 m, with 20% <100 and 23% >1000 m.

*Description.*—The vast majority of these worms are 1–6 mm long, a few measure 7–11 mm. Particular trunk length to width ratios are characteristic for many species, but given the plastic nature of sipunculans this value does vary. In 42 measured worms 71% have lengths 2–5 times the width, 21% are 6–8 times longer than wide, but 3 worms (7%) have lengths 10–13 times the width. These last 3 elongate worms approach the dimensions of *N. capilleforme*. The skin is generally smooth with low skin bodies more concentrated near the ends of the trunk. Some worms do have small digitiform papillae towards the posterior end, especially those taken from arenaceous foraminiferan tests. Introverts are rarely extended but most appear to be 50–100% (a few up to 150%) of the trunk length. While not always present, scattered pyramidal or triangular hooks generally 25–40  $\mu\text{m}$  tall, can be found. It is very possible that hookless members of this species have been identified as small *N. eremita*.

The single pair of introvert retractor muscles are fused for about one-half their length and they have their origins from the body wall 50–75% of the distance towards the posterior of the trunk. Developing ova were observed in 4 worms 5–6 mm long collected in October, February, and April, and sperm in a single 5 mm worm collected in February.

*Distribution.*—Cosmopolitan (from 82° N to 50° S) in cold water, most from bathyal and abyssal depths (down to 5300 m). This material significantly extends its known range into and around the Antarctic Ocean.

Genus *Phascolion* Théel, 1875

Subgenus *Phascolion* (*Isomya*) Cutler & Cutler, 1985

*Phascolion* (*Isomya*) *hedraeum* Selenka, de Man & Bülow, 1883

*Material examined.*—The 159 specimens are from 23 stations at 54–61.5° S, plus 1 at 74.5° S and longitudes 30.5–46° S plus 1 at 71° W at depths of 70–604 m (Fig. 5d).

*Description.*—The trunks are often coiled indicating a life within gastropod shells and are 2–25 mm long. The distinct holdfast papillae have granular borders that may not completely surround the papillae. In some worms this hardened protein is easily seen but on others may only be seen with the compound microscope. The slightly bent, scattered, spine-like hooks are 55–95 µm tall when present. These appear to be weakly attached, sometimes just a few present, and many worms, often the larger ones, have no hooks at all. Around the base of the introvert, which is shorter than the trunk, are large, densely packed, grey papillae, only a very few of these having more than a single tip. The two retractor muscles originate at the posterior end of the trunk. These muscles are usually slightly subequal in size, the ventral being 75–90% the diameter of the dorsal muscle. Developing ova were observed in 7 individuals ranging in length from 12–23 mm, having been col-

lected during the months of February, April and June.

Saiz (1995) identified 5 specimens as *P. convestitum* from the Weddell Sea, now considered as *P. hedraeum*, a closely related species and common representative in Antarctic waters. The main difference is the shape of the hooks; broad based and recurved in *P. convestitum*, but blunt and spine-like in *P. hedraeum*. Fig. 4a shows variation in this character, which includes both shapes.

*Distribution.*—Several southern Atlantic reports down to 65° S and a few from the southern Pacific, near Australia, and also off Japan. They live at shelf and slope depths, rarely over 800 m in gastropod or scaphopod shells. A single specimen from 4510 m was assigned to this taxon “with reservations”, and, as stated in that report (Cutler 1977), there are several questions about the reliability of the station data in these Galathea collections. These additions add to the one prior Antarctic record (Cutler & Cutler 1980) and show a broader, but still compact population in this Weddell Sea region.

Subgenus *Phascolion* (*Montuga*), Gibbs, 1985

*Phascolion* (*Montuga*) *lutense* Selenka, 1885

*Material examined.*—The 709 specimens came from 40 stations at latitudes from 53–68° S plus one station at 73.5° S. Longitudinally, there is a block of stations between 22–40° W, then scattered records across to 156° W, plus 3 in the east (108, 158, 164° E). This is clearly a deep-water taxon since they came from depths of 2160–5790 m, 50% of the stations and 40% of the specimens came from depths >4000 m (Fig. 5d).

*Description.*—Most of this material was 10–25 mm long but the total size ranged from 4–35 mm. The uniformly smooth skin free of visible holdfast papillae, and array of small papillae around the base of the introvert forming a grey cap, characterize this

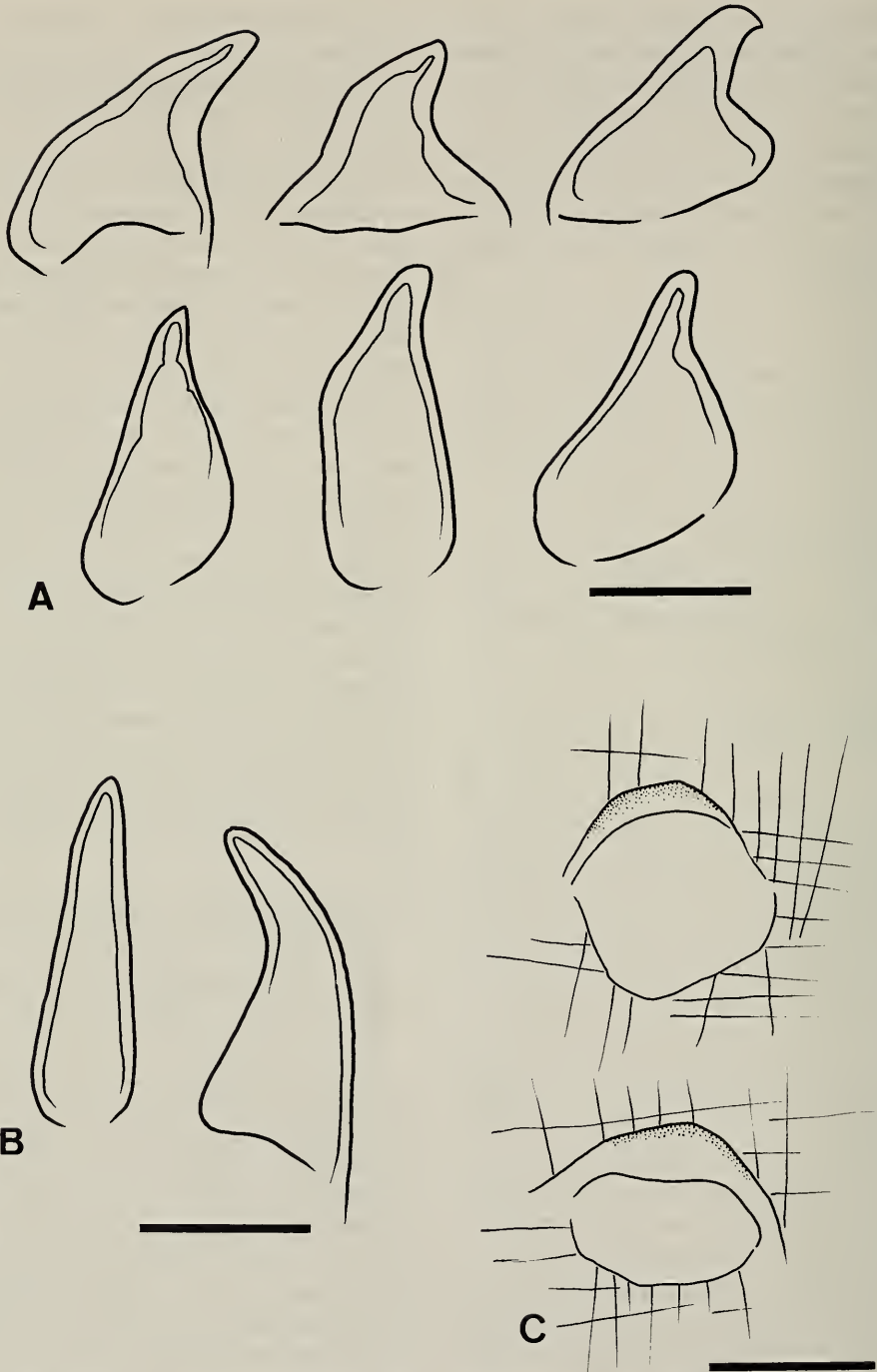


Fig. 4. A: *Phascolion (Isomya) hedraeum*, variation in hook shape. B: Hooks of *Phascolion (Montuga) lutense*. C: Weakly developed holdfast papillae of *P. (M.) lutense*. Scale bars: A = 50  $\mu\text{m}$ ; B = 35  $\mu\text{m}$ ; C = 200  $\mu\text{m}$ .



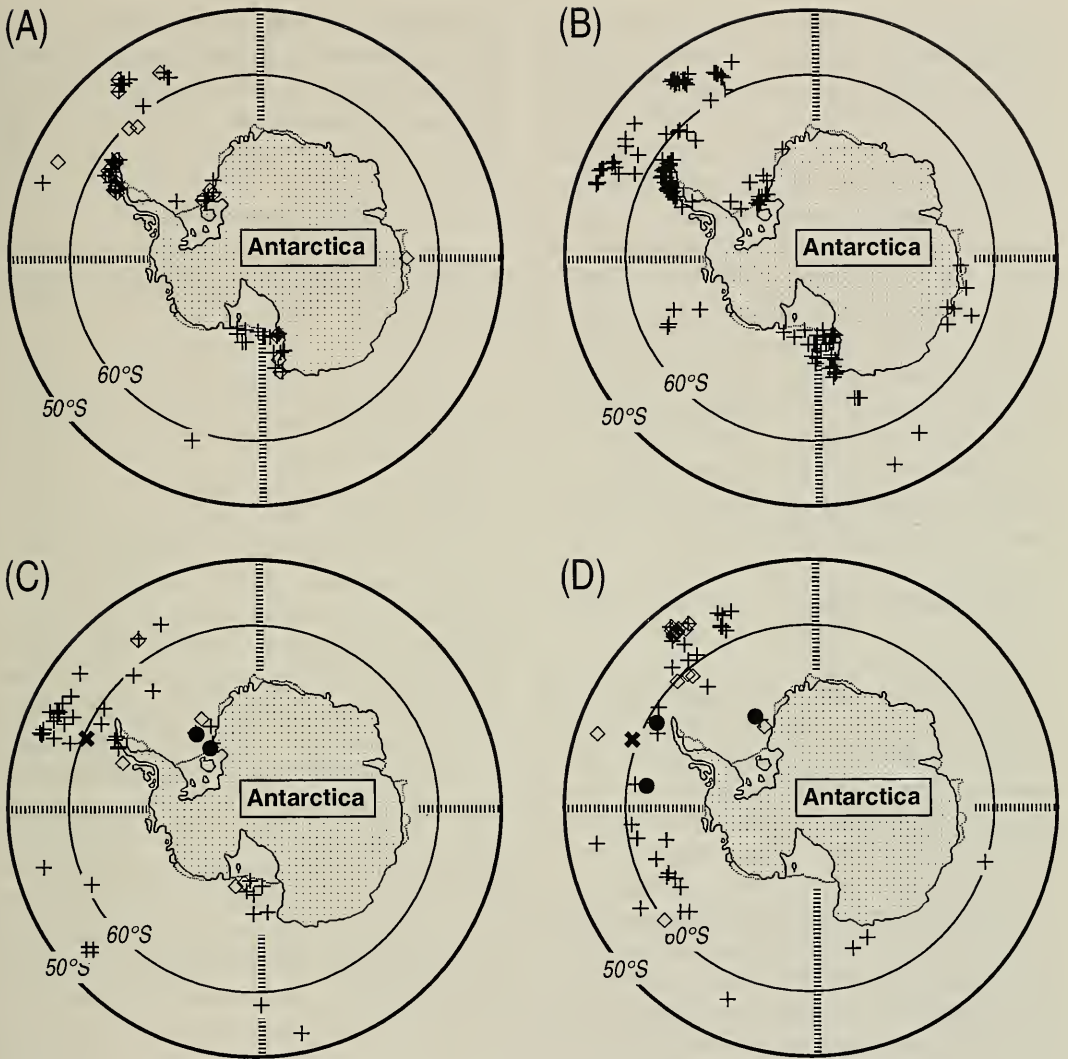


Fig. 5. A–D Distribution maps of the US-collected Antarctic sipunculans. A: (+) *Golfgingia anderssoni*, (◇) *G. muricaudata*. B: (+) *Golfgingia margaritacea*. C: (+) *N. diaphanes*; (◇) *Nephasoma abyssorum benhami*; (●) *N. capilleforme*; (X) *Apionsoma murinae murinae*; (#) *Apionsoma murinae bilobatae*. D: (+) *Phascolion (Montuga) lutense*; (◇) *Phascolion (Isomya) hedraeum*; (●) *Phascolion (Montuga) pacificum*; (X) *Phascolion* sp.

species. Papillae are present on the trunk that might have secreted some peripheral protein, but only a trace can be seen in a few larger worms (Fig. 4c). It is also the only known member of this genus to form a stable clay/mud tube as a dwelling place, an interesting adaptation to very deep life where empty calcareous mollusc shells or coral do not exist. The tentacular crown is reduced to a membranous ridge that may

have a few short lobes around the margin, another adaptation seen in other deep-sea species. Thin spine-like introvert hooks are seen only rarely and then in very small numbers measuring about 50 μm tall (Fig. 4b). It seems clear that these are not permanent structures. Living on the anterior end of a few worms were small clusters of epizoans, probably Entoprocta.

Internally the retractor muscles are fused

into a single column for almost their entire length, and the single nephridium is often quite large. Eggs were observed in only two worms 8 and 31 mm long, collected during August and October. Sperm were present in one 20 mm worm also collected in October.

*Distribution.*—A cold-water species (1000–6860 m) unknown from lower latitudes, even in deep water. Widely collected in the Southern Hemisphere in all three oceans, 36–66° S in the Pacific, 20–32° S in the Atlantic, and 32–38° S in the Indian Ocean. From northern waters it is recorded from the northwestern Pacific and the northeastern Atlantic, 47–56° N. This collection significantly broadens the longitudinal range at these high southern latitudes.

*Phascolion (Montuga) pacificum* Murina,  
1957

*Material examined.*—61°45'S, 61°14'W, 4758 m, 1 ind., 1 Aug 1962, USNM 170134; 63°00'S, 82°31'W, 4602 m, 2 ind., 24 Oct 1963, USNM 170681; 73°28'S, 30°26'W, 3111 m, 2 ind., 13 Mar 1969, USNM 170845 (Fig. 5d).

*Description.*—These 5 specimens are 5–17 mm long and differ from the other more common member of this deep-water subgenus by having holdfast papillae with thin but distinct U- or V-shaped hardened borders, and they do not construct the clay/mud houses of *P. lutense*. Both have retractor muscles almost totally fused into a single column, and tentacles reduced to lobes. This 17 mm worm was unusually thin (2 mm wide) thus not in its natural sausage shape. Small scattered hooks may be present near the tip of the introvert which is longer than the trunk in one, but shorter in another.

*Distribution.*—A bathyal and abyssal species (300–6860 m) widespread at high latitudes in the northwestern and southwestern Pacific, the northeastern and southern Atlantic, and the sub-Antarctic Indian Oceans. Two records from lower latitudes are the Peru-Chile Trench (5760–6860 m)

and 28° N (1760 m) in the eastern Atlantic. The only previous Antarctic record was at 77° E so these new records greatly expand the known range to the other side of the world in Antarctic waters.

*Phascolion* species?

*Material examined.*—59°14'S, 69°13'W, 3738 m, 1 ind., 6 Oct 1962 USNM 170211 (Fig. 5d).

*Description.*—This single 6 mm worm is interesting, but not sufficient for a positive identification. It most closely resembles the published description of *Phascolion ushakovi* (Murina, 1974). The similarities are of two types; long, thin, dark hooks 200–250 μm tall and mammiform papillae at both ends of the trunk. However, this set of retractor muscles are not of distinctly different sizes as is the case in *P. ushakovi* (i.e., ventral about 75% the diameter of the dorsal, not the expected 10–20%). This ventral muscle has two origins that quickly fuse. The mid-trunk region is smooth with no holdfast papillae.

Given that we have only a single small specimen, and the lack of congruity in retractor muscles, we hesitate to assign this a species name. Also, the location of our material is far from the only reported location of *P. ushakovi*, i.e., western Australia, at 330 m.

Genus *Apionsoma* Sluiter, 1902  
*Apionsoma murinae murinae* (Cutler,  
1969)

*Material examined.*—59°56'S, 65°18'W, 3687 m, 1 ind., 10 Aug 1962, USNM 170204 (Fig. 5c).

*Description.*—This single 17 mm specimen is large for this species and has a thin introvert about 110 mm long. The posterior trunk bears the larger mammiform papillae and the tip of the introvert carries rings of very small hooks. The nephridia are clearly single lobed and while the thin dorsal retractor muscles are partially hidden under the ventral pair they are present.

*Distribution.*—Widespread in cold water (100–5200 m) across the northern Atlantic and down to 15° S on the eastern side. In the Pacific it has been recorded from the Bering Sea and several deep water southern locations including the Peru-Chile Trench. Recent Indian Ocean records show it to be present there at depths from 250–3600 m as far south as 38° S. Therefore, this Weddell Sea specimen is the first for this taxon in Antarctic waters.

*Apionsoma murinae bilobatae* (Cutler, 1969)

*Material examined.*—54°50'S, 129°48'W, 1035 m, 2 ind., 7 Nov 1964, USNM 170774 (Fig. 5c).

*Description.*—These flask-shaped trunks are 8 and 11 mm long with prominent mammiform papillae posteriorly. Rings of small pale hooks show only very short spinelets almost as if they had been broken off. Since these are larger than most known specimens (1–7 mm) it is possible that the fragile spinelets wear down with age. This is similar to what Popkov (1993) observed in his 11 mm specimen from New Zealand that he called *Apionsoma claviformes*. The nephridia have the distinctive secondary lobe and two pair of introvert retractor muscles are long and very thin with their origins about 75–80% of the distance towards the posterior end.

*Distribution.*—Known from moderate depths in the northern Atlantic Ocean and Mediterranean Sea plus scattered reports from the eastern and western Indian Ocean, and one near New Zealand. Thus, this record is the first in the Antarctic region (far southern Pacific) for this taxon.

### Discussion

The taxa discussed above include all that have been reported by earlier authors, except these four:

*Golfingia elongata* (Hérubel 1906, 1907a, 1907b) What appears to be three records is actually one record repeated three

times. It is our supposition that this material is most likely a few *G. margaritacea* in which Hérubel saw some ordered array of hooks.

*Nephasoma confusum* (Murina 1957, 1972) This species is very similar to *N. abyssorum* with moderate sized, dark hooks. If the ill-defined spiral order of these hooks was not evident these two taxa could be easily confused. Hook shape has also been used as a diagnostic character. The original description of *N. confusum* by Sluiter (1902) said there is a reinforced rim in the hook. However Sluiter illustrated a hook with a rim not especially thick. Murina (1972) identified material from Antarctic waters with large hooks and stated that their hooks were similar to those drawn by Sluiter in 1902. Specimens identified as *N. confusum* sent to one of us (EC) by Murina, have large hooks with the suggestion of a thin reinforced rim. These hooks are not pyramidal as are the 'typical' hook of *N. abyssorum*. Ditadi & Migotto (1981) stated: "As pointed out by Sluiter (1902) a very characteristic feature of this species is the chitinous reinforcement of the hooks, a trait we have also found and shown in Fig. 4h4." They illustrate several hooks showing variation, some are only partially reinforced. Cutler & Cutler (1986) and Cutler (1994) draw a hook with a thick reinforced rim and a little bend in the apex. Saiz & Villafranca (1990) found specimens in South Spain with the same shape as shown in the Cutlers' work. The typical *N. abyssorum* hook in Théel (1905) is pyramidal. However he drew a specimen with the introvert out in which the 'spiral arrangement' of the hooks is not obvious.

In this study we have identified as *N. abyssorum benhami* worms with diverse hooks, some having pyramidal edges, others triangular in shape, and others in between. It seems that hook shape is more variable than previously reported. Therefore, we consider it very likely that what Murina named *N. confusum* we would have called *N. abyssorum benhami*.

*Nephasoma eremita* (Fischer 1928, Murina 1972, Saiz 1995) Given the experience of one of us (JISS) it now seems probable that these specimens represent a few *N. diaphanes* that lack hooks.

*Phascolion strombus* (Fischer 1920, Stephen 1948, Murina 1972) It is most likely that these records are what we are here calling *P. hedraeum*.

Thus, we suggest that this report includes all the known members of this phylum living in Antarctic waters.

**Morphology.**—The impermanent or deciduous nature of introvert hooks has been observed in a few isolated cases previously, but this study affirms the more widespread reality of this condition in most of these Antarctic species (all three *Golfingia* species, *Nephasoma diaphanes*, and all three *Phascolion* species). As a rule hooks are less numerous in larger individuals. One strong message here is that the absence of hooks in a few individuals does not warrant the naming of a new species. None of the species we encountered are new to science and all have been well described from large sample sizes, the unnamed *Phascolion* being the single exception.

**Ecology.**—*Golfingia margaritacea*, with 46% of the specimens, dominates this fauna, but by adding *Phascolion lutense* with 22% and *Nephasoma diaphanes* with 19%, we have 87% of the collection in three species. A second tier of species each making up 2–5% consists of *P. hedraeum*, *G. anderssoni*, and *G. muricaudata*. The remaining 5 species if added together comprise just 1.1% of the total.

Of the 456 stations, 395 contained a single sipunculan species, but 58 yielded 2 species and 3 contained 3 species. Eight of the 11 species were found together with a second. The remaining 3 were the least common with only 1–5 representatives each.

**Zoogeography.**—The numbers of specimens examined (3156) and species identified (10) in this study are comparable to others previously reported from Antarctica (cf. Murina 1972, Saiz 1995). All species have been

previously collected by other expeditions, except for *Apionsoma murinae*, here recorded for the first time south of the Antarctic Convergence. Concerning spatial horizontal distribution within Antarctic waters, the most ubiquitous species is *Golfingia margaritacea*, present along almost the entire coastline of Antarctica with a few gaps such as off 'Dronning Maud Land' (between longitude 0–45° E) and 'Marie Byrd Land' (120–150° W). Several other common species (*G. anderssoni*, *G. muricaudata*, *N. diaphanes*, *P. lutense*, *P. hedraeum*) appear a more restricted in those areas heavily sampled by oceanographic vessels such as the Antarctic Peninsula, the Ross and Weddell Seas. The remaining species: *N. abyssorum benhami*, *N. capilleforme*, *P. pacificum*, and *A. murinae* are represented by only a very few specimens from widely scattered locations. With regard to the vertical distribution, most sipunculan species in the US Antarctic collections were found at sub-littoral (1–200 m) and bathyal (200–3000 m) depths, whereas only two, *Phascolion lutense* and *P. pacificum*, showed a preference for deeper water (>2000 m).

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Appendix.—Station data for sipunculan species found at more than 5 locations. See text for less common taxa.

Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
<i>Golfingia anderssoni</i>					
5340	W07015	0307	2	79.04.28	170193
5357	W03721	0033	1	75.05.16	170147
5403	W03724	0070	2	75.05.16	170074
5414	W03754	0173	1	75.06.10	170156
5417	W03828	0243	1	86.12.03	170986
5422	W03828	0220	1	86.12.03	170987
5431	W03535	0265	4	75.05.19	170149
5506	W03955	2975	2	66.02.08	170708
5629	W02646	2270	1	75.05.30	170084
5723	W02634	2325	1	75.05.26	170151
5739	W02600	2500	4	75.05.27	170152
5855	W15945	0750	3	64.08.12	170761
5908	W03649	2817	7	64.04.10	170172
6157	W05553	2340	10	64.03.14	170170
6203	W06109	1437	1	62.08.08	170203
6205	W05823	0048	1	72.01.15	170399
6207	W05558	1133	2	63.01.01	170158
6221	W05848	0082	3	72.01.16	170976
6233	W05801	1680	2	63.01.04	170159
6241	W05443	0215	1	64.03.15	170957
6241	W05443	0215	2	64.03.15	170253
6242	W05610	0430	1	63.01.02	170220
6252	W05927	0910	1	63.01.07	170862
6256	W06048	0100	1	72.01.08	170395
6326	W06215	0122	1	69.02.10	170348
6419	W06259	0045	1	63.02.06	170820
6437	W06251	0655	18	82.03.25	171032
6446	W06404	0028	3	72.03.10	170438
6447	W06419	0047	1	71.12.04	170403
6447	W06407	0055	1	72.01.03	170392
6447	W06410	0208	1	83.03.20	170125
6503	W06354	0365	1	72.03.01	170421
7120	E16955	0439	2	59.01.25	170803
7208	E17210	0434	1	58.01.13	170785
7400	W05456	0438	1	68.02.12	170852
7432	E16817	0876	5	68.01.18	170143
7457	E17206	0525	2	68.01.18	170180
7458	E16534	1124	2	78.02.08	175516
7531	W03008	0412	3	69.02.25	170853
7607	W16837	0514	1	68.02.03	170309
7625	W17034	0558	1	68.01.30	170188
7650	W04055	0513	1	69.03.01	170855
7704	E16819	0916	10	68.01.22	170182
7705	W03504	0793	3	69.02.26	170854
7709	W03858	0851	3	69.04.05	170843
7716	W04238	0512	10	69.03.01	170133
7716	W04238	0512	1	69.03.01	170841
7720	E17239	0633	1	67.01.24	170141
7730	E16800	0107	1	48.01.29	021097
7731	W16305	0606	5	68.02.05	170190
7736	E16609	0249	1	56.12.26	170780
<i>Golfingia margaritacea</i>					
7736	W04230	0585	3	69.03.02	170842
7742	E17712	0746	1	78.01.23	175509
7750	W04205	0659	4	69.03.04	170858
7759	E17811	0647	1	68.01.25	170185
7809	W17832	0695	1	78.01.24	175514
7810	W16230	0500	1	56.01.27	170775
7824	W16858	0565	1	68.01.27	170138
5306	W06704	0086	3	70.03.05	175492
5306	W06704	0086	2	70.03.05	175493
5320	W06651	0080	2	62.09.27	170210
5331	W07050	0001	2	69.04.24	170049
5336	W03735	0310	1	75.05.11	170064
5338	W03754	0133	1	75.05.13	170068
5338	W03802	0137	1	75.05.12	170067
5340	W06620	0081	1	64.02.10	170248
5340	W07024	0100	56	69.05.13	171090
5342	W03757	0147	2	75.05.14	170070
5349	W07025	0021	1	70.04.29	170837
5351	W03738	0100	38	66.02.07	171004
5357	W03721	0033	7	75.05.16	170147
5400	W03741	0074	4	75.05.15	170073
5401	W03651	0112	1	75.05.17	170075
5402	W03740	0058	4	75.05.15	170072
5402	W03740	0065	3	75.05.15	171037
5408	W05208	0450	1	66.01.30	170274
5411	W03802	0160	1	86.12.05	170988
5412	W03736	0069	1	75.06.10	170105
5412	W03740	0080	12	75.06.10	170104
5412	W03741	0074	1	75.06.09	170102
5412	W03741	0074	19	75.06.09	170103
5412	W03743	0085	2	75.06.09	170101
5414	W03754	0200	1	75.05.12	170066
5422	W03359	0155	9	75.05.19	170148
5424	E15901	0086	5	65.02.10	170764
5431	W03535	0265	6	75.05.19	170149
5432	E15902	0093	6	65.02.10	170765
5434	W06430	0074	1	71.11.07	170382
5439	W06350	0136	17	71.10.26	170377
5439	W06420	0048	1	71.10.20	170829
5440	W05705	0126	1	66.03.14	170276
5443	W03649	0188	2	75.05.17	170076
5445	W06410	0022	1	71.05.20	170363
5447	W06404	0040	1	71.10.29	170379
5451	W03503	0170	1	86.12.10	170971
5456	W03550	0151	47	75.06.06	170098
5500	W06450	0543	2	71.11.03	170381
5503	W05857	N.R.	13	62.12.04	170216
5507	W03547	0131	4	75.06.06	170097
5509	W03545	0130	11	75.06.06	170096
5542	W03539	0240	1	86.12.11	170972
5549	W02211	4256	1	66.03.04	170710
5606	W06619	0440	2	63.09.18	170769

## Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
5616	W02730	0290	15	75.06.02	170092
5616	W02735	0132	22	75.06.03	170093
5619	W02729	0175	27	66.03.06	170711
5620	W02729	0175	9	66.03.06	171003
5620	W02730	0130	5	75.06.04	170094
5623	W02723	0185	1	75.06.02	170091
5624	W02725	0186	2	75.06.02	170090
5642	W02700	0107	29	75.05.30	170083
5643	W02700	0125	6	75.05.31	170087
5644	W02659	0337	1	75.05.31	170086
5644	W02702	0146	2	75.05.31	170088
5645	W02654	0740	5	75.05.31	170085
5700	W02610	2742	1	75.05.22	170150
5722	E14937	3299	1	69.04.19	170320
5730	W05858	3533	2	62.12.07	170217
5739	W02600	2500	1	75.05.27	170152
5741	W02622	0412	3	75.05.26	170082
5839	W06407	0024	1	71.05.17	170362
5900	W04900	3867	1	63.03.08	170677
5928	W02703	0093	1	76.02.27	170061
5953	W03219	0600	2	76.02.25	170869
6026	W04622	0105	2	76.02.16	170108
6026	W04623	0155	6	76.02.16	170109
6026	W04628	0110	6	76.02.16	170110
6027	W04550	0103	1	76.02.15	170106
6030	W04643	0126	4	76.02.16	170058
6030	W04643	0129	10	76.02.17	170059
6116	W05611	0224	4	62.12.31	170218
6117	W04429	0295	1	76.02.22	170060
6119	W05609	0230	31	62.12.31	170135
6119	W05609	0230	1	62.12.31	170953
6125	W05630	0300	1	64.03.13	170251
6202	W05905	0101	2	63.01.12	170230
6205	W05823	0048	1	72.01.15	170399
6206	W05600	1200	2	63.01.01	170219
6218	W05835	0066	1	71.12.21	170384
6219	W05911	0044	2	71.12.19	170414
6219	W05911	0044	4	71.12.19	170415
6219	W05911	0044	2	71.12.19	170866
6219	W05911	0044	1	71.12.19	170867
6219	W05912	0073	9	71.12.26	170386
6221	W05845	0050	1	72.01.16	170400
6221	W05848	0082	6	72.01.16	175495
6222	W05912	0670	1	81.02.21	170128
6230	W05758	1058	4	63.01.05	170161
6240	W05445	0265	18	64.03.15	170252
6240	W05445	0265	1	64.03.15	175498
6240	W05610	0365	18	63.01.02	170222
6241	W05443	0215	1	64.03.15	170253
6241	W05443	0215	4	64.03.15	170690
6241	W05443	0215	1	64.03.15	170999
6241	W05443	0215	5	64.03.15	170254
6241	W05602	0225	1	83.04.01	170127
6243	W06101	0059	3	72.01.14	170397

## Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
6243	W06102	0073	7	72.01.14	170398
6249	W05610	0378	1	63.01.02	175502
6255	W05927	0915	1	63.09.07	170162
6257	W06051	0154	2	70.03.28	171042
6257	W06051	0154	1	70.03.28	175490
6258	W06041	0087	1	70.03.25	170357
6258	W06047	0140	1	70.03.25	170356
6258	W06048	0057	1	70.03.25	170355
6259	W06034	0056	3	82.03.13	171014
6259	W06035	0060	1	82.04.03	170992
6301	W06044	0040	1	74.01.12	175517
6313	W11038	0036	31	61.12.28	170129
6314	W05845	0073	5	63.01.08	170225
6314	W05845	0073	1	63.01.08	170226
6324	W04451	3622	1	63.02.24	170234
6324	W06210	0074	1	85.03.31	170969
6324	W06214	0093	1	69.02.10	170449
6326	W06215	0122	14	69.02.10	170348
6351	W06238	0147	1	63.01.09	170228
6351	W06238	0147	5	63.01.09	170229
6351	W06238	0147	1	63.01.09	175500
6400	W06100	0570	1	83.03.23	118765
6402	W06407	0075	7	72.03.01	170432
6402	W06407	0075	1	72.03.01	170978
6406	W11517	4873	1	66.04.30	170984
6409	W06240	0097	3	69.02.10	170448
6413	W06105	0115	1	71.12.16	170410
6413	W06105	0131	4	71.12.16	170411
6413	W06105	0129	3	71.12.16	170412
6414	W06158	0260	2	82.03.24	171029
6414	W06235	0085	1	82.03.24	175494
6414	W06235	0085	1	82.03.24	171031
6418	W06258	0170	2	82.03.22	171024
6419	W06259	0045	1	63.02.06	170810
6419	W06259	0045	2	63.02.06	170819
6419	W06259	0107	34	82.03.22	171023
6419	W06300	0067	5	82.03.22	171022
6420	W06358	0005	4	69.02.03	171038
6421	W06128	0132	1	82.03.23	171025
6421	W06135	0093	17	82.03.24	171028
6422	W06128	0105	6	82.03.23	171026
6422	W06128	0106	4	82.03.23	171027
6429	W06229	0120	1	82.03.24	171030
6434	W06200	0045	5	63.02.09	170821
6442	W06238	0097	2	71.12.15	170408
6442	W06238	0098	4	71.12.15	170409
6444	W06405	0067	1	72.03.07	170434
6445	W06439	0014	1	63.03.01	170825
6445	W06408	0193	1	82.03.29	171034
6445	W06439	0038	2	63.03.01	170823
6445	W06439	0014	1	63.03.01	170824
6446	W06404	0021	1	73.02.18	170111
6446	W06404	0028	2	72.03.10	170437
6446	W06404	0020	4	73.02.18	170443

## Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
6446	W06404	0027	1	63.01.25	170814
6446	W06405	0020	3	71.12.31	170388
6446	W06406	0224	1	73.11.08	175513
6446	W06407	0111	2	72.01.02	170391
6447	W06407	0027	1	73.02.20	175508
6447	W06326	0125	1	73.03.11	170122
6447	W06403	0031	1	69.01.27	170057
6447	W06404	0037	7	73.03.06	170118
6447	W06404	0048	1	73.03.06	170119
6447	W06404	0048	1	73.03.06	171045
6447	W06405	0017	1	73.01.27	175510
6447	W06406	0213	1	74.10.23	175512
6447	W06407	0069	4	73.02.19	170112
6447	W06407	0100	2	73.02.20	170114
6447	W06407	0055	2	72.01.03	170392
6447	W06407	0107	1	72.01.26	170402
6447	W06407	0108	2	72.02.23	170417
6447	W06407	0100	9	72.02.23	170418
6447	W06407	0100	1	72.02.23	171043
6447	W06407	0077	3	72.03.17	170440
6447	W06410	0208	3	83.03.20	170125
6447	W06411	0245	1	82.03.29	171035
6448	W06330	0056	1	63.01.26	170815
6448	W06404	0055	3	72.03.10	170436
6448	W06407	0100	45	72.01.28	170416
6448	W06407	0100	5	72.02.23	171044
6448	W11430	4886	3	64.01.11	170683
6449	W06205	0075	1	63.03.01	170812
6449	W06330	0024	1	70.03.16	170352
6449	W06330	0023	1	70.03.16	171041
6449	W06333	0053	1	73.03.09	170120
6449	W06333	0053	1	73.03.09	171046
6449	W06407	0093	4	82.03.29	171036
6452	W06340	0290	1	73.02.19	170113
6453	W06253	0268	3	73.03.11	170123
6453	W06333	0115	1	73.03.09	175489
6454	W06447	0480	1	72.03.04	170433
6504	W06401	0024	3	72.03.13	170439
6504	W06456	0355	2	73.03.03	170117
6505	W06455	0270	5	73.03.03	170116
6512	W06413	0060	1	63.???	170817
6514	W06412	0335	1	82.03.19	171020
6514	W06412	0335	62	82.03.19	171021
6514	W06412	0335	10	82.03.19	175505
6514	W06415	0054	4	82.03.16	171017
6514	W06415	0060	1	82.03.15	170980
6515	W06412	0295	1	82.03.19	171019
6525	E10113	0183	1	48.01.14	170794
6554	W06517	0258	5	82.03.16	170981
6605	W06521	0086	2	82.03.16	170990
6608	W06635	0175	1	82.03.18	171018
6610	E11041	0128	2	61.12.29	170872
6610	E11641	0036	2	61.12.29	170871
6613	E11038	0036	2	61.12.28	170874

## Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
6613	W11038	0038	2	61.12.29	170055
6615	E11029	0045	3	58.01.23	170784
6617	E11031	0137	7	62.02.12	170052
6618	E11032	0101	14	61.12.11	170050
6621	E11027	0210	33	61.12.06	170053
6621	E11028	0238	5	61.12.03	170056
6622	E11029	0315	9	61.12.13	170051
6622	E11029	0254	3	61.12.13	170054
6622	E11029	0247	3	61.12.13	170870
6633	E09254	0080	1	58.01.29	170786
6637	E16256	0217	1	67.02.05	170453
6650	E16432	3515	1	67.02.05	170451
6653	E16319	0100	8	74.02.10	170047
6718	E11019	0135	12	58.01.27	170793
6730	W06800	0073	1	48.02.22	021091
6730	W06800	0073	1	48.02.22	021092
6730	W06800	0074	1	48.02.22	021089
6730	W06800	0074	1	48.02.22	021093
6848	W06407	0100	5	56.02.07	170796
7003	W11451	0366	3	56.02.06	170795
7055	E17155	2273	1	59.01.18	170801
7122	E17043	0162	1	68.02.13	170303
7130	E16930	0250	5	56.02.07	170796
7132	E17018	0027	3	56.02.06	170795
7150	W01550	1102	1	59.01.18	170801
7206	E17215	0392	2	58.01.12	170792
7208	E17210	0434	2	58.01.13	170785
7216	E17018	0134	1	59.01.12	170799
7217	E17018	0134	2	59.01.12	170800
7304	E17903	0570	1	68.02.11	170311
7319	E16915	0100	31	56.02.12	170797
7359	E17051	0597	1	68.01.13	170296
7400	W05456	0438	1	68.02.12	170852
7401	E17853	0257	2	68.01.14	170298
7406	W03938	0731	1	68.02.06	170850
7406	W17911	0256	4	68.01.05	170300
7407	W03938	0650	1	68.02.06	170838
7428	W03032	0513	19	69.02.24	170131
7431	E17010	0320	4	67.01.16	171008
7500	E17642	0336	2	68.01.17	170179
7531	W03008	0412	9	69.02.25	170853
7600	E17210	0575	2	68.01.19	170181
7600	W05500	0457	2	68.02.09	170851
7600	W17648	0567	1	68.01.20	170305
7600	W17648	0567	2	68.01.20	170961
7602	E17822	0487	1	67.01.20	170286
7602	E17822	0487	1	67.01.20	171009
7602	E17950	0394	1	72.02.08	170340
7602	W17957	0352	1	72.02.09	171011
7602	W17957	0352	2	72.02.09	170341
7610	E16817	0075	2	67.01.18	170285
7630	E17040	0643	5	67.01.21	170140
7650	W04055	0513	2	69.03.01	170855
7701	E16838	0917	2	68.01.22	170307



## Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
7702	W16644	0411	2	68.02.04	170189
7704	E16819	0916	1	68.01.22	170182
7706	W15817	0200	6	60.12.24	170811
7709	W03858	0851	4	69.03.05	170859
7716	W04238	0512	35	69.03.01	170133
7719	E16548	0832	2	68.01.23	170183
7720	E17239	0663	1	67.01.24	170141
7720	W03641	1079	2	69.02.27	170132
7727	E16630	0321	2	56.02.18	170798
7730	E16800	0102	9	48.01.29	021094
7730	E16604	0364	2	56.12.?	170777
7730	E16800	0107	6	48.01.29	021097
7734	E17443	0728	2	67.01.25	170142
7735	E17458	0731	2	68.01.25	170144
7736	W04230	0585	2	69.03.02	170856
7739	E16616	0315	1	60.02.19	170877
7739	W04450	0256	1	58.01.16	170787
7740	E16614	0382	1	56.11.04	170778
7740	W03530	0391	1	59.01.28	170804
7740	W03530	0410	1	59.01.30	170806
7743	E16621	0419	5	56.12.29	170782
7750	E16636	0020	9	60.01.03	170887
7750	E16636	0087	1	58.12.30	170876
7750	E16637	0020	6	59.12.16	170885
7750	E16637	0020	2	59.12.31	170886
7750	W04205	0659	24	69.03.04	170858
7751	E16634	0124	4	58.02.05	170788
7751	E16637	0051	1	58.12.30	170875
7751	E16638	0016	1	61.04.01	170888
7751	E16638	0021	2	61.05.14	170895
7752	E16641	0190	2	61.04.14	170891
7752	E16641	0136	1	61.05.22	170892
7752	E16641	0129	3	61.10.11	170893
7752	E16641	0128	1	61.10.31	170894
7752	E16643	0284	1	61.06.03	170889
7752	E16643	0282	9	61.11.02	170890
7752	E17733	0770	1	67.01.25	170177
7753	E16644	0585	1	60.11.30	170882
7753	E16649	0585	1	61.03.08	170884
7754	W04513	0252	4	69.03.03	170857
7758	E17802	0655	3	68.01.25	170184
7759	E17811	0647	1	68.01.25	170185
7820	W17300	0456	1	72.02.18	170343
7823	E17306	0474	1	68.01.26	170186
<i>Golfingia muricaudata</i>					
5351	W03738	0100	1	66.02.07	175501
5444	W06353	0044	1	71.05.11	170827
5506	W03955	2975	2	66.02.08	170708
5619	W02729	0175	2	66.03.06	170711
6055	W04441	0237	1	76.02.22	175507
6125	W04155	0595	1	64.04.13	171000
6219	W05912	0073	7	71.12.26	170386
6240	W05610	0365	9	63.01.02	170222

## Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
6241	W05751	0892	1	63.01.05	170224
6241	W05443	0215	1	64.03.15	170999
6258	W06050	0123	1	70.03.28	170358
6413	W06105	0118	4	71.12.16	170413
6442	W06238	0098	2	71.12.15	170409
6446	W06405	0054	1	72.03.07	170435
6447	W06407	0143	1	72.01.26	170977
6447	W06407	0108	1	72.02.23	170417
6448	W06407	0100	2	72.01.28	170416
6449	W06251	0075	2	63.02.04	170818
6452	W06333	0114	1	73.03.09	170121
6453	W06253	0268	4	73.03.11	170123
6504	W06456	0355	1	73.03.03	170117
6635	E09040	0278	2	47.12.30	021096
7120	E16955	0439	2	59.01.25	170803
7319	E16915	0100	7	56.02.12	170797
7730	E16800	0107	3	48.01.29	021090
7736	W04230	0585	4	69.03.02	170856
7740	W03530	0393	1	59.01.28	170802
7740	W03530	0410	2	59.01.30	170805
7740	W03530	0391	1	59.01.28	170804
7743	E16619	0391	1	60.02.19	170878
7750	E16636	0020	2	60.01.03	170887
<i>Nephasoma diaphanes</i>					
5311	W07050	0001	1	66.03.27	170277
5329	E16948	0591	2	68.01.01	170289
5333	W06457	0121	3	64.02.12	170249
5335	W06945	0041	1	69.05.17	170124
5346	W07053	0288	472	64.02.06	170982
5349	W07025	0021	3	70.04.29	170360
5408	W05208	0450	4	66.01.30	170274
5427	W06612	N.R*	1	63.01.21	170231
5429	W06350	0840	2	71.10.27	170378
5434	W06410	0073	1	71.10.20	175488
5434	W06420	0091	1	71.10.20	170375
5445	W06100	0001	2	71.05.20	170371
5445	W06353	0044	11	71.05.11	170361
5446	W06423	0051	2	71.05.24	170974
5458	W06503	0247	28	64.02.10	170687
5459	W10510	4180	1	65.11.20	170704
5502	W05857	0120	1	62.12.04	170952
5542	W07035	0174	2	62.08.20	170208
5606	W06619	0440	1	63.09.18	170680
5606	W06619	0440	6	63.09.18	170769
5606	W06619	0436	1	63.09.18	170995
5624	W02719	0950	2	75.06.02	170089
5651	W03425	3170	1	63.09.06	170242
5706	W06321	3975	1	62.07.28	170199
5800	W07056	4010	1	62.11.03	?EL311
5829	E17948	0592	1	68.01.01	170288
6051	W04255	0300	5	64.04.14	170259
6056	W05652	2850	1	64.03.13	170689
6057	W11453	5033	2	64.01.06	170682

## Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
6145	W06114	4728	1	62.08.01	170201
6442	W06238	0097	2	71.12.15	170830
6446	W04130	4575	1	69.03.19	170861
6447	W06410	0198	1	83.03.20	175491
6535	W06540	0200	1	73.03.01	175511
6558	W06651	0200	1	59.04.04	170809
7316	W17705	1210	1	68.02.10	170310
7340	E17517	0519	1	57.11.09	170781
7406	W03938	0731	2	68.02.06	170130
7406	W03938	0731	2	68.02.06	170850
7428	W03032	0513	1	69.02.24	170839
7604	W17640	0564	1	68.01.21	170306
7658	W17107	0431	1	68.02.02	170308
7705	W03504	0743	2	69.02.26	170840
7705	W03504	0793	9	69.02.26	170854
7752	E17733	0770	1	67.01.25	171002
7823	W17306	0474	1	68.01.26	1710962
<i>Phascolion (Montagu) lutense</i>					
5302	W03740	3080	1	63.09.17	170245
5403	W03340	2690	21	63.09.09	170160
5501	W09915	3931	1	65.06.05	118738
5501	W09915	2160	4	65.06.05	118728
5506	W03955	2975	2	66.02.08	170708
5508	W02559	5440	128	63.03.29	170679
5508	W02559	5440	3	63.04.29	170758
5549	W02211	4256	9	66.03.04	170710
5552	W02449	5790	54	63.04.30	170759
5618	W15613	3694	4	66.11.11	170445
5653	W03733	3141	1	83.08.28	170240
5700	W02610	2742	39	75.05.22	170150
5723	W02634	2325	109	75.05.26	170151
5739	W02600	2500	113	75.05.27	170152
5806	W12008	4173	1	64.10.31	170772
5808	W04456	2800	4	63.02.15	170676
5811	W02548	2400	14	63.05.03	170164
5814	W02544	2492	55	63.05.03	170776
5900	W03945	2825	4	66.02.10	170767
5903	W03649	2817	41	64.04.10	170172
6056	W05652	2850	1	64.03.13	170689
6100	W09502	4941	2	64.10.11	170763
6120	W08237	4455	1	63.10.22	170863
6127	E10800	5043	8	66.04.25	170713

## Appendix.—Continued.

Latit. South	Longit.	Depth in m.	Num. ind.	Date y.m.d.	USNM #
6144	W09952	5046	1	65.07.16	170700
6145	W06114	4758	1	62.08.01	170200
6239	W06406	3737	1	62.08.06	170202
6307	W12812	4682	5	66.11.03	170444
6353	W10839	4948	46	66.03.27	170983
6406	W11517	4873	2	66.04.30	170984
6408	W04048	4510	2	64.03.21	170255
6417	W13013	4645	8	64.06.22	170173
6417	W13013	4695	2	64.06.22	170757
6448	W11430	4886	2	64.01.11	170683
6520	W11730	4845	1	64.06.15	170756
6537	W12106	4781	1	64.06.17	170262
6612	W10228	4713	6	64.06.10	170755
6650	E16432	2515	2	67.02.05	170451
6748	E15812	2315	3	67.02.05	170178
7328	W03027	3111	6	69.03.13	170860
<i>Phascolion (Isomya) hedraeum</i>					
5302	W03740	3080	1	63.09.17	170245
5338	W03802	0137	2	75.05.12	170067
5342	W03757	0147	3	75.05.14	170070
5344	W03759	0133	3	75.05.13	170069
5346	W07053	0288	2	64.02.06	170982
5351	W03738	0100	78	66.02.07	170707
5403	W03724	0070	1	75.05.16	170074
5406	W03631	0135	1	75.05.19	170078
5411	W03802	0160	1	86.12.05	170988
5412	W03740	0070	4	75.06.10	170100
5414	W03754	0200	1	75.05.12	170065
5422	W03359	0155	40	75.05.19	170148
5439	W03851	0267	1	75.06.09	170155
5451	W03503	0170	1	86.12.10	170971
6009	W12709	4375	1	65.10.09	170835
6022	W04650	0350	3	64.04.15	170697
6051	W04255	0300	4	64.04.14	170696
6125	W04155	0396	3	64.04.13	170258
6125	W04155	0595	1	64.04.13	170694
6125	W04155	0595	1	64.04.13	170137
6125	W04155	0595	3	64.04.13	170695
6127	W04155	0604	1	64.04.12	170257
6127	W04155	0604	1	64.04.12	170692
6127	W04155	0604	1	64.04.12	170693
7428	W03032	0513	3	69.02.24	170839

## Two new species of *Nereis* (Polychaeta: Nereididae) from the Mexican Pacific

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*Abstract.*—Two new species of *Nereis* from the Mexican Pacific are described. *N. inflata*, is characterized by an enlarged dorsal ligule in posterior notopodia and long shafted notopodial homogomph falcigers; *N. casoae* belongs to the group of species with short dorsal ligules and elongate ventral ligules, but it can be differentiated by the presence of long blades in notopodial homogomph falcigers, with many small teeth on the interior margin and an apical blunt tooth.

The descriptions included in this study are part of an exhaustive revision of specimens from the family Nereididae in Mexican shores (de León-González 1997). So far, 22 species of the genus *Nereis* are known from the Mexican Pacific. The species newly described herein were collected either by María Elena Caso in Chivos Island in front of Mazatlán harbor, Sinaloa State, Mexico in the intertidal zone, by one of us (VSW) in soft bottoms of the continental shelf along the Sinaloa coast with personnel from the Lab de Ecología Costera, ICML-UNAM, as part of the Institutional projects SIPCO and CORTES (1981–1982), on board the R/V *El Puma*, of UNAM, and by the first author (JALG), those last separated from the endolithic fauna in sandy rocks collected by shrimp trawls in the western coast of the Baja California peninsula.

The type material is deposited in the polychaetological collections of both the Universidad Autónoma de Nuevo León (UANL), and the Instituto de Ciencias del Mar y Limnología, U.N.A.M. (CPICML)

*Nereis casoae*, new species  
Figs. 1, 2

*Material examined.*—55 specimens. Col. Dra. Maria Elena Caso, Isla los Chivos,

Mazatlán, Sinaloa, 9 May 1979 (Holotype UANL 4832, 6 Paratypes UANL 4833); Project SIPCO I, Stn. A-2(14), 22°17'N, 106°10'W, 61 m, 23 Apr 1981; Stn. C-1 (1), 23°37'N, 106°56'W, 40 m, 24 Apr 1981; C-2 (7), 23°34'N, 106°57'W, 66 m, 24 Apr 1981; SIPCO II, Stn. A-2 (2), 22°18'N, 106°10'W, 66 m, 22 Aug 1981; Stn. C-2 (2), 23°36'N, 107°02'W, 72 m, 23 Aug 1981; SIPCO III, Stn. A-2 (2), 22°17'N, 106°11'W, 74 m, 15 Jan 1982; Stn. C-2 (17), 23°32'N, 107°08'W, 76 m, 16 Jan 1982; Project CORTESI, Stn. 33 (1), 29°54'N, 114°20'W, 75–80 m, 8 May 1982; Stn. 48 (1), 28°13'N, 111°28'W, 54 m, 11 May 1982.

*Epitokous material examined.*—SIPCO II, Stn. A-2 (1).

*Description.*—Holotype incomplete with 71 setigers, 40 mm long, 3 mm wide. Body reddish-brown, with dorsal dark band in median anterior region, beginning on setiger 2. Prostomium pentagonal, one pair of slender frontal antennae. Two pairs of eyes in trapezoidal arrangement, anterior pair as a lens, posterior oval. Biarticulate palps with cylindrical palpostyle. Expanded peristomium, with four pairs of tentacular cirri, the longest extending to setiger 4 (Fig. 1a).

Pharynx with paragnaths in all areas, except area V, paragnaths arrangement as follows: I = 1 small cone, II = 2 cones in a triangle; III = 23 cones in a square; IV = 22 cones in a crescent; VI = 4 cones in a diamond; VII–VIII = 4 cones in a row.

Anterior notopodia with dorsal ligules triangular, median ligule conical, superior lobe reduced as a ridge; neuropodia with postsetal lobe rounded, ventral ligule subulate; dorsal cirrus basally inserted, ventral cirrus smaller (Fig. 1b). Median and posterior parapodia similar to anterior ones, but with ventral ligule notoriously elongate. Ventral cirrus becoming smaller in posterior parapodia (Fig. 1c, d).

Setae in anterior parapodia arranged as follows: notosetae in supracicular position homogomph spinigers; supracicular neurosetae homogomph spinigers and heterogomph falcigers strongly denticulate (Fig. 1e); infracicular spinigers and falcigers heterogomph, the latter with a slightly longer blade (Fig. 1f). Median and posterior parapodia with setae in the following arrangement: notosetae in supracicular position homogomph spinigers and falcigers with the anterior region of blade rounded (Fig. 1g); supracicular neurosetae homogomph spinigers and heterogomph falcigers, the latter with a short blade, strongly denticulate in inner margin and an apical tooth directed downwards (Fig. 1h); infracicular neurosetae homogomph spinigers and heterogomph falcigers, with blade slightly larger than supracicular ones (Fig. 1i).

Pygidium absent in this specimen; in another one, pygidium with terminal anus and two longanal cirri.

*Epitokous male*.—Specimen complete, light yellow, with 67 setigers, 13 mm long atokous region 2 mm wide, epitokous region 2.5 mm wide.

Prostomium pentagonal, as long as wide, one pair of cirriform antennae, two pairs of enlarged eyes, biarticulate palps with rounded palpostyles. Peristomium as wide as the next two setigers; longest peristomial cirrus extends posteriorly to setiger 6.

Body divided in two regions: anterior one atokous, first 9 setigers with dorsal and ventral cirri slightly modified, all with distal cirristyles (Fig. 2a, b). From setigers 11 to 14, parapodia similar to atokous specimens (Fig. 2c). Parapodia from heteronereidid region strongly modified, with lamellae associated with lobes, ligules and cirri; dorsal cirrus in anterior parapodia with up to 9 ventral crenulations, ventral cirrus short (Fig. 2d). Dorsal cirrus smooth in posterior parapodia, ventral cirrus almost twice dorsal cirri size (Fig. 2e). Natatory setae from modified region with oar-like appendages.

*Discussion*.—The presence of the ventral elongate ligule is a characteristic seldom observed, being only known in *Nereis apalie* Wilson (1985) from Australia, *N. fauchaldi* de León-González & Díaz-Castañeda (1998), from western Mexico and probably *N. latrescens* Chamberlin (1918) from California, since in the latter the ventral ligule is not so elongate as in the former species but more so than in other species of *Nereis*. This structure is present in *N. casoae*, new species, as in the species formerly mentioned, but it can be differentiated by the presence of the long blade in notopodial homogomph falcigers, with many small teeth on the interior margin, and an apical blunt tooth; in *N. apalie* and *N. latrescens*, for the above mentioned falciger, the blade is short and with 5 and 3 teeth, respectively, whereas in *N. fauchaldi* the blade is short and smooth.

*Etymology*.—This species is dedicated to Dr. María Elena Caso who collected part of the material which was used in the description.

*Distribution*.—This species is known from the Mazatlán area (Sinaloa State), and two localities in the Gulf of California.

*Habitat*.—Among algae fixed to coral-line rocks, and in sandy bottom of the Gulf of California.

*Nereis inflata*, new species

Fig. 3

*Material examined*.—7 specimens. Col. J. A. de León-González, in front of Punta

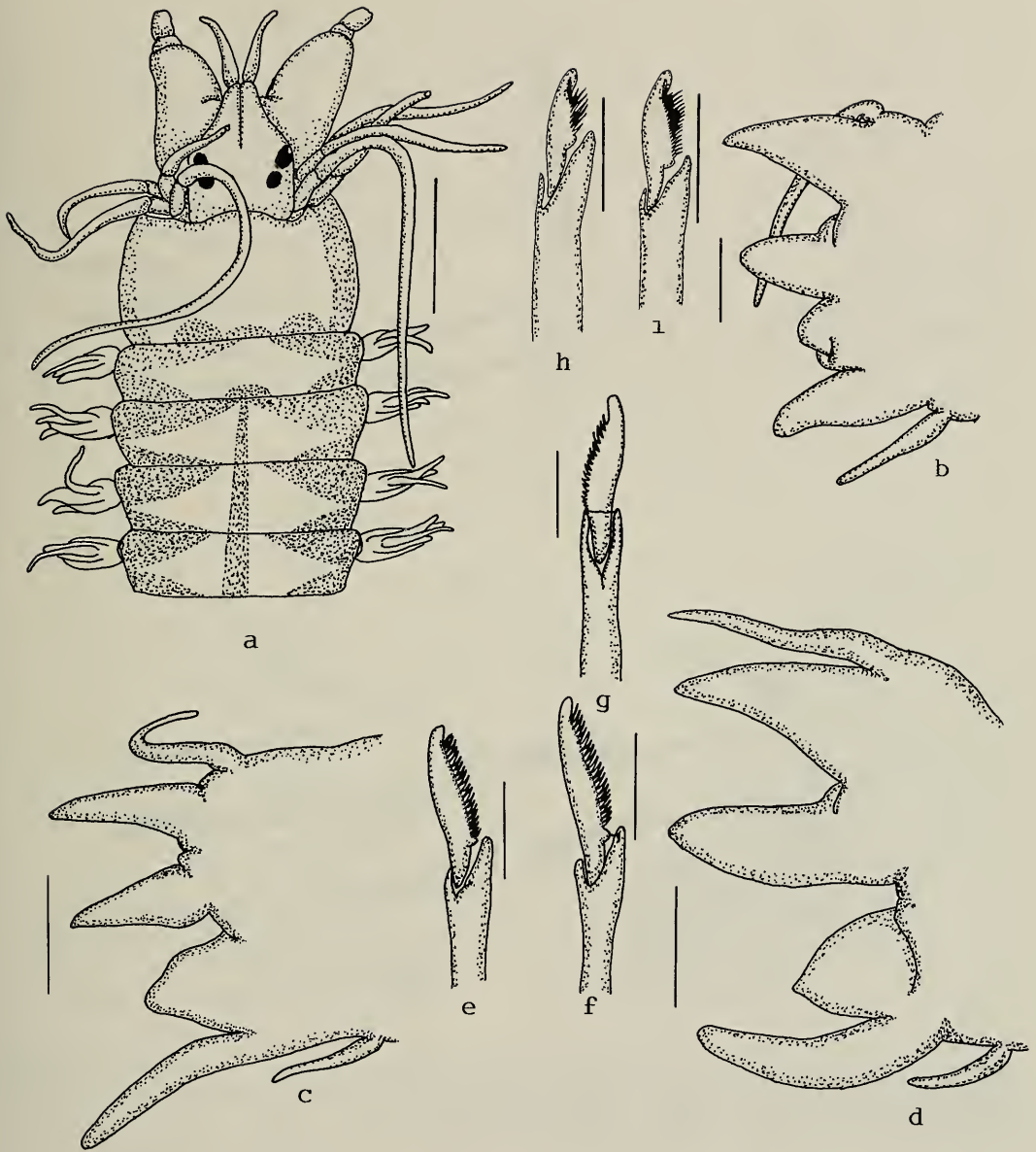


Fig. 1. *Nereis casoae*, new species: a. Anterior region, dorsal view; b. Parapodium, setiger 10, anterior view; c. Parapodium, setiger 37, anterior view; d. Parapodium, setiger 71, anterior view; e. Notopodial heterogomph supracicular falciger from setiger 10; f. Neuropodial infracicular heterogomph falciger from setiger 10; g. Notopodial homogomph falciger from setiger 71; h. Neuropodial supracicular heterogomph falciger from setiger 37; i. Neuropodial infracicular heterogomph falciger from setiger 37. Scale bars: a = 1 mm; b–c = 250  $\mu\text{m}$ ; d = 150  $\mu\text{m}$ ; e–i = 30  $\mu\text{m}$ .

San Juanico, Baja California Sur, 26°13'N; 112°32'W, 30 m, 28 Feb 1989 (Holotype UANL 4834, 5 Paratypes UANL 4835, 1 Paratype CPICML).

*Description.*—Holotype complete, with

56 setigers, 11 mm long, 2 mm wide, including setae; body reddish, prostomium strongly pigmented, posterior region of anterior setigers with transverse dark narrow band. Prostomium pentagonal, a pair of

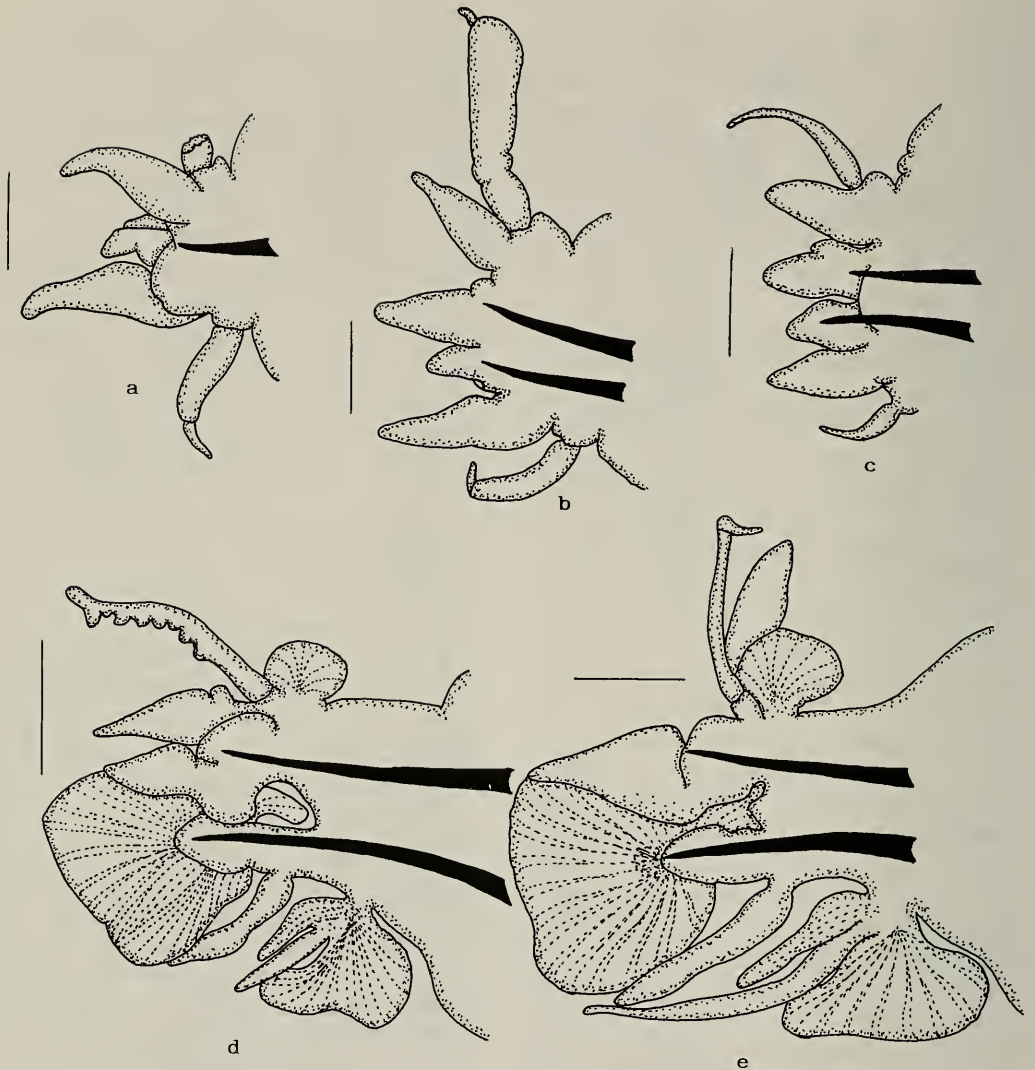


Fig. 2. *Nereis casoae*, new species (epitoke): a. Parapodium, setiger 1, anterior view; b. Parapodium, setiger 5, anterior view; c. Parapodium, setiger 10, anterior view; d. Parapodium, setiger 20, anterior view; e. Parapodium, setiger 50, anterior view. Scale bars: a = 100  $\mu$ m; b-e = 150  $\mu$ m.

slender antennae which do not extend to anterior margin of palps. Two pairs of rounded small eyes. Biarticulate palps, conical palpostyle. Prostomium as large as the next setiger; 4 pairs of tentacular cirri, the longest extending posteriorly to setiger 4 (Fig. 3a).

Pharynx with paragnaths in following arrangement: I = 2 cones in a row; II = 11 cones in 2 rows; III = 11 cones in an oval

group; IV = 17 cones in a crescent; V = 6 cones in a group; VI = 6 in a stellate group; VII-VIII = 60 cones in 3 rows.

Anterior parapodia with notopodia formed by one median and one dorsal conical ligules, and subulate superior lobes; neuropodia formed by a postsetal mammiliform lobe and a digitiform ventral ligule. Dorsal cirrus slender inserted in the median posterior region, ventral one inserted basal-

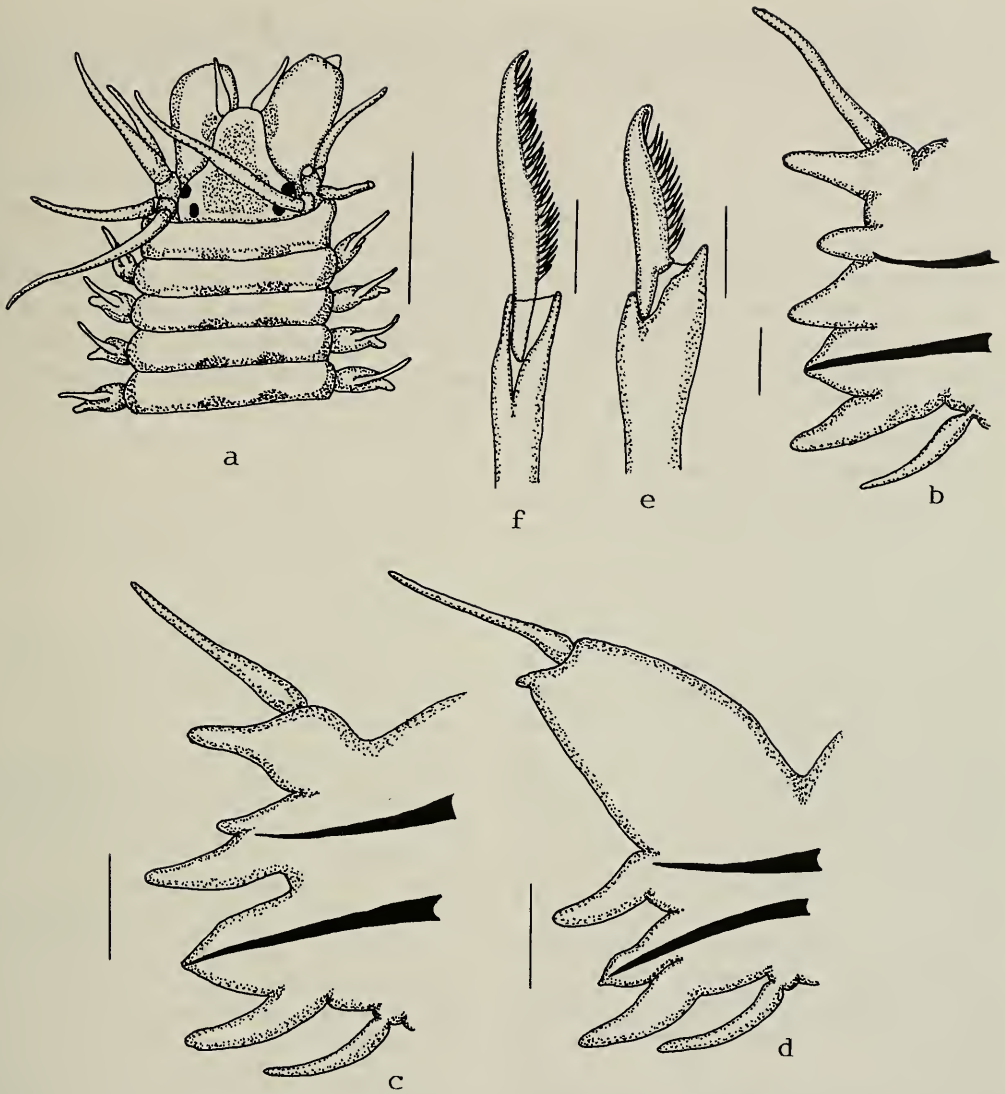


Fig. 3. *Nereis inflata*, new species: a. Anterior region, dorsal view; b. Parapodium, setiger 10, anterior view; c. Parapodium, setiger 23, anterior view; d. Parapodium, setiger 41, anterior view; e. Neuropodial infracircular heterogomph falciger from setiger 23; f. Homogomph notopodial falciger from setiger 41. Scale bars: a = 1 mm; b–d = 150  $\mu$ m; e–f = 15  $\mu$ m.

ly, smaller (Fig. 3b). Median parapodia with reduced superior lobes, dorsal cirrus inserted medially (Fig. 3c). Posterior notopodia with expanded dorsal ligule, superior lobe absent; neuropodia with reduced post-setal lobe. Dorsal cirrus inserted distally (Fig. 3d).

Setae in anterior parapodia in the following arrangement: notosetae supracicular

homogomph spinigers; neurosetae supracircular homogomph spinigers and heterogomph falcigers; infracircular setae heterogomph spinigers and falcigers, the latter with apical tooth directed downwards (Fig. 3e). Median and posterior parapodia with setation similar to those of anterior parapodia; they only differ in the notopodium where in addition to the homogomph spi-

nigers homogomph falcigers are present, with slender blades strongly denticulate in interior margin, with a small distal tooth directed downwards (Fig. 3f).

Pygidium with anus terminal and with two long ventral cirri.

*Discussion.*—*Nereis inflata*, new species, belongs to the group of species with notopodial superior lobes expanded in posterior setigers and notopodial homogomph falcigers with long and strongly denticulate blades; this group includes: *N. callaona* (Grube, 1857) from Peru, *N. lamellosa* Ehlers, 1868 from the Adriatic sea and *N. profundus* Kirkegaard, 1956 from western Africa; however, only in *N. lamellosa* is the superior lobe present in notopodia of anterior setigers, but in contrast to *N. lamellosa*, in *N. inflata* an apical tooth directed downwards is present in notopodial homogomph falcigers. On the other hand, in *N. inflata* in area V of the pharynx there are 6 cones in a group, whereas in *N. lamellosa* there are 0 to 3 cones in a triangle. According to Ehlers (1868), in this species 10 small cones are present in an irregular arrangement on area VI, whereas in the *N. inflata* 6 cones are present in a perfect stellate shape.

*Etymology.*—The specific name “*inflata*” derives from the Latin “*inflatus*” (= puffed or swollen) in reference to the shape of the notopodial superior lobes in posterior parapodia.

*Distribution.*—Endemic. Only known from one locality in the western coast of Baja California Sur.

*Habitat.*—The species was collected in the cavities of sandy rocks obtained in a shrimp trawl.

#### Acknowledgments

We would like to thank M.Sc. Francisco Solís Marín for allowing us to examine and

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## The genus *Pseudoxomysis* (Crustacea: Mysidacea: Mysidae: Leptomysini), with description of a new species from the Timor Sea

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*Abstract.*—Two species of *Pseudoxomysis* are discussed. The present occurrence of *P. caudaensis* in coastal waters of Indonesia is only the second record for the species since Nouvel established it based on specimens from Vietnam. A new species, *Pseudoxomysis incisa*, is described from the Sahul Shelf, Timor Sea. The new species is distinguished from the other species of the genus, *P. caudaensis*, by the smooth body, the third segment of the mandibular palp furnished with two series of setae on the outer margin, the endopod of the fourth male pleopod extending to the distal end of the fourth exopod segment, and the endopod of the uropod armed with 50 spines on the inner margin.

The genus *Pseudoxomysis* was established by Nouvel (1973) to accommodate *P. caudaensis* collected from near Nha Trang, Vietnam. At that time he moved *Doxomysis longiura* Pillai, 1963, to this genus. Since then, no further reports of this genus have been presented. The *Pseudoxomysis* specimens in my possession are composed of two species, *P. caudaensis* Nouvel, 1973, and an undescribed species. Those identified as *P. caudaensis* were collected in Tegal, located in the northern coast of Java Island, Indonesia, by Mulyadi and were presented in my study. The specimens of the supposed new species were collected off the Sahul Shelf in the Timor Sea during a cruise (KH-72-1) of *Hakuho Maru* of the Ocean Research Institute, University of Tokyo. This latter species is described herein. All the specimens examined are deposited in the National Science Museum, Tokyo (NSMT).

### Systematics

Genus *Pseudoxomysis* Nouvel, 1973

*Pseudoxomysis* Nouvel, 1973: 131-132.

*Diagnosis.*—Carapace produced anteri-

orly into triangular rostral plate with rounded apex. Antennal scale lanceolate with rounded apex, setose all around. Labrum provided with strong frontal process. Distal segment of endopod of maxilla expanded distally, shorter than broad, distal margin nearly straight, with about 10 similar-sized strong spines, outer margin naked, clearly longer than inner. Endopods of third to eighth thoracic limbs with carpopropodus divided into 3 subsegments by transverse articulation, terminal claw setiform. Exopod of fourth pleopod of male 7-segmented; ultimate segment small, with 2 simple setae on terminal end, penultimate and antepenultimate segments armed with strong modified seta. Endopod of fourth pleopod of male 6-segmented, considerably shorter than exopod, without modified setae. Female pleopods rudimentary. Female with 3 pairs of oostegites. Endopod of uropod armed with spines along inner margin. Telson with deep apical incision furnished with spinules on either side and pair of plumose setae arising from anterior end. Lateral margin of telson with spines throughout.

*Type species.*—*Pseudoxomysis caudaensis* Nouvel, 1973.

*Remarks.*—Nouvel (1973) mentioned

three major characters that distinguish *Pseudoxomysis* from the closely allied genus, *Doxomysis*, and its related genera, as follows; the labrum with a strong frontal process, the distal endopod segment of the maxilla with the outer margin longer than the inner, and the endopods of the third to eighth thoracic limbs with the carpopropodus divided into 3 subsegments by the transverse articulation.

When Nouvel (1973) established *Pseudoxomysis*, he suggested that *Doxomysis longiura* Pillai, 1963, should be transferred to this genus, because *D. longiura*, described and illustrated by Pillai (1963, 1964), was in agreement with this genus in the characteristics of the maxilla and thoracic endopods, and with respect to the labrum he received a private letter from Pillai that the lip is anteriorly prolonged into a spine though short and apically broad and rounded (Nouvel 1973). In 1973, however, Pillai described and illustrated this species in detail, but omitted to describe the labrum. Liu & Wang (1986) also examined *D. longiura* specimens from northern areas of the South China Sea and stated that the anterior margin of the labrum was not armed with a spine.

At least, the labrum in *D. longiura* lacks such a strong frontal process as seen in *P. caudaensis*. Furthermore, *D. longiura* is different from *Pseudoxomysis* in having a notable papilla on the eyestalk and fine spinules between proximal two lateral spines of the telson. Considering these circumstances, it is judged that the transfer of *D. longiura* to *Pseudoxomysis* should be canceled. As a result, the genus *Pseudoxomysis* comprises only two species which are described in this paper.

*Pseudoxomysis caudaensis* Nouvel, 1973  
Figs. 1, 2

*Pseudoxomysis caudaensis* Nouvel, 1973:  
132–141, figs. 1–25.

*Material*.—(NSMT-Cr 13404) 1 adult female with embryos (5.4 mm), 1 adult male

(4.5 mm), 1 immature female with half-grown marsupium (4.4 mm) and 1 juvenile (2.7 mm); Tegal, northern coast of central Java, Indonesia, 3 June 1994, plankton net, collected by Mulyadi.

*Description*.—Carapace produced anteriorly into triangular rostral plate with rounded apex extending to proximal third of first segment of antennular peduncle (Fig. 1A, B), posteriorly shortened, last 2 thoracic somites visible dorsally. Anterolateral corner of carapace rounded.

Eye slightly compressed dorso-ventrally, 1.5 times as long as broad; cornea developed, as broad as eyestalk; eyestalk 1.5 times longer than cornea, without papilliform process on dorsal surface (Fig. 1A, B).

Antennular peduncle of female more slender than that of male; first segment twice as long as broad, armed with several setae at outer distal corner and 1 seta at inner distal corner; second segment short, wider than long, armed with 1 long seta near distal end of inner margin and 1 short seta on middle of outer margin; third segment connected with second obliquely, as long as first, twice as long as broad, armed with 1 long seta on middle of inner margin and 1 short and 2 long setae at inner distal corner (Fig. 1A). In male, first peduncular segment 1.5 times as long as broad, armed with several setae at outer distal corner and 1 seta at inner distal corner; second segment short, armed with 1 short seta on middle of outer margin, no setae on inner margin; third segment longer than first, 1.5 times as long as broad, armed with 1 long and 1 minute setae at inner distal corner (Fig. 1B).

Antennal scale extending slightly beyond distal margin of antennular peduncle in female and to distal end in male, lanceolate with rounded apex, more than 6 times as long as widest part at proximal fourth; outer margin nearly straight, apical suture at about distal tenth (Fig. 1C). Antennal peduncle barely reaching middle of scale, 3-segmented, second segment longest (Fig. 1C). Antennal sympod with 1 stout spine at anterolateral corner (Fig. 1C).

Mandible with masticatory edge developed; palp narrow, third segment half as long as second, with 7 feathered setae on distal third of outer margin (Fig. 1D). Maxillule with outer lobe armed with 12 stout spines on distal margin and 3 setae on ventral surface; inner lobe armed with 3 strong and 1 slender setae on distal margin, 4 setae on outer margin, 2 setae on inner margin and 4 setae on ventral surface (Fig. 1E). Maxilla with second segment of endopod greatly expanded distally, shorter than broad; outer margin naked, 1.5 times longer than inner, so that distal margin clearly inclined towards mouth; distal margin very slightly concave, nearly 3 times as broad as at base, armed with 9 strong spines and 2 setae; inner distal corner with 6 barbed setae (Fig. 1F). Labrum with strong frontal process (Fig. 1G).

Endopod of first thoracic limb robust; lobe from basis rather small, armed with many stout plumose setae; preischium and ischium expanded medially, wider than long; merus relatively slender, twice as long as broad; dactylus wider than long, furnished with stout setae (Fig. 1H). Endopod of second thoracic limb rather slender; merus as long as carpopropodus and dactylus combined; dactylus as long as broad, armed with setae arranged radially (Fig. 1I). Endopods of third to eighth thoracic limbs lost in all specimens. Exopods of first to eighth thoracic limbs with flagelliform portion 8- or 9-segmented; basal plate small, with outer distal corner pointed (Fig. 1H, I).

First to fifth abdominal somites subequal, sixth somite 1.5 times longer than fifth. Second to sixth abdominal somites hispid. Each of second to fifth abdominal somites with small process along ventral median line.

Pleopods of male biramous, natatory. First pleopod with endopod reduced into short, unsegmented lobe, exopod 7-segmented (Fig. 2A). Second and third pleopods with 7-segmented exopod and 6-segmented endopod, exopod longer than endopod. Exopod of fourth pleopod slightly

less than twice as long as endopod, 7-segmented, ultimate segment small, with pair of simple setae on terminal end; penultimate segment 3 times as long as ultimate segment, with 1 strong seta overreaching tip of terminal setae for half of its length; antepenultimate segment shorter than succeeding one, with 1 strong seta extending slightly beyond apex of terminal setae; each of proximal 4 segments with pair of ordinary plumose setae (Fig. 2B). Endopod of fourth pleopod 6-segmented, only extending to distal margin of third segment of exopod, without modified setae (Fig. 2B). Endopod of fifth pleopod 6-segmented, first segment with triangular lobe tipped with seta on outer margin in addition to usual side lobe; exopod 7-segmented, longer than endopod (Fig. 2C).

Endopod of uropod overreaching distal end of telson for  $\frac{1}{4}$  of its length, armed along inner margin with about 37 spines of variable length (Fig. 2D, E). Exopod of uropod overreaching apex of telson for more than  $\frac{1}{2}$  of its length (Fig. 2E).

Telson (Fig. 2E, F) as long as last abdominal somite, 1.7 times as long as broad at base, abruptly narrowing towards proximal third, parallel-sided in middle third and then gradually narrowing distally. Lateral margin armed with about 21 spines throughout, spines longer in female than in male; each apex with single stout spine. Apical cleft  $\frac{1}{3}$  as long as telson and U-shaped in female,  $\frac{1}{4}$  as long and V-shaped in male, furnished on either side with 2 distal spines and 16–18 spinules; pair of plumose setae arising from anterior end of cleft.

*Remarks.*—The present specimens agree in main characteristics with the description of *Pseudoxomysis caudaensis* Nouvel, 1973, but some minor differences are apparent. The endopod of the fourth male pleopod is slightly less than half as long as exopod and extends to the distal end of the third segment of the exopod in the present specimen, while in the type specimens it is slightly more than half as long as exopod

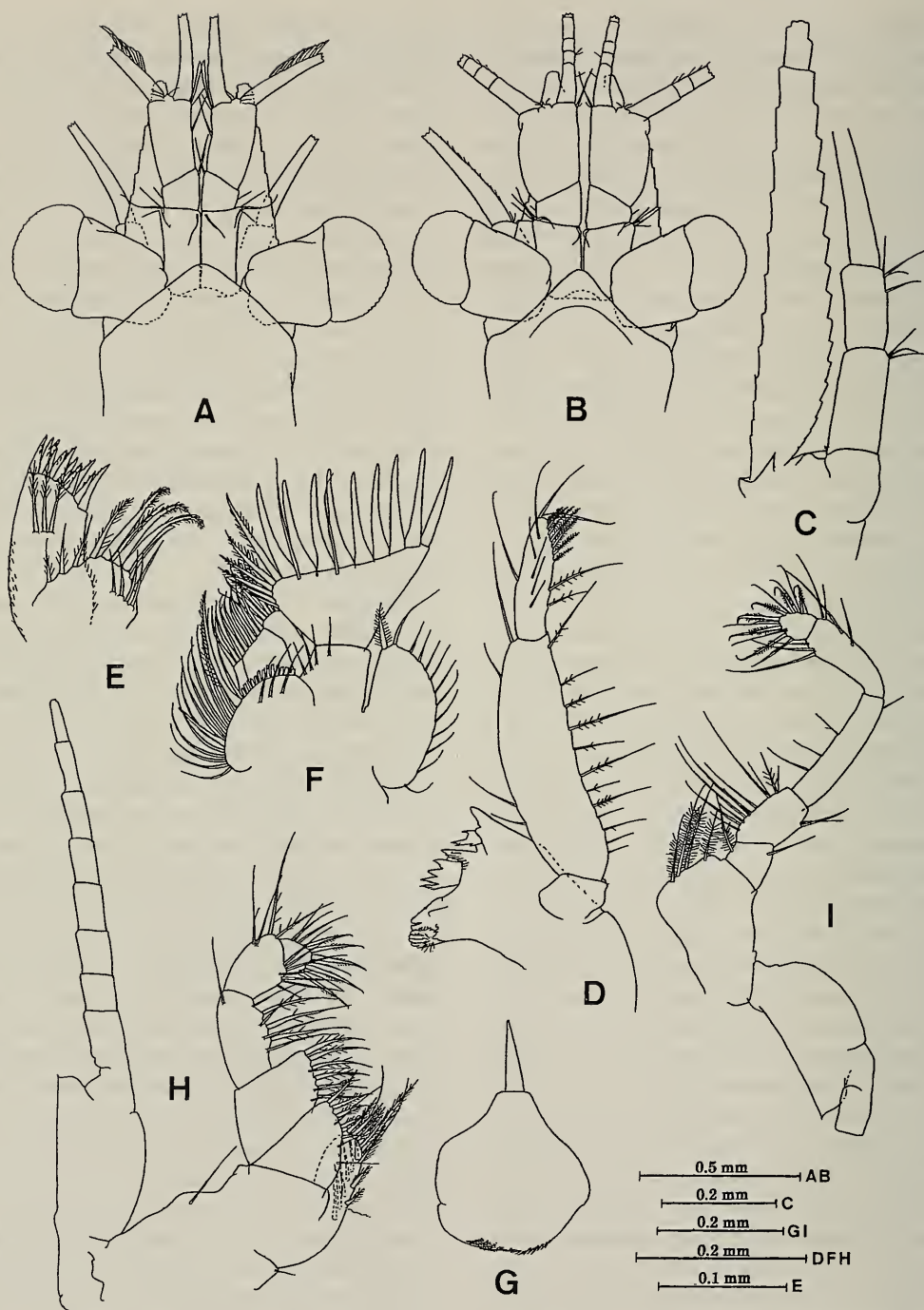


Fig. 1. *Pseudoxomysis caudaensis* Nouvel, A, C-I, adult female; B, adult male. A, anterior end of adult female; B, anterior end of adult male; C, antenna; D, mandible and mandibular palp; E, maxillule; F, maxilla; G, labrum; H, first thoracic limb; I, endopod of second thoracic limb.

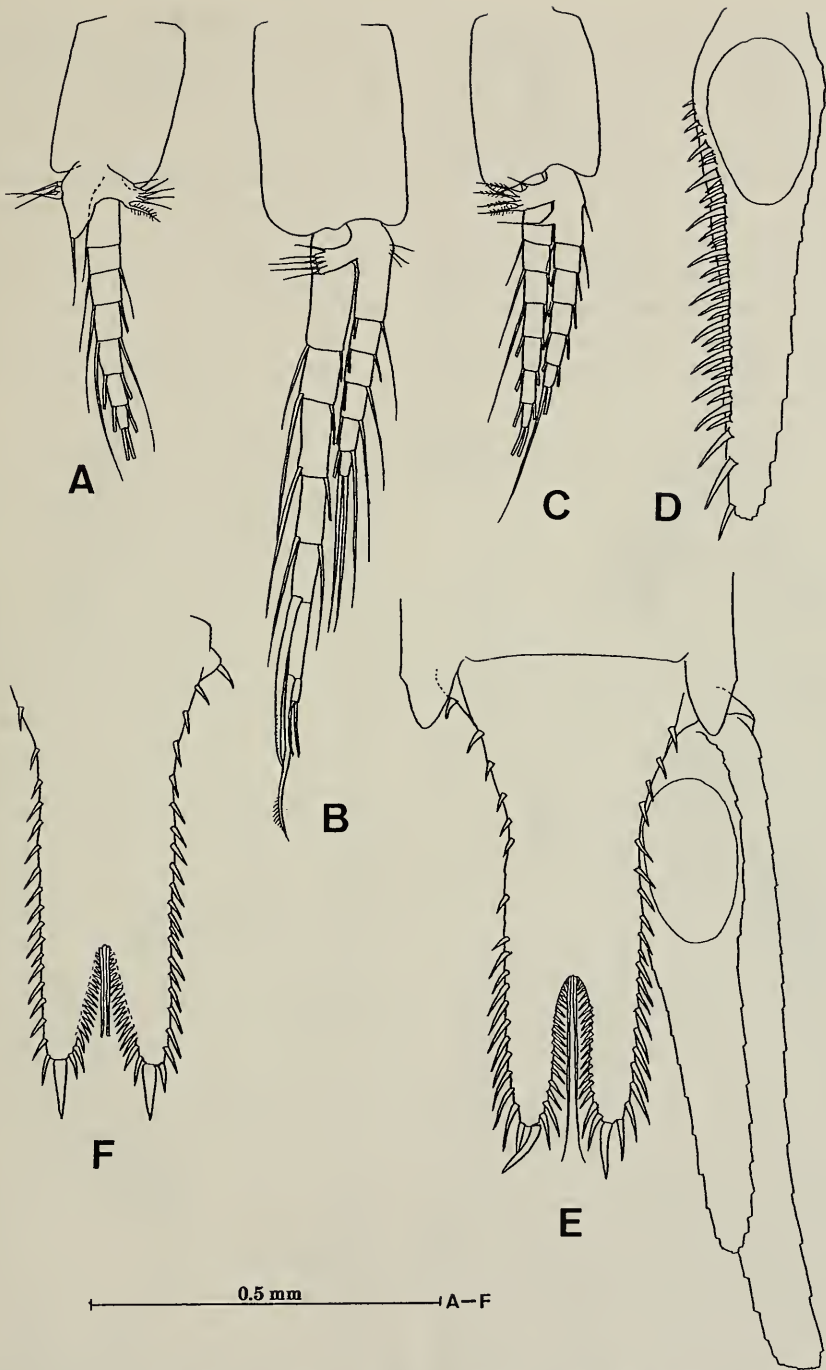


Fig. 2. *Pseudoxomysis caudaensis* Nouvel, A-C, F, adult male; D, E, adult female. A, first pleopod of male; B, fourth pleopod of male; C, fifth pleopod of male; D, endopod of uropod; E, uropod and telson, female; F, telson, male.

and extends to the middle of the third segment. In the type specimens the telson is narrower and several proximal lateral spines arise from the dorsal surface rather than from the lateral margin, while in the present specimens the spines arise from the lateral margin.

*Distribution.*—The type specimens were collected from Cauda Bay near Nha Trang, Vietnam, and the present specimens from Tegal, northern coast of the central Java, Indonesia. This species seems to be a coastal form in Southeast Asia.

*Pseudoxomysis incisa*, new species

Figs. 3, 4

*Type series.*—Holotype (NSMT-Cr 13401), adult male (6.4 mm); allotype (NSMT-Cr 13402), adult female with embryos (5.4 mm); paratypes (NSMT-Cr 13403), 6 adult males (5.2–5.8 mm), 6 adult females (4.7–5.9 mm), 3 of which (4.7, 5.6, 5.9 mm) bear embryos; Sahul Shelf, 12°17.3'S, 129°40.9'E to 12°17.2'S, 129°41.8'E; 49–52 m; 24 June 1972; collected with plankton net installed in mouth of 3-m beam trawl during Hakuho Maru Cruise (KH-72-1).

*Other material.*—17 adult males (5.2–6.4 mm), 13 adult females (4.7–5.9 mm), 4 immature males, 9 immature females; collection data same as type series.

*Description.*—Body smooth. Carapace produced frontally into triangular rostral plate with narrowly rounded apex extending to proximal third to middle of first segment of antennular peduncle, lateral margin of rostrum slightly concave or straight (Fig. 3A, B). Anterolateral corner of carapace rounded. Posterior margin slightly emarginate, leaving last 2 thoracic somites exposed dorsally.

Eye relatively large; cornea occupying about half of whole eye, slightly wider than eyestalk; eyestalk hispid on proximal corners, without papilliform process on dorsal surface (Fig. 3A, B).

Antennular peduncle of male more robust

than that of female. In male first segment with several setae on anterolateral corner and 1 seta on anteromedial corner, second segment shortest, third segment about as long as first, 1.3 times longer than broad, with 3 setae on anteromedial corner (Fig. 3A). In female first segment more than twice as long as broad, second segment with 1 seta on anteromedial corner, third segment slightly shorter than first, slightly less than twice as long as broad, with 1 seta on middle of medial margin and 6 setae on anteromedial margin (Fig. 3B).

Antennal scale lanceolate with rounded apex, extending beyond distal end of antennular peduncle for 1/7 of its length in male and for 1/6 in female, about 5.5 times as long as maximum breadth at about proximal third, with suture at distal tenth, setose all around; inner margin convex; outer margin straight (Fig. 3A–C). Antennal peduncle short, reaching middle of antennal scale, second segment longest. Antennal sympod with spine at anterolateral corner.

Mandible with masticatory edge developed. Mandibular palp narrow, third segment half as long as second, outer margin armed with 2 series of setae, 10 proximal setae becoming longer distally, feathered on proximal half, 5 distal setae of equal length feathered along whole length (Fig. 3D). Maxillule, outer lobe armed with 11 stout spines on distal margin and 3 setae on ventral surface; inner lobe armed with 3 strong and 1 slender setae on distal margin, 4 setae on outer margin, 3 setae on inner margin and 7 setae on ventral surface (Fig. 3E). Maxilla with second segment of endopod greatly expanded distally, outer margin longer than inner, naked, distal margin truncate, 3 times broader than basal margin, armed with 9 stout, naked spines, outer 2 spines, especially outermost one, considerably longer than others (Fig. 3F). Labrum armed on frontal margin with pointed, long, robust process (Fig. 3G).

Endopod of first thoracic limb robust; lobe from basis armed with many stout plumose setae, preischium and ischium ex-

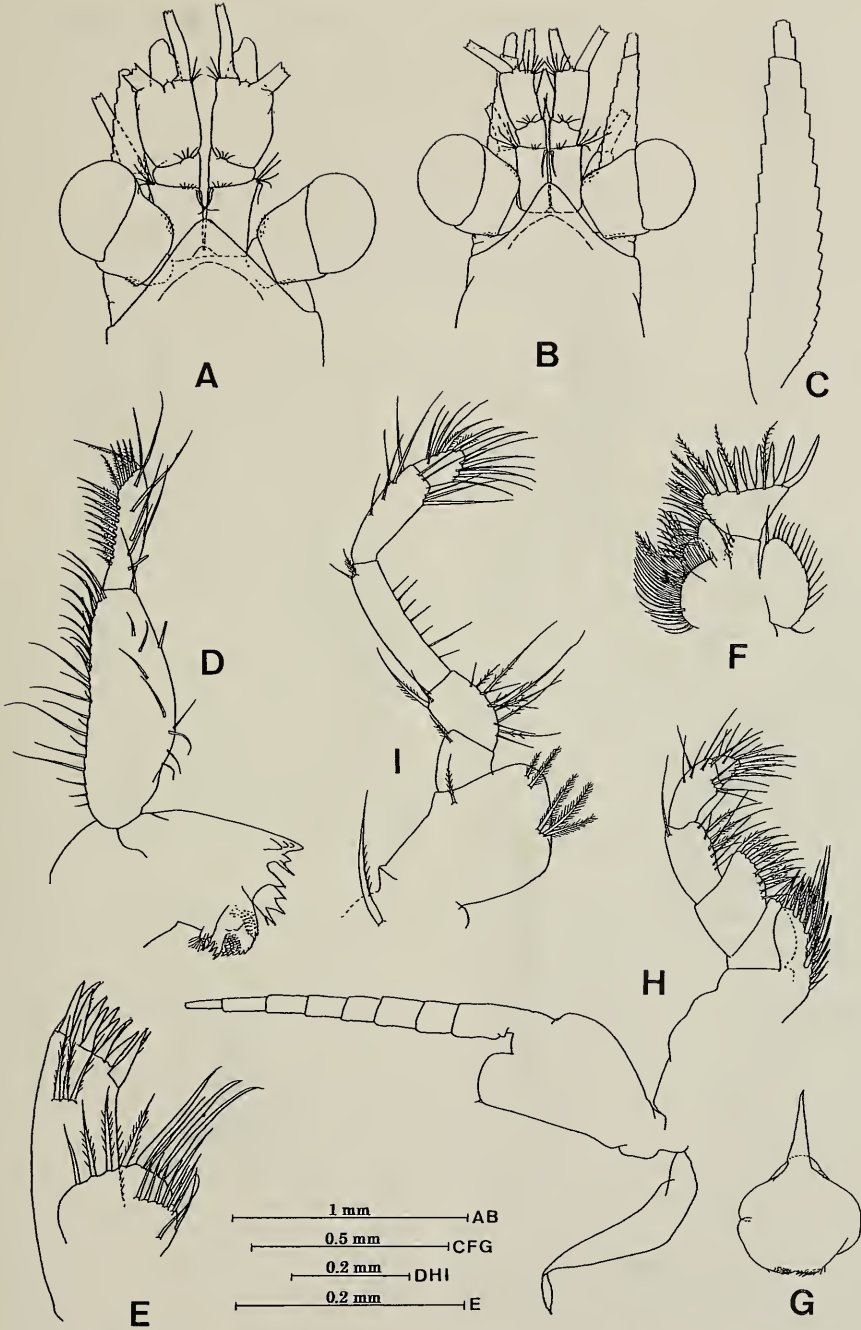


Fig. 3. *Pseudoxomysis incisa*, new species, A, C-I: holotype; B: allotype. A, anterior end of adult male; B, anterior end of adult female; C, antennal scale; D, mandible and mandibular palp; E, maxillule; F, maxilla; G, labrum; H, first thoracic limb; I, endopod of second thoracic limb.

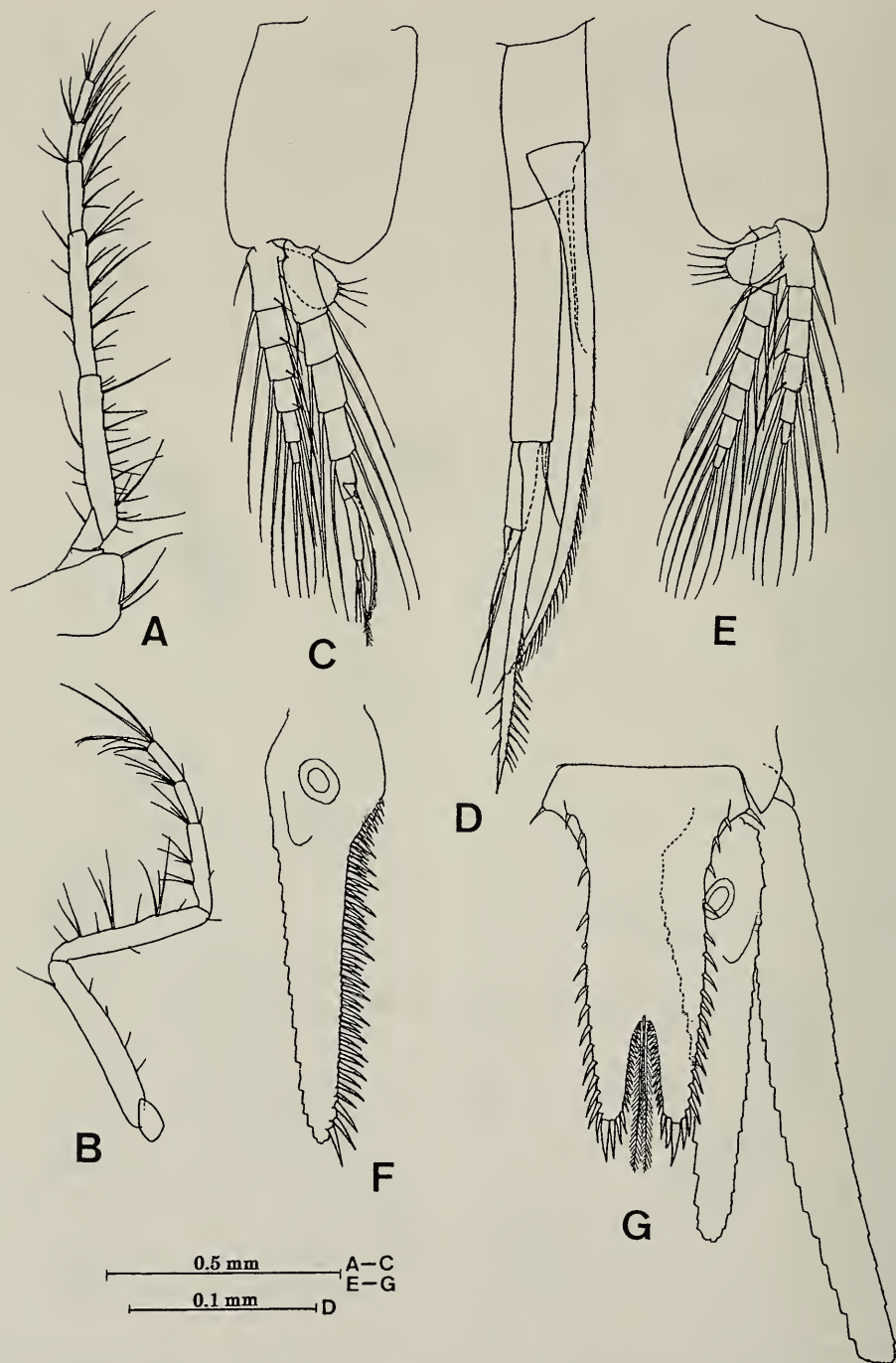


Fig. 4. *Pseudoxomysis incisa*, new species, A, allotype; B, one of male paratypes; C-G, holotype. A, endopod of third thoracic limb without dactylus; B, endopod of seventh thoracic limb; C, fourth pleopod of male; D, distal part of exopod of fourth male pleopod; E, fifth pleopod of male; F, endopod of uropod; G, uropod and telson.



Table 1.—Morphological differences between *Pseudoxomysis caudaensis* Nouvel, 1973 and *P. incisa*, new species.

	<i>P. caudaensis</i> Nouvel, 1973	<i>P. incisa</i> , new species
Abdomen	Hispid	Smooth
Mandibular palp	Third segment with a single series of setae on outer distal margin	Third segment with 2 series of setae on outer margin
Fourth pleopod of male	Exopod slightly less than twice as long as endopod; endopod extending to middle to distal end of third exopod segment	Exopod 1.5 times as long as endopod; endopod extending to distal end of fourth exopod segment
Uropod	Endopod armed with 37 spines along inner margin; exopod overreaching distal end of telson for more than $\frac{1}{2}$ of its length	Endopod armed with about 50 spines along inner margin; exopod overreaching distal end of telson for nearly half of its length

panded medially, wider than long, merus relatively slender, twice as long as broad, dactylus wider than long, hirsute (Fig. 3H). Endopod of second thoracic limb rather slender, merus as long as carpopropodus and dactylus together, dactylus longer than broad, with terminal claw strong (Fig. 3I). Endopods of third to eighth thoracic limbs slender, with carpopropodus divided into 3 subsegments by transverse articulations (Fig. 4A, B).

First 5 abdominal somites subequal, sixth somite 1.3 times longer than preceding one.

Male pleopods developed, biramous. First pleopod with unsegmented endopod and 7-segmented exopod. Second and third pleopods with 7-segmented exopod and 6-segmented endopod, endopod shorter than exopod. Exopod of fourth pleopod 1.5 times longer than endopod, 7-segmented; antepenultimate segment shorter than preceding one, armed with 2 setae, one short, arising from outer distal corner, the other markedly robust, arising from near distal end and reaching tip of terminal setae, curved inwardly; penultimate segment 1.5 times longer but narrower than preceding one, armed with 2 unequal setae on distal margin, shorter one as long as ultimate segment, longer one 1.5 times longer than segment supporting it, straight, with short spine-like setae on distal half; ultimate seg-

ment small, nearly  $\frac{1}{3}$  of preceding one in length, armed with 2 naked, equal-sized setae on distal end (Fig. 4C, D). Endopod of fourth pleopod extending to distal margin of fourth segment of exopod, 6-segmented, without modified setae, first 4 segments with naked accessory seta (Fig. 4C). Fifth pleopod with 7-segmented exopod and 6-segmented endopod; first segment of endopod with slender lobe tipped with seta in addition to usual side lobe; third and fourth segments of endopod with naked accessory seta (Fig. 4E). Side lobe on second to fifth endopods broad (Fig. 4C, E).

Uropod slender, setose all around; endopod extending beyond distal end of telson for  $\frac{1}{4}$  of its length, furnished with about 50 spines on inner margin from statocyst region to apex; exopod overreaching telson for nearly half of its length (Fig. 4F, G).

Telson slightly shorter than last abdominal somite, 1.7 times as long as maximum basal width, abruptly narrowing near base, then gradually towards apex. Lateral margin of telson armed with 16–19 acute spines arranged sparsely in proximal half and densely in distal half, proximalmost spine stout, arising at widest part, proximal second and third spines arising from dorsal surface near margin. Each apical lobe armed with 1, occasionally 2, strong spines on apex and 2 spines near distal end of cleft

margin. Cleft extending to about  $\frac{1}{3}$  of telson length, armed with 16 or 17 spinules on either side, anterior end with pair of plumose setae between which small sinus is present (Fig. 4G).

*Etymology.*—The specific name *incisa* is from the Latin *incisus* = cut into, derived from *caedo* = to cut, in reference to the apical cleft of the telson.

*Remarks.*—The present new species distinctly belongs to the genus *Pseudoxomysis* in the characters of the maxilla, labrum and third to eighth thoracic endopods. From the other species of the genus, *P. caudaensis*, the new species is distinguished as shown in Table 1.

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**Redescription of *Lepeophtheirus marginatus* Bere, 1936 (Copepoda: Caligidae) and relegation of *L. christianensis* Wilson, 1944 and *L. orbicularis* Shiino, 1960 as its synonyms**

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*Abstract.*—*Lepeophtheirus marginatus* Bere, 1936 is redescribed based on examination of type specimens. Studying the type materials of *L. christianensis* Wilson, 1944 and *L. orbicularis* Shiino, 1965 from sea catfish (*Galeichthys* sp.) collected in the Gulf of Mexico and Peru, respectively, led us to recommend relegating both of them as synonyms of *L. marginatus* Bere.

In their report on a new species of *Lepeophtheirus* parasitic on the bullseye puffer (*Sphoeroides annulatus* Jenyns) taken off Sinaloa, Mexico, Ho et al. (in press) suspected that *L. christianensis* reported by Wilson (1944) may be synonymous with *L. marginatus* Bere, 1936, because these nominal species resemble one another and probably were reported from the same species of sea catfish (*Galeichthys* sp.) caught at the same locality (off Pass Christian, Mississippi). Therefore, type specimens of both species deposited at the National Museum of Natural History, Smithsonian Institution in Washington, D.C. were examined. Unexpectedly, in the process of reviewing the species of *Lepeophtheirus* reported from the sea catfish, it was discovered that not only is *L. christianensis* synonymous with *L. marginatus*, but also is *L. orbicularis* Shiino, 1965.

Based on these studies we herein redescribe *L. marginatus* and then discuss the establishment of *L. christianensis* and *L. orbicularis* as junior synonyms of *L. marginatus*.

#### Materials and Methods

The specimens kept in 70% ethanol in the collections of National Museum of Nat-

ural History, Smithsonian Institution in Washington, D.C. and Faculty of Biore-sources, Mie University in Tsu, Japan were cleared in lactic acid for 1 hr before examination. Two specimens (one female and one male) of *L. marginatus* from USNM 79163 were dissected in a drop of glycerin and the removed body parts and appendages were mounted on slides using glycerin as mounting medium and examined using a compound microscope. All drawings were made with the aid of a camera lucida. In this report a full description is given of the female and only those parts and appendages showing sexual dimorphism are given of the male.

#### *Lepeophtheirus marginatus* Bere, 1936 Figs. 1-6

*Material examined.*—Type-material 1 ♀ and 1 ♂ (USNM 69860) from “outside skin” of *Arius felis* (Linnaeus) (= *Galeichthys felis*) collected at Englewood, Florida and another collection containing 3 ♀, 2 ♂, and 1 young ♀ (USNM 79163) from Lemon Bay, Florida (no host designated on label).

*Female.*—Body (Fig. 1A) 3.12 (2.94–3.44) mm long, excluding setae on caudal

rami. Cephalothoracic shield nearly as long (1.59 mm) as wide (1.43 mm), excluding marginal hyaline membranes. Fourth pediger distinctly wider (373  $\mu\text{m}$ ) than long (193  $\mu\text{m}$ ). Genital complex (Fig. 1B) slightly longer than wide (942  $\times$  878  $\mu\text{m}$ ) and scattered with setules in central part of dorsal surface and posteroventral surface near leg 5; median portion of anterior margin protruded to form a short stem that connects to 4th pediger, posteroventral portion between 5th legs with or without shield-like cement plate (originating from a male with whom female mated) holding spermatophores. Abdomen (Fig. 1B) not clearly separated from genital complex, distinctly wider than long (210  $\times$  388  $\mu\text{m}$ ) and with convex sides. Caudal ramus (Fig. 1A, B) small, wider than long (51  $\times$  70  $\mu\text{m}$ ), carrying 3 short (mediodorsal seta broken off on both rami in dissected specimen) and 3 long plumose setae (broken off on both rami in dissected specimen). Egg sacs (not shown in Fig. 1A) longer than half body length.

Frontal plate (Fig. 1A) with 1 setule on anterior margin near midline. Antennule (Fig. 2A) 2-segmented; proximal segment with 27 plumose setae on anterodistal surface, distal segment 2.69 times longer than wide, with isolated seta about midway on posterior margin and 11 setae plus 2 aesthetascs on distal margin. Antenna (Fig. 2B) 3-segmented; proximal segment smallest, with bluntly pointed postero-medial process; 2nd segment robust, with ventral corrugated pad near tip; distal segment with sharply pointed, bent tip, with small seta in proximal region and slender seta in middle region. Postantennal process (Fig. 2B) comprising massive, globular base with 2 setule-bearing papillae and broadly rounded shaft. A spherical outgrowth located between bases of antenna and postantennal process. Mandible (Fig. 2C) with 4 sections, bearing 12 teeth on medial margin of distal blade. Maxillule (Fig. 2B) consisting of long, slender, pointed process and papilla with 3 unequal setae. Maxilla (Fig. 2D) 2-segmented; proximal segment (lacertus)

large, with transverse ridge across middle region and cuneiform process on medial surface; slender, distal segment (brachium) carrying small subterminal process on outer edge and 2 unequal elements (calamus and canna) terminally and subterminally. Maxilliped (Fig. 2E) 2-segmented; proximal segment (corpus) largest, with basal flange on medial surface; distal segments sharply pointed claw carrying small knob in proximal region and simple, medial seta in middle region. Sternal furca on dissected specimen (Fig. 2F) with bluntly tipped tines bearing marginal hyaline membranes, but tines of other specimens appears spatula-like as shown in Fig. 6C.

Armature on rami of legs 1–4 as follows (Roman numerals indicating spines and Arabic numerals, setae):

	Exopod	Endopod
Leg 1	I-0; III, I, 3	(vestigial)
Leg 2	I-1; I-1; II, 5	0-1; 0-2; 6
Leg 3	I-1; I, II, 5	0-1; 6
Leg 4	I-0; I-0; III	(absent)

Leg 1 (Fig. 3A) protopod with plumose outer seta and another plumose inner seta; endopod short, bluntly tipped pinnate process; first segment of exopod with row of setules on posterior edge and short spini-form seta at anterior-distal corner; middle 2 of 4 terminal elements on last segment of exopod with accessory process, 3 terminal elements bearing crescent membrane terminally on both sides assuming spoon-like structure, and 3 posterior plumose setae short. Leg 2 (Fig. 3B) coxa small, with large plumose seta on posterior edge; basis with small, naked outer seta; both lateral and medial edge of protopod with large marginal membranous fringe, proximal lateral spines on third segment of exopod semipinnate with naked anterior side, next spine pinnate and appearing setiform. Leg 3 (Fig. 4A) protopod with large lateral and posterior marginal membranous fringe in addition to lateral and medial plumose setae. Both rami 2-segmented; proximal seg-

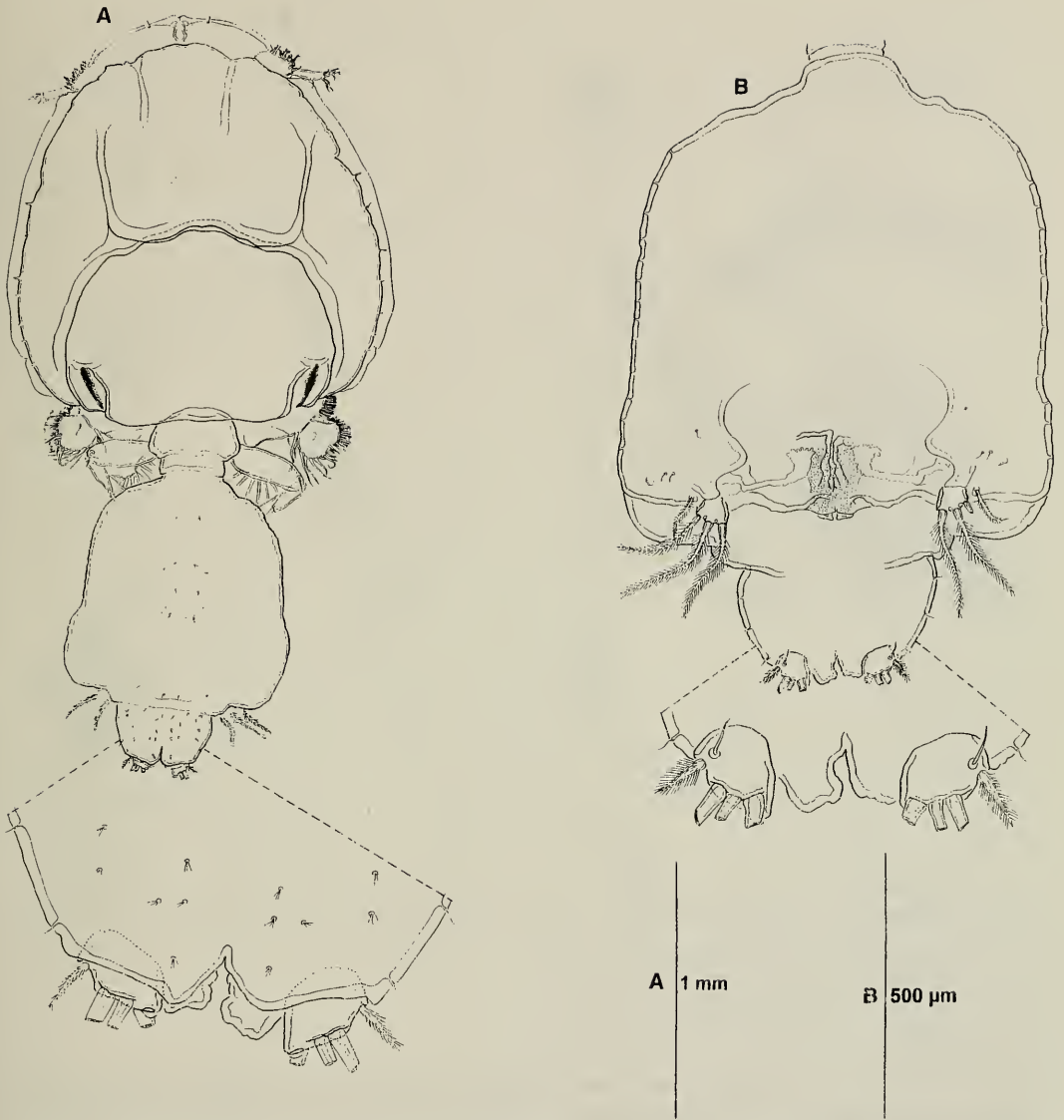


Fig. 1. *Lepeophtheirus marginatus* Bere, 1936. Female. A, habitus, dorsal. B, genital complex and abdomen, ventral.

ment of exopod round, with marginal membranous fringe membrane and slender setiform process; second and terminal segments incompletely fused, with 2 setules proximal to lateral spines on terminal segment. Leg 4 (Fig. 4B) protopod with short, naked distal-lateral seta; pectens on exopod segments at insertion of each lateral spine (Fig. 4C).

Leg 5 (Fig. 4D) represented by pinnate

seta and small process tipped with 3 plumose setae.

*Male*.—Body (Fig. 5A) 2.27 (1.90–2.48) mm long, excluding setae on caudal rami. Cephalothoracic shield about as long (1.19 mm) as wide (1.13 mm), excluding marginal hyaline membranes. Genital complex (Fig. 5C) longer than wide,  $916 \times 786 \mu\text{m}$ , sparsely covered with setules on dorsal surface and lateral margins; ventral surface

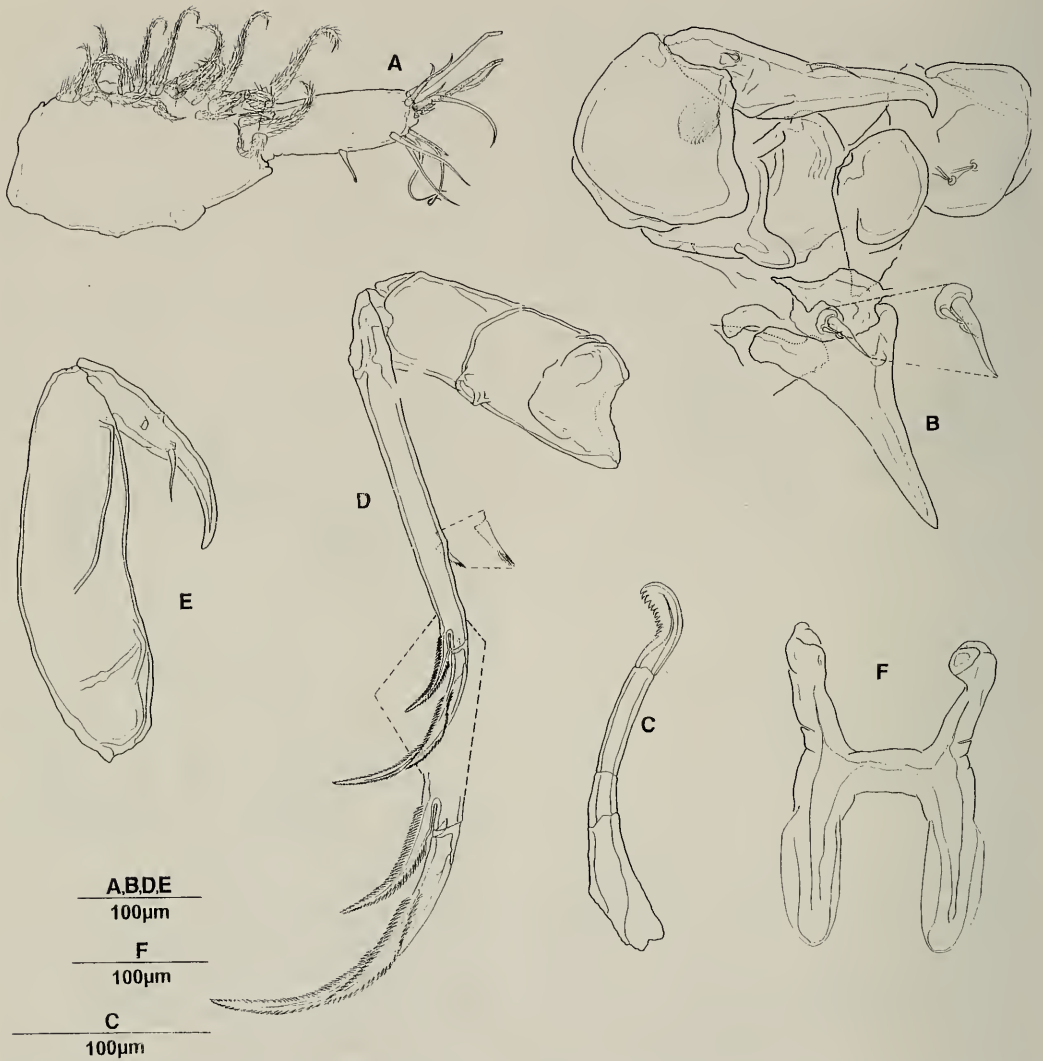


Fig. 2. *Lepeophtheirus marginatus* Bere, 1936. Female. A, antennule (not showing all setae), dorsal. B, antenna, postantennal process, and maxillule; ventral. C, mandible. D, maxilla. E, maxilliped. F, sternal furca.

showing two posterolateral lobes bearing leg 6 at their tip. Abdomen (Fig. 5C) short and slightly wider (488  $\mu\text{m}$ ) than long (461  $\mu\text{m}$ ). Caudal ramus (Fig. 5B) wider (68  $\mu\text{m}$ ) than long (50  $\mu\text{m}$ ). Antenna (A1 in Fig. 6A) 3-segmented; proximal segment with large corrugated pad; middle segment largest, robust and armed with 2 corrugated pads (Fig. 6B); terminal segment prehensile, quadrifurcate distally and armed with 2 spiniform setae. Corrugated pad on sternum (A3 in Fig. 6A) posterior and medial

to maxillule (A2 in Fig. 6A). Dentiform process of maxillule with small protuberance near base (A2 in Fig. 6A). Corpus of maxilliped (Fig. 6D) with 2 transverse ridges near base; shaft bearing subspherical protuberance basally and spiniform seta distally; claw with denticulate medial protrusion near base (see insert drawing in Fig. 6D). Sternal furca (Fig. 6C) with broad, spatula-like tines. Leg 5 (Fig. 5C) consisting of small plumose seta and papilla tipped with 1 simple and 2 plumose setae located

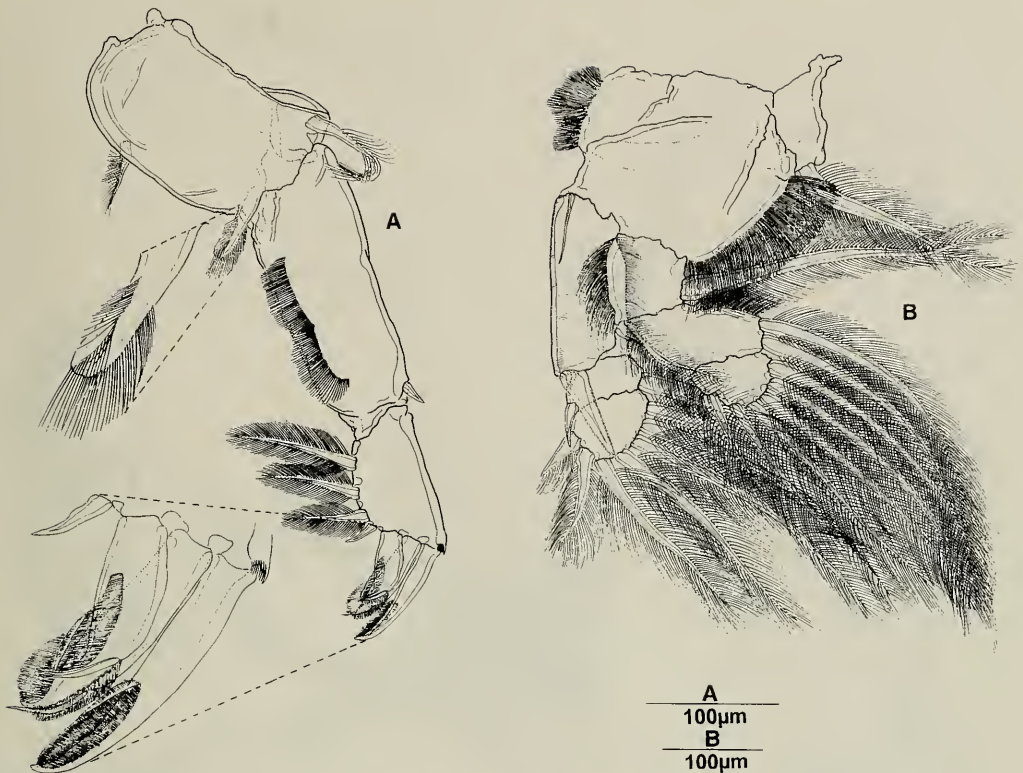


Fig. 3. *Lepeophtheirus marginatus* Bere, 1936. Female. A, leg 1, anterior. B, leg 2, anterior.

on lateral side of genital complex. Leg 6 (Fig. 5C) represented by 3 plumose setae at tip of ventral ridge on genital complex.

#### Discussion

The most distinguishing characteristics of *L. marginatus* are the possession of: a maxillule with simple (instead of bifid) dentiform process (see Figs. 2B and 6A); a 2-segmented (instead of 3-segmented) exopod of leg 3 with slender setiform element (instead of robust, claw-like spine) on proximal segment (see Fig. 4A); and a 3-segmented exopod of leg 4 with long (instead of minute), proximal, outer spine (see Fig. 4B). Due to an incomplete original description of *L. marginatus* and the lack of supplemental information in Causey (1955), the first two of these three unusual features of *L. marginatus* were unknown until now. Interestingly, these three features are also

found in *L. orbicularis* Shiino and *L. simplex* Ho, Gómez & Fajer-Avila (2001). However, *L. simplex* is distinguishable from *L. marginatus* in the shape of the genital complex (oval in *L. simplex*) in both sexes, the structure of the sternal furca (with pointed and curved tines in *L. simplex*), the morphology of the terminal spines on the exopod of leg 1 (lacking crescent membrane in *L. simplex*), and the structure of the terminal claw of male antenna (bipartite and equipped with a tridentate medial protuberance in *L. simplex*).

One hundred and eight species of caligid copepods are currently classified in the genus *Lepeophtheirus*. Among them, six species were reported from the sea catfishes (Ariidae). They are *L. dissimulatus* Wilson, 1905; *L. monacanthus* Heller, 1865; *L. unispinosus* Pearse, 1952, *L. christianensis*, *L. marginatus* and *L. orbicularis*. *Lepeo-*

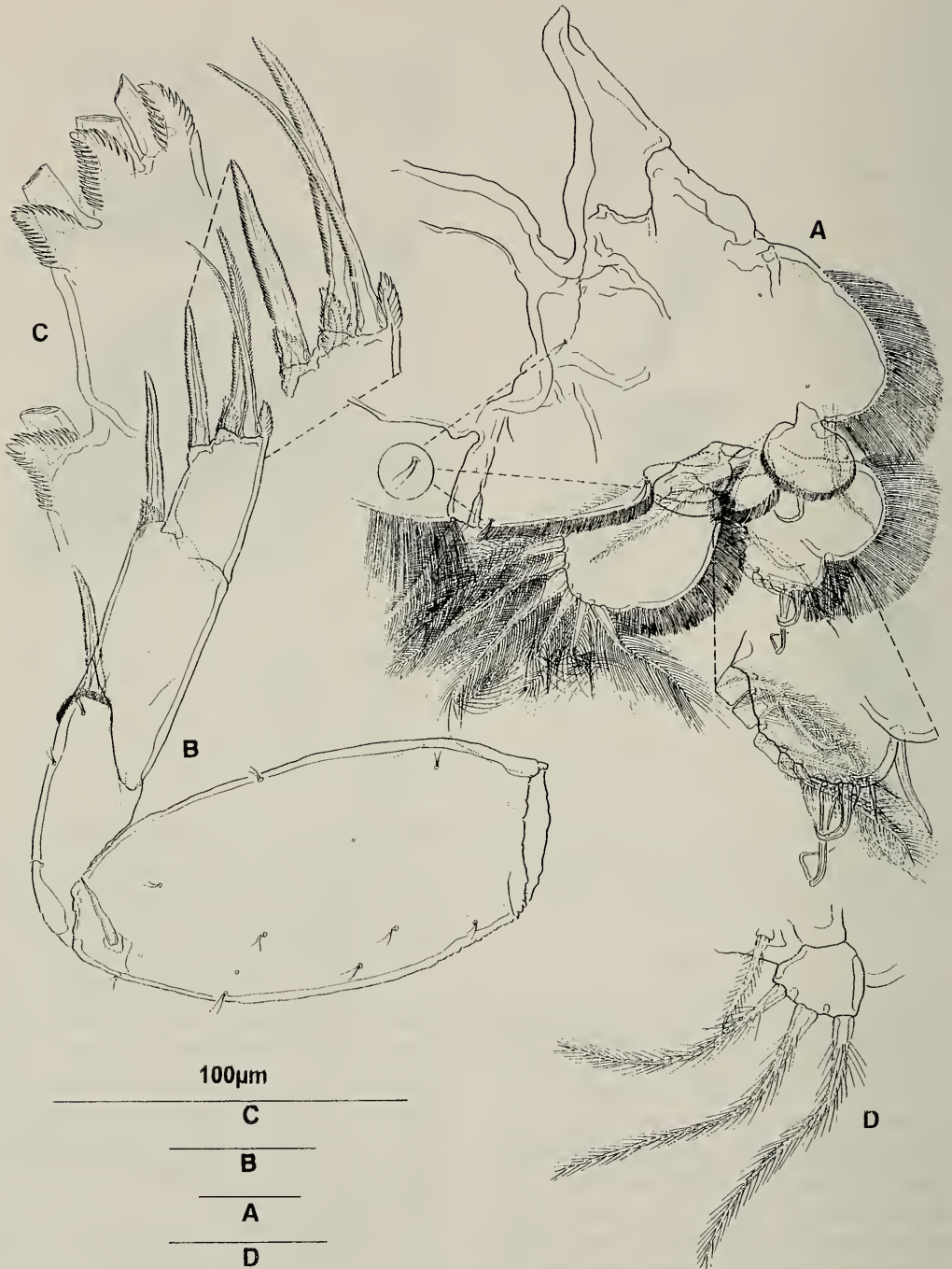


Fig. 4. *Lepeophtheirus marginatus* Bere, 1936. Female. A, leg 3, ventral. B, leg 4, anterior. C, terminal part of leg 4 exopod. D, leg 5.



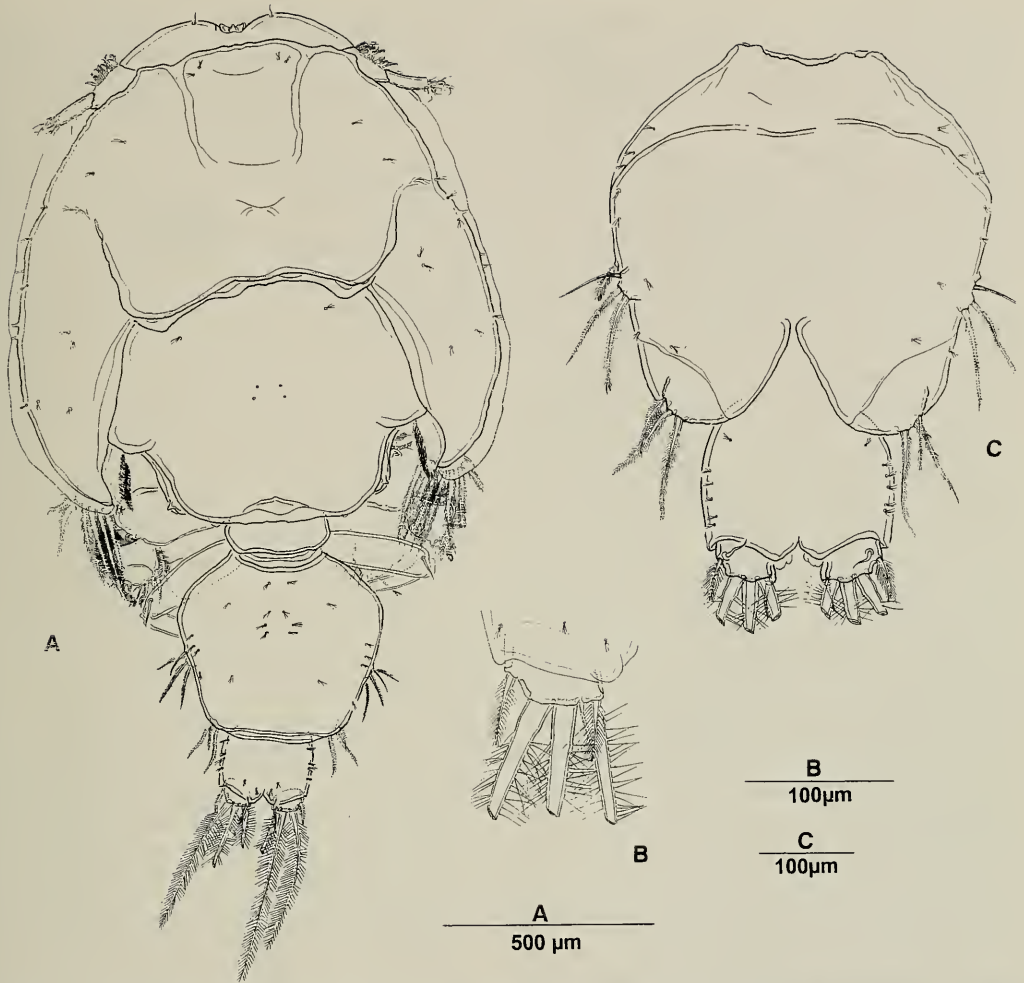


Fig. 5. *Lepeophtheirus marginatus* Bere, 1936. Male. A, habitus, dorsal. B, caudal ramus, dorsal. C, genital complex and abdomen, ventral.

*phtheirus dissimulatus* differs from *L. marginatus* in the structure of leg 3, and *L. monacanthus* and *L. unispinosus* are distinguishable easily from *L. marginatus* by the terminal armature on the exopod of leg 1. Thus, only *L. christianensis* and *L. orbicularis* remain to be scrutinized further.

In her original report of *L. marginatus*, Bere (1936: 587) stated: "A single male and female have been selected for the types of the new species with U.S.N.M. No. 60548." Curiously, Wilson (1944) listed the same catalogue number for his type material of *L. christianensis*. He (Wilson 1944:

533) stated: "The female holotype and male allotype are U.S.N.M. No. 60548." The type collections kept at Smithsonian Institution show that the catalogue number of USNM 60548 is for the type lot of *L. christianensis* and that of *L. marginatus* is USNM 69860. Strangely, although *L. christianensis* was published eight years later than *L. marginatus* it is assigned a smaller (i.e., earlier) catalogue number.

Another curiosity about Wilson's report of *L. christianensis* concerns the number of specimens he collected, examined, and deposited in the National Museum of Natural

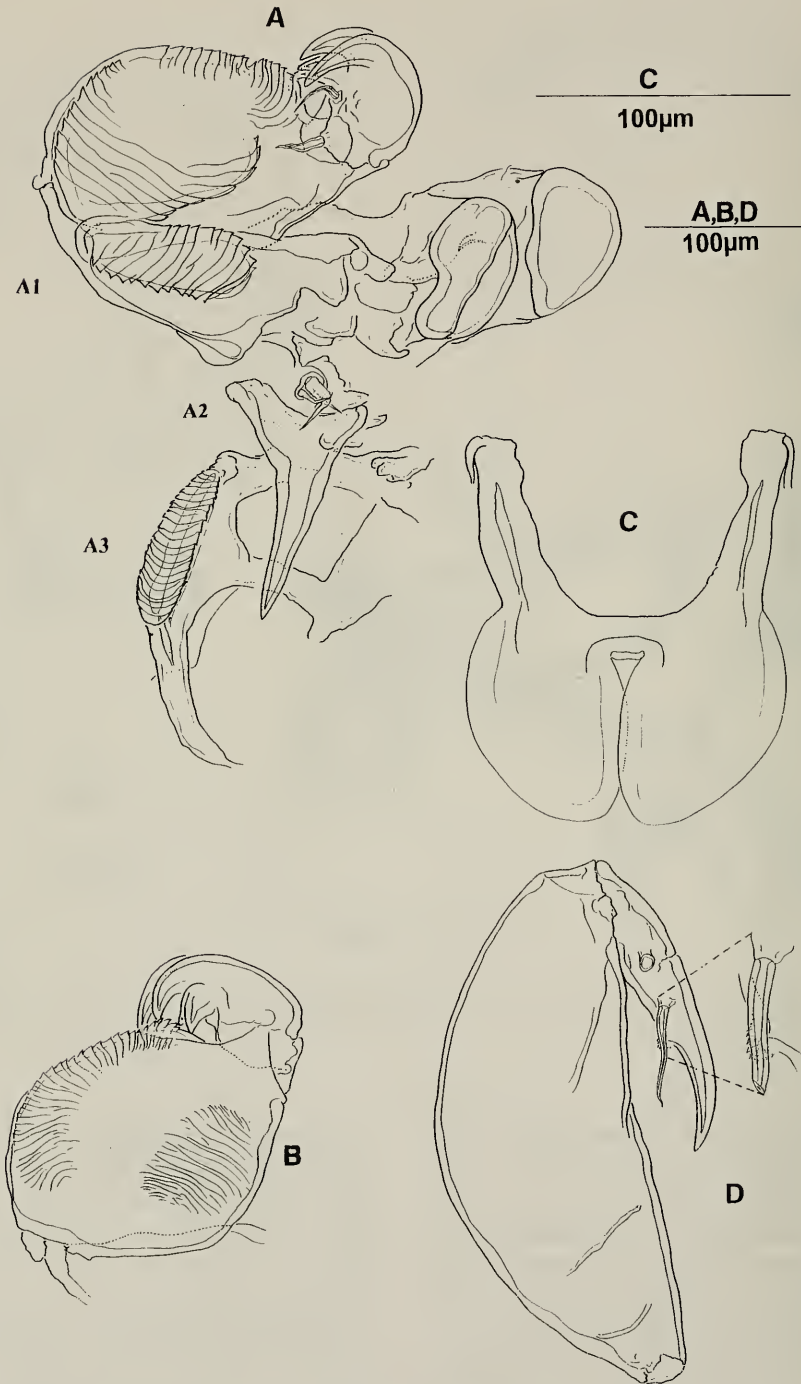


Fig. 6. *Lepeophtheirus marginatus* Bere, 1936. Male. A, antenna (A1), maxillule (A2), and corrugated pad (A3), ventral. B, middle and terminal segments of antenna, anterior. C, sternal furca. D, maxilliped, anterior.

History. Wilson (1944: 533) stated that, "Thirty specimens, including both sexes, were obtained from a sea catfish (*Galeichthys* sp.) at Pass Christian, Miss.," but museum records list a total of 32 specimens kept in two lots, two (one holotype female and one allotype male) in a lot carrying the catalogue number of USNM 60548 and 30 (18 adult females, nine adult males, one pair in amplexus, and one juvenile female) in another lot identified as USNM 60549.

Of the three distinguishing characteristics enumerated above for *L. marginatus*, the segmentation of the exopod of leg 3 and the armature on its proximal segment are the most remarkable feature of this species. In the original description of *L. marginatus*, Bere (1936: 588) stated: "The second and third legs are of the usual type" and thus omitted the illustrations of these two appendages. On the other hand, in Wilson's (1944: 534) report of *L. christianensis*, these two appendages were neither mentioned nor illustrated. As shown in Fig. 4A, leg 3 in *L. marginatus* is not "of the usual type." It is rather unusual in bearing a 2-segmented exopod carrying a setiform element on the proximal segment. These unusual features are found in all 32 specimens of *L. christianensis* deposited at the National Museum of Natural History. A check of their other features revealed that, indeed, all 32 specimens are compatible with our re-description of *L. marginatus*. Accordingly, we recommend relegating *L. christianensis* Wilson, 1944 as a junior synonym of *L. marginatus* Bere, 1936.

When Shiino (1965) reported *L. orbicularis*, no comments on or comparison with *L. marginatus* were made. However, after observing the morphology of *L. marginatus* and noting its close resemblance to *L. orbicularis*, we felt it was necessary to examine the type material of the latter, which was kept in the Faculty of Bioresources at Mie University in Tsu, Japan.

The type material of *L. orbicularis* (S-577) is kept in three vials marked 1, 2, and 3, with each of them containing one, nine,

and five specimens, respectively. In his original description of *L. orbicularis*, Shiino (1965: 447) stated "No. 577. Ten females and five males. The largest female is selected as holotype." But, close examination of each specimen in a drop of lactic acid disclosed that while specimens in vial 1 (containing holotype ♀) and vial 2 (containing 5 ♀ ♀ and 4 ♂ ♂) agree with Shiino's (1965) description of *L. orbicularis*, the five specimens (4 ♀ ♀ and 1 ♂) kept in vial 3 are not. They differ from Shiino's original description in the shape of the abdomen (with straight sides) and structures on leg 3 (with longer velum) and leg 4 (with slender exopod). At this time, those five specimens kept in vial 3 should be excluded from *L. orbicularis*.

Shiino's (1965) description of *L. orbicularis* is clear and no supplemental information from our reexamination of the type material is significant to this study, except for the segmentation of the exopod of leg 3, which is clearly 2-segmented as in *L. marginatus*. Although some minor differences were detected in the fine structures of the maxillule (length of the dentiform process), maxilla (length of the subterminal process and ornamentation on calamus and canna), leg 2 (ornamentation on the two outer spines on the terminal segment of the exopod), and leg 4 (relative length of the lateral spine on the proximal segment of the exopod), these differences are considered geographical variation, because Shiino's (1965) material came from Peru, a different locality from Bere's (1936). Hence, we recommend that the name *L. orbicularis* Shiino, 1960 be relegated as junior synonym of *L. marginatus* Bere, 1936.

#### Acknowledgments

We thank Chad Walter for arranging the loan of type-materials of *L. marginatus* and *L. christianensis* from the collection of the National Museum of Natural History, Smithsonian Institution, and Izawa Kunihiro for the visit by one of us (JSH) to Mie Univer-

sity in Tsu, Japan to examine the type-material of *L. orbicularis* at that institution. Z. Kabata and two other reviewers are acknowledged for their comments and suggestions for the improvement of this paper. The completion of this manuscript was aided by a fellowship from the JISTEC (Japan International Science and Technology Exchange Center) and a grant from the Paramitas Foundation to the senior author (JSH).

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**Observations on Cumacea (Malacostraca: Peracarida) from Antarctic and subantarctic waters. I. *Ekleptostylis debroyeri* (Diastylidae), a new species from waters off the Antarctic Peninsula**

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*Abstract.*—Eighteen species of diastylid cumaceans have been described from Antarctic and subantarctic waters. A nineteenth species, *Ekleptostylis debroyeri*, n. sp., was collected in depths of 83 to 530 m off the Antarctic Peninsula. The new species appears to be closely allied to *Ekleptostylis heardi* McLelland & Meyer, 1998; *E. inornata* (Hale, 1937), n. comb.; *E. pseudoinornata* (Ledoyer, 1977); and *E. vemae* (Băcescu-Mester, 1967), all of which are known from subantarctic and Antarctic waters. *Ekleptostylis debroyeri* is distinguished from these species by a combination of characters including the size of the anterior-most pair of lateral spiniform setae of the telson and the proximal article of the uropodal endopod subequal to the combined length of the two distal most articles. The genera *Diastylis* Say, 1818, *Ekleptostylis* Stebbing, 1912, and *Leptostylis* G. O. Sars, 1869 have morphological features that appear to be transitional, especially among the subadults and females. The generic status of many species within these genera can only be determined with certainty by the morphology (length of antenna, structure of the second pereopod, ornamentation of telson) of the terminal male stage. Although the mature male of *E. debroyeri* is unknown, it is tentatively placed in *Ekleptostylis* based on the similarity of the female to other known species of the genus.

This report represents the first in a series on the distribution, taxonomy, and systematics of Cumacea from the Antarctic and subantarctic waters in depths ranging from 3 to over 5000 m. Members of the cosmopolitan family Diastylidae are found throughout the world's oceans and seas; however, most of the described species come from depths of greater than 1000 m (Day 1980, Jones 1969). In Antarctic and subantarctic waters (south of 50°S) diastylids are presently represented by 18 nominal species and subspecies belonging to four genera. Table 1 lists these currently known diastylids.

An examination of Antarctic and subant-

arctic Cumacea from the collections in the Smithsonian Institution and Antarctic Biology Program of the University of Łódź revealed an undescribed species tentatively referable to the genus *Ekleptostylis* Stebbing, 1912. The description of the new species, which comes from waters in the vicinity of the Antarctic Peninsula, is the subject of this report.

Type material has been deposited in the collections of the National Museum of Natural History (USNM) and University of Łódź. Measurements are in mm unless otherwise stated and total body length (TL) is measured from the tip of pseudorostrum to tip of telson.

Table 1.—Type locality and depth of species and subspecies of the family Diastylidae presently known from Antarctic and subantarctic waters south of 50°E.

Species	Type Locality	Depth (m)
<i>Diastylis anderssoni anderssoni</i> Zimmer, 1907	South Georgia	64–385
<i>Diastylis anderssoni aramata</i> Ledoyer, 1993	Weddell Sea (Halley Bay?)*	270–810
<i>Diastylis corniculata</i> Hale, 1937	66°45'S, 62°03'E	218
<i>Diastylis enigmatica</i> Ledoyer, 1993	75°14.2'S, 26°59.4'E	270–280
<i>Diastylis galeronae</i> Ledoyer, 1993	74°32.2'S, 29°18.7'E	1165–1223
<i>Diastylis horrida</i> Sars, 1887	Kerguelen Islands	20–540
<i>Ekleptostylis inornata</i> (Hale, 1937), n. comb.	66°45'S, 62°03'E	150
<i>Diastylis mawsoni</i> Calman, 1918	66°55'S, 145°06'E	200–582
<i>Diastylis zimmeri</i> Ledoyer, 1977	Kerguelen Islands	18–90
<i>Diastylis annulata</i> (Zimmer, 1902)	South Georgia	4–355
<i>Diastylis diaphanes</i> Zimmer, 1907	66°02'S, 89°03'E	385
<i>Diastylis goekei</i> Roccatagliata & Heard, 1992	King George Island	2–399
<i>Ekleptostylis debroyeri</i> , n. sp.	South Shetlands, King George Is.	90–400
<i>Ekleptostylis heardi</i> McLelland & Meyer, 1998	Argentina (54°04'S, 58°46'W)***	119
<i>Ekleptostylis pseudinornata</i> (Ledoyer, 1977)	Kerguelen Islands	90
<i>Ekleptostylis vemae</i> (Băcescu-Meşter, 1967)**	Argentina (41°16'S, 60°03'W)	70–665
<i>Holostylis helleri</i> (Zimmer, 1907)	South Georgia	12–640
<i>Leptostylis antipa</i> Zimmer, 1907	South Georgia	12–310
<i>Leptostylis crassidauda</i> Zimmer, 1907	66°02'S, 89°03'E	123–385
<i>Makrokyllindrus baceskei</i> Lomakina, 1968	64°03'W, 161°59.2'E	2938
<i>Makrokyllindrus inscriptus</i> Jones, 1971	75°15'S, 166°15'E	808

\* No specific type locality designated.

\*\* See Roccatagliata & Mühlenhardt-Siegel (2000) for records from <50°S.

\*\*\* See remarks in this report concerning a probable error for the original type-locality designation.

*Ekleptostylis debroyeri*, new species  
Figs. 1–3

*Material examined*.—Holotype, adult ♀ with developed oostegites, body length 10 mm; USNM 1000896, Admiralty Bay (King George Island, South Shetland Islands, Antarctic), depth 290 m, transect Thomas Point–Urbanek Crag (sample no. OC-321), 17 Mar 1981, dredge, R/V *Professor Siedlecki*, BIOMASS-FIBEX Expedition (leg. Jażdżewski and Kittel).—Paratypes (1♂, 2♀), same collection data as holotype, Laboratory of Polar Biology and Oceanobiology, University of Łódź, Poland.

*Other material examined*.—Admiralty Bay (King George Island, South Shetlands): 1♀, OC-324, 19 Mar 1981, depth 430 m; 1 manca, OC-477, 11 May 1985, depth 211 m, 1 manca, OC-487, 4 Sep 1985, depth 162 m, 3♀, OC-733, 7 Dec 1988, depth 400–530 m, 2 manca OC-354, 13 Apr

1983, depth 70 m; 1♀, 5 manca, OC-517, 30 Oct 1985, depth 212 m; 1 manca, OC-353, 13 Apr 1983, depth 286 m; 2♂♂ OC-341, 23 Mar 1981, depth 400–530 m; 1♀, OC-726, 10 Oct 1988, depth 240–280 m; 2♀♀, OC-341, 23 Mar 1981, depth 400–530 m; 1♀, OC-348, 61°44.2'S–58°16.7'W; 1♀, OC-347, 58°56.6'S–61°45.5'W, depth 260–285 m, 26 Mar 1981.—R/V *Polarstern*: 50+ specimens, Cruise 42, ANT XIV/2/175, 63°18.90'S–58°41.70'W 23 Dec 1996, depth 491 m.—R/V *Hero*: 1♀, Cr. 731/1847, 67°52.00'S–68°56.00'W, 26 Feb 1973, depth 185 m; 1 subadult ♂ Cr. 731/1823, 64°47.23'S–64°07.20'W; 20 Feb 1973, depth 90–110 m.—R/V *Eltanin*: 5♀♀ Cruise 6, Sta. 439, 63°50.10'S–62°35.90'W, 9 Jan 1963, depth 128–165 m.

*Diagnosis*.—Carapace approximately 0.25 total body length, lacking spines, sparsely covered in fine hair-setae. Pseu-

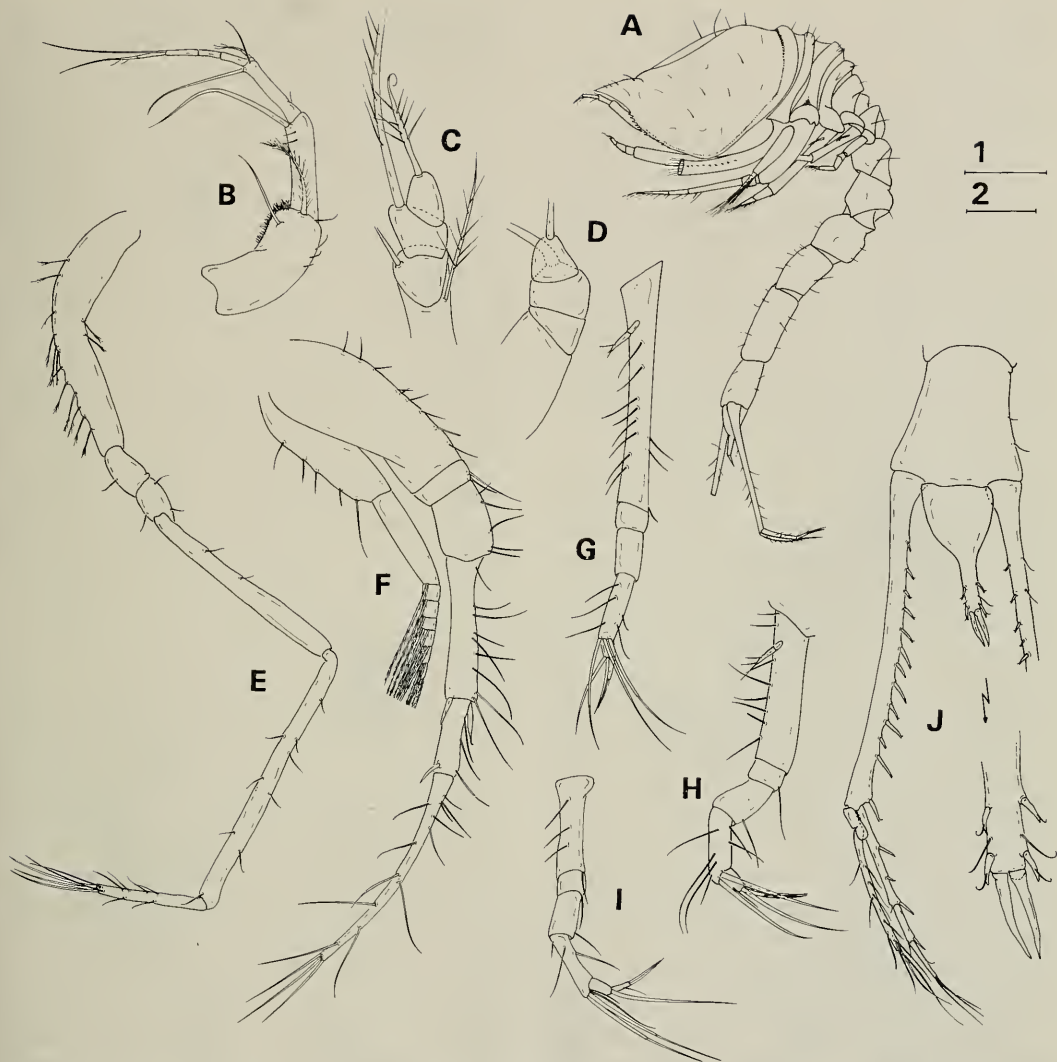


Fig. 1. *Diastylis debroyeri*, n. sp. (female) A, lateral view of adult; B, antenna 1; C, antenna 2; D, antenna 2, another aspect (setae on 2 proximal article not shown); E-I, pereopods 1-5 (exopod not illustrated for pereopod 1); J, left uropod, telson last abdominal somite. Scales: 1 = 1.0 mm for A; 2 = 0.2 mm for B-D; 0.3 mm for E-J.

dorostral lobes slightly downturned with dorsal margins straight. Antennal notch absent in both sexes. Telson slightly longer than last abdominal segment, constricted posteriorly, bearing 2 pairs of lateral, setulate spiniform setae with pair of simple, fine, dorsal-lateral setae between them; posterior tip with terminal pair of spiniform setae strongly developed. Carpus and propodus of pereopod 1 and 2 with short stout

distal setae. Uropods slender, more than twice as long as telson.

*Description.*—Female (based on adults unless stated otherwise). Body length 9–11 mm, sparsely covered with fine simple setae (Fig. 1A). Carapace approximately 1.5 as long as deep, twice as long as combined length of pereonites and approximately  $\frac{1}{4}$  total body length. Pseudorostral lobes deflected slightly downward, dorsal margins

straight. Distinct antennal notch not evident.

Abdomen subequal in length to cephalothorax; pleomeres increase successively in length until 5th; 6th subequal to 4th.

Telson (Fig. 1J). Constricted posteriorly, length (excluding terminal spiniform setae) subequal to last abdominal segment; postanal region subequal in length to preanal, bearing 2 pairs of spiniform (setulate) setae laterally, 1 pair of subdistal, dorsal-lateral fine simple setae between lateral spiniform pairs; tip of telson armed with pair of well-developed terminal spiniform setae.

First antenna (Fig. 1B). Peduncle and flagellum having 3 and 5 articles, respectively. Peduncle article 1 stout, bearing 1 subdistal simple seta, 1 distal plumose seta, and cluster of numerous hair setae distoventrally; peduncle articles 2 and 3 attenuated, much narrower than article 1, each with large distal simple seta. Flagellum with 5 articles; accessory flagellum minute, with 3 articles.

Second antenna (Fig. 1C, D). Small, poorly developed, having 3 short articles on buttressed carina with plumose seta near attachment with article 1; article 1 wedge shaped with 1 simple spiniform seta; article 2 asymmetrical, broadest distally, with long well-developed plumose setae on distal lobe; terminal article small, rounded distally with single terminal plumose seta.

Mandible (Fig. 2A, B). Slender (typical diastylid shape); left mandible bearing lacinia mobilis and 9 spiniform setae, 4 dentate and 5 finely serrate, between molar and incisor process; right mandible with 1 distal palmate comb seta and 9 finely serrate setae.

Labium (Fig. 2C). As illustrated.

Epignath (Fig. 2D). As illustrated.

First maxilla (Fig. 2E). Outer endite with 14 relatively slim setae of various shapes; inner endite with 5 setae (4 of different shapes and 1 accessory); palp with 2 distal setae of different lengths armed distally with microspinules.

Second maxilla (Fig. 2F). Protopodite wide with numerous setae of different

shapes, outer endite with 6 spiniform setae; inner endite with 4 spiniform setae (3 bluntly serrate, 1 non-serrate with basal setule).

First maxilliped (Fig. 2G, J). Siphon long with terminal lobes wide and relatively short, appearing fused (Fig. 2J). Endopodal articles stout and wide with numerous setae along inner margin, ischium reduced, carpus with 2 long plumose setae distally (other setation as illustrated), dactyl slender bearing 5 terminal or subterminal setae.

Second maxilliped (Fig. 2H). Basis equal to combined length of merus and carpus, with 1 long sparsely plumose seta and 4 small simple, needle-like setae distally; ischium approximately 0.5 length of merus with 1 plumose seta on inner margin. Merus approximately length of carpus with plumose setae on middle of inner margin and subdistal on outer margin; carpus twice as long as propodus with numerous setae on inner margin and 2 subdistal plumose setae on outer margin; propodus with numerous setae on inner margin, 1 long, plumose seta medially and 1 subproximal long plumose seta; dactyl slender, tipped by 4 simple terminal and subterminal simple setae.

Third maxilliped (Fig. 2I). Endopod: Basis approximately 1.5 longer than remaining articles combined; inner margin with 12 plumose setae; distal process well-developed with 3 stout, relatively short plumose setae (not reaching tip of propodus); ischium 0.5 length of merus with small plumose seta on inner margin; merus twice as long as ischium, inner margin with 3 small plumose setae, outer with 1 distal plumose seta; carpus, propodus and dactyl subequal; carpus with plumose setae along inner margin, 1 distal seta on outer margin; propodus slender with simple setae distally on inner margin and 1 plumose on outer; dactyl with simple terminal and subterminal setae. Exopod: well-developed, excluding setae, nearly reaching to distal end of basis of endopod.

First pereopod (Fig. 1E). [based on subadult ♀] Attenuate, long with ischium, merus, carpus, propodus, and dactyl with few



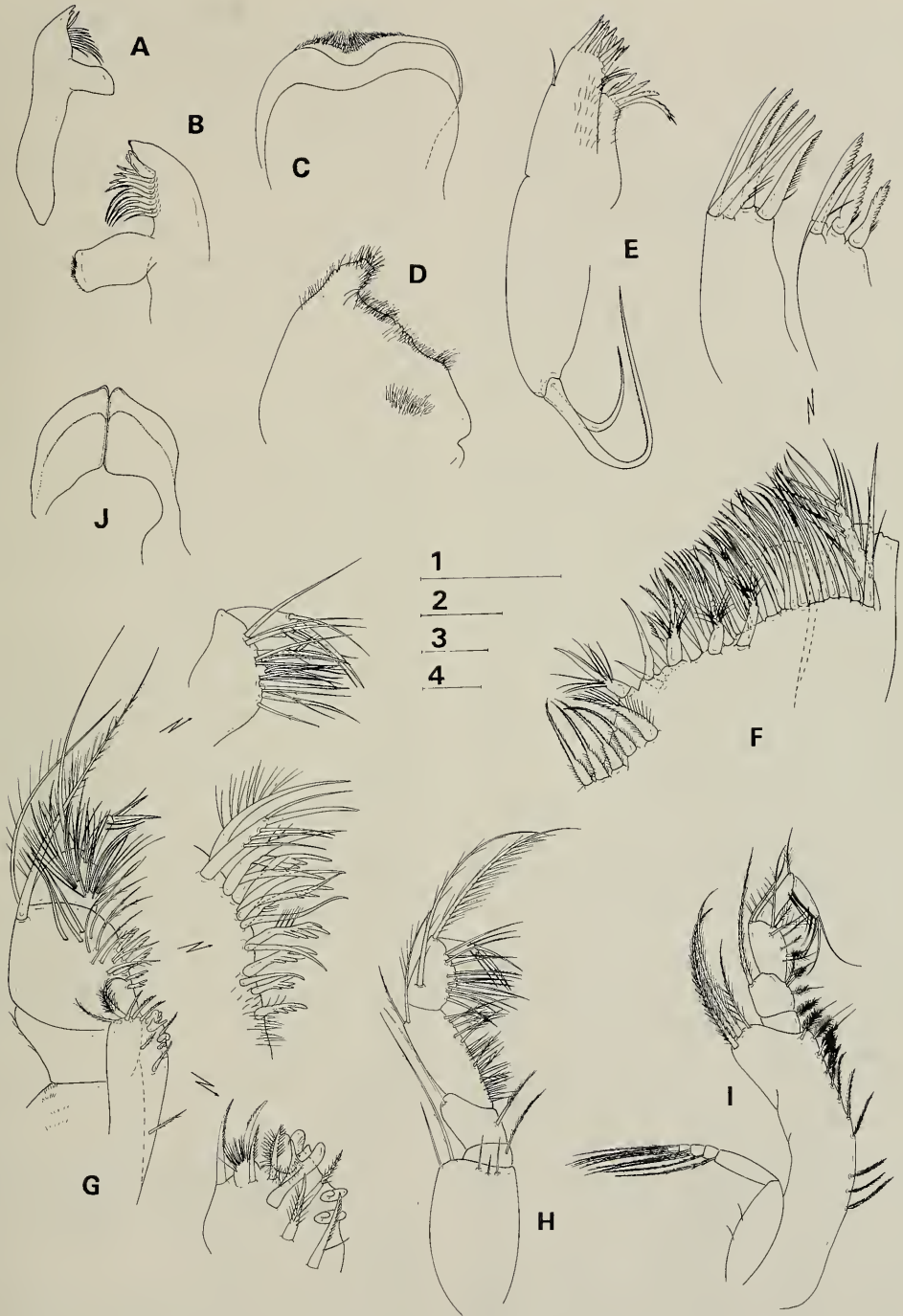


Fig. 2. *Diastylis debroyeri*, n. sp. A-B, mandible; C, labium; D, epignath; E, maxilla 1; F, maxilla 2, with detail (above) of outer and inner endite viewed from outer face; G, maxilliped 1, inner face (with detail of setation); H, maxilliped 2; I, maxilliped 3; J, terminal lobes of siphon (ex. maxilliped 1). Scales: 1 = 0.1 mm for A; 0.2 mm for B; 2 = 0.2 mm for C-E; 0.1 mm for F; 3 = 0.2 mm for G, J; 4 = 0.4 mm for H, I.

simple setae; basis less than 0.33 total length of appendage, ventral margin fringed with plumose setae; ischium and merus subequal; carpus elongate, subequal to propodus; dactyl about 0.33 length of propodus. Exopod well-developed excluding setae, reaching to carpus of endopod.

Second pereopod (Fig. 1F). Basis subequal in length to carpus; merus subequal to propodus; dactyl about 1.5 as long as propodus; each article with numerous simple setae with carpus and propodus also having stout spiniform setae distally. Exopod well-developed, as in first pereopod.

Third pereopod (Fig. 1G). Basis slender, approximately 1.5 as long as remaining articles combined, with some simple setae; ischium approximately 0.5 length of merus; carpus as long as ischium and merus combined, simple lateral setae present, 3 long simple setae on distal margin (extending past tip of dactyl); propodus as long as dactyl, with 1 distal seta; dactyl slightly longer than wide, tipped by 2 simple setae. Exopod greatly reduced, with 2 articles, distal article twice as long as proximal.

Fourth pereopod (Fig. 1H). Similar to third, but stouter, basis as long as remaining articles combined; ischium and merus with simple seta. Exopod reduced, as in third pereopod.

Fifth pereopod (Fig. 1I). Similar to fourth, but basis shorter than remaining articles combined. Exopod lacking.

Uropod (Fig. 1J). Slender, elongate. Peduncle over twice as long as telson with 12–14 spiniform setae along inner margin; outer margin with some fine simple setae. Endopod with 3 articles; article 1 longer than 2 and 3 combined, bearing 3 spiniform setae along inner margin; articles 2 and 3 subequal, article 2 with distal spiniform seta on inner margin, article 3 simple terminal and subterminal setae. Exopod with simple setae only, reaching just beyond article 2 of endopod; proximal article reduced, distal article with marginal setae along distal 0.75 and 3 terminal setae.

Subadult male, paratype (Fig. 3A).

Length 9.2 mm. Similar to female in external view, except for much greater development of exopods and broadening of basis on pereopods 3 and 4.

Telson (Fig. 3I). Having 3 pairs of lateral, setulate, spiniform setae (instead of 2 as in female).

First antenna (Fig. 3B). Peduncle with 3 stout articles decreasing in length distally, article 3 cubbed (stout, rounded); flagellum with 7 articles; accessory flagellum with 3 articles, extending to mid-region of flagellum article 3.

Second antenna (Fig. 3C). Flagellum about 0.5 body length.

First pereopod (Fig. 3D). Basis longer than combined length of ischium, merus and carpus, with numerous simple setae; ischium subequal to merus; carpus elongate; propodus and dactyl lost.

Second pereopod (Fig. 3E). Basis broad subequal to combined length of ischium, merus, carpus and propodus; dactyl elongate, 3 times longer than propodus; each article with some simple setae; carpus and propodus with stout distal spiniform setae.

Third pereopod (Fig. 3F). Basis broad, longer than remaining articles combined; ischium approximately 0.5 of merus length with 2 distal seta; carpus as long as combined length of ischium and merus, with few lateral setae and 2 distal setae; propodus subequal to dactyl, with one terminal seta; dactyl with 2 terminal setae. Exopod well developed.

Fourth pereopod (Fig. 3G) similar to third.

Fifth pereopod (Fig. 3H) as in female.

Uropod (Fig. 3I). Similar to female, but with 16 lateral spiniform setae along inner margin of peduncle and endopod, and more simple setae on rami.

*Etymology.*—This species is named in honor of Claude DeBroyer, Institut Royal Sciences Naturelles de Belgique, in recognition of his many significant contributions to carcinological research in the Antarctic.

*Remarks.*—*Ekleptostylis debroyeri* is similar to *Ekleptostylis heardi* McLelland &

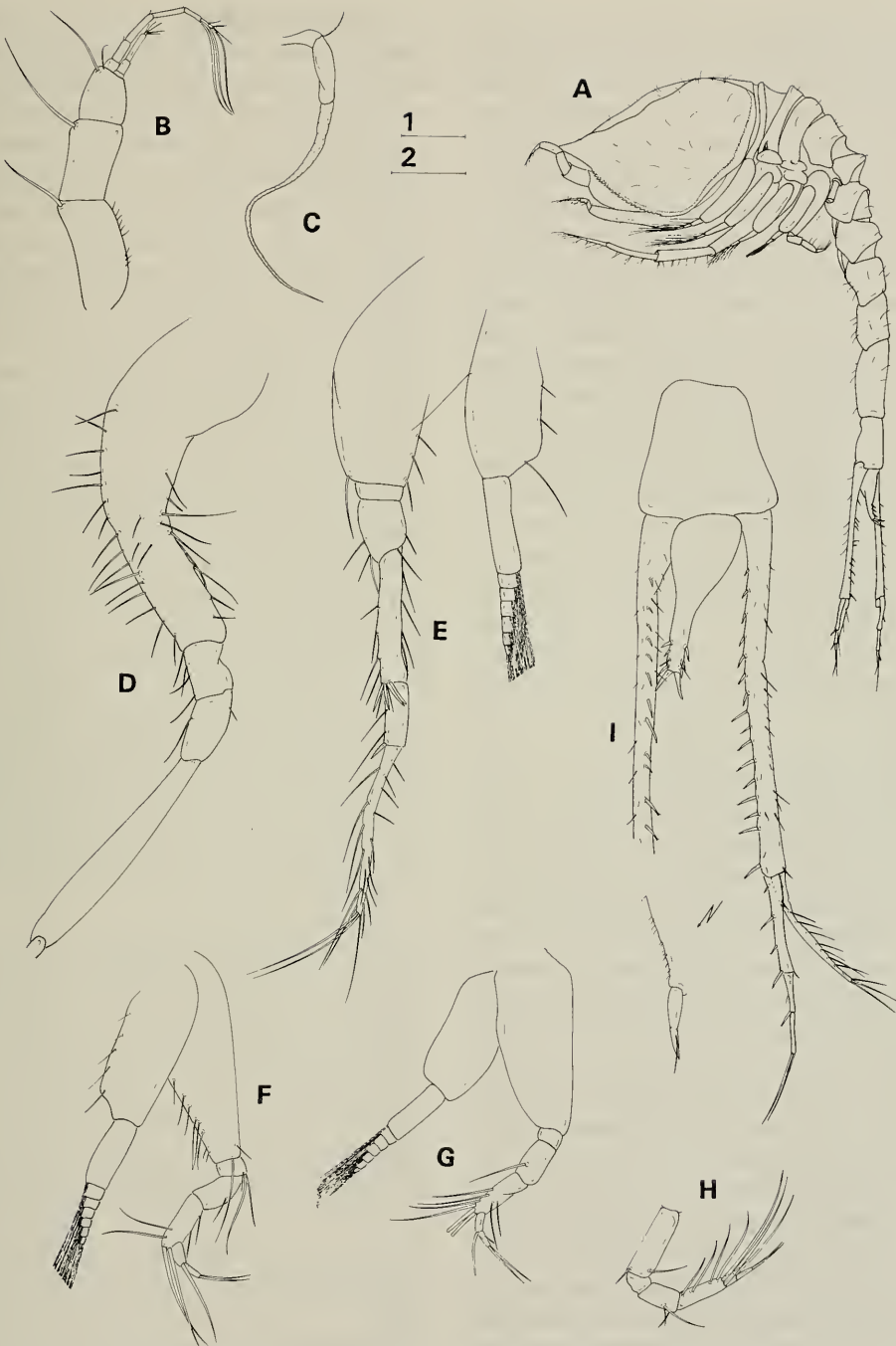


Fig. 3. *Diastylis debroyeri*, n. sp. (subadult male) A, lateral view of adult; B, antenna 1; C, antenna 2 of subadult; D-H, pereopods 1-5 (propodus and dactyl missing on pereopod 1, exopod illustrated only for pereopod 2); I, uropods, telson, and last abdominal somite. Scales: 1 = 1.0 mm for A, C; 2 = 0.2 mm for B-H; 0.3 mm for I.

Meyer, 1998; *E. pseudoinornata*, (Ledoyer, 1977); *E. vema*e Băcescu-Mester, 1967; and *Diastylis inornata* Hale, 1937, all of which are known from subantarctic waters. Based on the descriptions and illustrations of *D. inornata* given by Hale (1937), Ledoyer (1977) and examination of the type material from the Kerguelen Islands, *E. debroyeri* can be distinguished from it by: the proximal article of the uropodal endopod subequal to the combined length of the two distal articles; differences in the setation on the third maxilliped; carpus of pereopod 2 armed with short, stout, distally located spiniform setae; the carpal setae of the third, fourth, and fifth pereopods extending beyond those of dactyl; more slender uropods; telson half or less as long as uropodal peduncle with an additional pair of delicate setae. *Ekleptostylis debroyeri* is further distinguished from *D. inornata* by the relatively straight dorsal margin of its pseudo-rostrum.

*Ekleptostylis pseudinornata*, recently transferred from the genus *Diastylis* Say, 1818 by Roccatagliata & Mühlenhardt-Siegel (2000), is distinguished both from *E. debroyeri* and *D. inornata* by possessing an antennal notch. Ledoyer (1977) described *D. pseudoinornata* based on two specimens, an adult (marsupial) female holotype bearing oostegites and a male paratype, collected in Kerguelen Islands. He distinguished his female specimen of *E. pseudoinornata* from *D. inornata* primarily on the presence of a pair of anterior-dorsal projections on the first two pereonites, the presence of an antennal notch, and the dentition of the anteroventral margin of the carapace. Study of material attributable to *D. inornata* in the Institut Royal Sciences Naturelles de Belgique, Brussels, revealed that adult females with developed oostegites also have these same dorsal projections on the first two pereonites, but those of smaller subadult, preincubatory females lack these tubercles. We reexamined the holotype and paratype of *D. inornata*, which are both subadult females, and found no indication

of anterodorsal projections observed in the adult females of *E. pseudoinornata*, *E. heardi*, and those in the Brussels collection, which were referred to *D. inornata*.

Although no adult males or incubatory females are known for *D. inornata*, based on the features of the carapace, uropods, and telson, we believe that it represents another member of the genus *Ekleptostylis* and transfer *D. inornata* to the genus *Ekleptostylis* here. In addition to the descriptions of the antenna, second pereopod, and telson for the terminal male of *Ekleptostylis inornata* (Hale, 1937), n. comb, detailed descriptions and illustrations of the mouth parts of adult males and females with fully developed oostegites collected from the Kerguelen Islands are needed.

The adult female of *E. debroyeri* can be distinguished from those of *E. walkeri* (Calman, 1907) (type species), *E. heardi*, and *E. vema*e, by a having a telson bearing only two pairs of lateral spiniform setae plus a pair of characteristic simple setae (Figs. 1J, 3I). The telson of adult female *E. walkeri*, *E. vema*e, and *E. heardi* are armed with 10+, 3–4 and 4–5 pairs of lateral spiniform setae, respectively.

The adult female of *E. debroyeri* is further distinguished from that of *E. vema*e by having: a maxilliped 3 without an inner distal spine (or spines) on basis; different proportions for the articles in pereopods 1 and 2; a distinctly larger and longer (10 mm) body; a distinctly longer pair of terminal setae on the telson; the peduncle of the uropod two or more times longer than the telson; first article of the uropodal endopod distinctly longer than both two distal articles combined (not subequal as in *E. vema*e).

Besides the larger number of lateral spiniform setae, *Ekleptostylis debroyeri* can be separated from *E. heardi* by its relatively shorter telson. In *E. heardi* the telson is over 2/3 the length of the uropodal peduncle.

There is confusion concerning the type

locality of *E. heardi* and the depth and locality data for the type material presented by McLelland & Meyer (1998) appears to be in error. Based on the written label, some specimens of *E. heardi*, including the type material, came from the abyssal depth of 3590 m. There is strong circumstantial evidence that *Eltanin* Station "363" (Cruise 6) was an apparent mislabeling of one of the fractions of the large "rock dredge" sample taken at *Eltanin* Station 343. Station 363 was a Phleger corer sample taken at a depth of 3477–3590 m. In addition to *Ekleptostylis heardi*, three other diastylid species, *Diastylis hammoniae* Zimmer, 1902, *Diastylis planifrons* Calman, 1912, and *Diastylodes goekei* Roccatagliata & Heard, 1992 were also present in the vial labeled "Station 363." All three species were previously known from Antarctic and subantarctic waters in depths of less than 400 m (Roccatagliata & Heard 1992, Calman 1912). When received from the University of Southern California where the *Eltanin* samples were sorted, the vials labeled Stations 343 & 363 were placed together in a large vial (Heard, per. obs.), further supporting our supposition of a mislabeling error.

Due to this apparent mislabeling during the sorting process, McLelland & Meyer (1998) listed (p. 279) their type material of *Ekleptostylis heardi* as coming from "Sta. 363" at a depth of 3590 m." We recommend that all their material should now be referred to a single locality, *Eltanin* Station 343 (Cruise 6), and that the type locality of *E. heardi* be changed to accommodate this apparent error.

*Discussion.*—Subadult specimens that we attribute to *E. debroyeri*, appear to be nearly indistinguishable from the genus *Leptostylis* G. O. Sars, 1869, sensu lato. Day (1980) noted that the distinction between *Diastylis* and *Leptostylis* cannot be determined without the adult males, since other generic characters appear to be too plastic. This situation also appears to apply to the females and subadults of *Ekleptos-*

*tylis*. As defined by Day (1980), the telson of *Diastylis* is usually longer than the last pleomere and has at least three pairs of lateral spiniform setae. In contrast, the telson of *Leptostylis* is short and supposedly never longer than the last pleomere (Day 1980). Another important diagnostic character attributed to *Leptostylis* is based on the length of second antenna of the adult male, so complete determination has not been possible because the males for some species remain unknown. The descriptions of four species attributed to *Leptostylis* are based solely on subadult males. These species, *Leptostylis faurei* Day, 1980, *L. gilli* Day, 1980, and *L. menziesi* Băcescu-Mester, 1967, have a "cub-shaped" article 3 on second antenna and the flagellum of the second antenna barely reaches half the body length. According to the definition of *Leptostylis* sensu Stebbing (1912), this character would distinguish them from *Diastylis*. However, since their descriptions, as well as ours for *E. debroyeri*, are based on subadult males, there is a possibility that the terminal male forms might have considerably longer second antennae and thus affinities with the genus *Diastylis* sensu Day 1980. Also, the telsons of these species are subequal, or even longer than sixth pleomere, and with the exception of *L. menziesi*, they have 3 or more pairs of lateral spiniform setae on the post-anal region of the telson. These characters further suggest affinities to *Diastylis* sensu lato or possibly *Ekleptostylis*.

The generic status of these three species will not be settled with certainty until adult males and females are available for study or until a more reliable set of characters can be established to separate *Diastylis*, *Ekleptostylis*, and *Leptostylis*. The taxonomy of these three genera also requires designation of a type species for both *Diastylis* and *Leptostylis*.

The taxonomic status of *D. arenaria* Say, 1818, the type species and genotype for the family Diastylidae may be nearly resolved (see Gerken 1999). The type material for *D. arenaria* is poorly defined and no longer

extant (Holthuis 1969). The brief and vague species description was based on specimens collected from the east coast of the United States ["Coast of Georgia and Florida" (Say 1818:315)]. *Diastylis arenaria* may be conspecific with *Oxyurostylis smithi* Calman, 1912, the well-described type species of the genus *Oxyurostylis* Calman, 1912, which also was described from the shallow waters of the U. S. East Coast (Holthuis 1969, Roccatagliata & Heard 1995). As suggested by Day (1980), Gerken (1999) petitioned the International Commission on Zoological Nomenclature to suppress *D. arenaria* as the type species in favor of the well established *Diastylis rathkei* (Kröyer 1841). At this time her case (3078) is still pending. With regard to genus *Leptostylis*, apparently Sars (1869) did not designate a type species for one of the four initial species assigned to the genus (see Day 1980: 276).

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***Probopyrus insularis*, a new species (Isopoda: Bopyridae), a parasite of *Macrobrachium fastinum* (Saussure de, 1857) (Decapoda: Palaemonidae), with criteria to differentiate species of *Probopyrus***

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*Abstract.*—*Probopyrus insularis* n. sp. parasiting *Macrobrachium fastinum* (Saussure de, 1857) from the Caribbean Islands is mainly distinguished by the shape of the: pleotelson in both sexes; carina of the seventh legs in females; palp of the maxillipeds in females; and pleon in males. Characters used to distinguish species of *Probopyrus* Giard & Bonnier, 1888 are discussed.

Two new American species of *Probopyrus* recently have been described as part of an ongoing taxonomic study of these parasitic isopods. *Probopyrus pacificensis* Román-Contreras, 1993, and *P. markhami* Román-Contreras, 1996, both were described from the west coast of Mexico. Here a new *Probopyrus* parasitizing *Macrobrachium fastinum* (Saussure de, 1857) from Jamaica, Puerto Rico, Guadeloupe and Cuba is described. Other American species new to science are expected as taxonomic research continues.

Holthuis (1977) recorded *M. fastinum* parasitized by “bopyrids” from Cuba; and Kensley & Schotte (1989), and Bunkley-Williams & Williams (1998) have assigned *M. fastinum* as host of *Probopyrus pandalicola* (Packard, 1879). These records, however, might be a misidentification of the new species described here. *Macrobrachium fastinum*, the only host known for this new species, has been reported from the United States, Venezuela and the Antilles by Chace & Hobbs Jr. (1969), Holthuis & Provenzano (1970), Chace (1972), Dugger & Dobkin (1975), Pereira (1991), Fièvet (1998, 1999a, 1999b, 2000), Fièvet et al. (1996, 1999) and Bowles et al. (2000). The new isopod may be present in these areas.

In a previous paper Román-Contreras (1993) summarized and proposed a series of diagnostic characters for the genus *Probopyrus*. These characters are updated and applied to this description (Tables 1 and 2).

Genus *Probopyrus* Giard & Bonnier, 1888  
*Probopyrus insularis*, new species  
Figs. 1–22

*Holotype female.*—USNM 120073. Allotype male USNM 306876, prepared for SEM; C. W. Hart Jr. coll., 7 Jan 1960, Tributary of Trunnels River, St. Mary Parish, Jamaica.

*Other material examined.*—USNM 235988: one young female, Río Cruces, 1500 m W of Sabana Grande, Puerto Rico. USNM 235990: one female, one male, 8 May 1953, Río Lajas, 3000 m S of Vega Alta, Puerto Rico. USNM 63309: one female, one male, J. C. Welsh Jr. coll., Cuba. One female, one male, Serre coll., 1910, Cuba (in the Muséum National d’Histoire Naturelle, Paris). Twenty one females and males, Y. Thèrèzien coll. and det. hosts, 2 Dec 1977, Belle Eau, village de l’Habituée, Guadeloupe. Ten females, eight males, Y. Thèrèzien coll. and det. hosts, 30 Oct 1978, Lèzarde estuary, Guadeloupe. Twenty nine



females, 26 males, E. Fièvet coll. and det. hosts, Dec 1996, Bananie River, Guadeloupe. Material from Guadeloupe deposited at collections of the authors.

*Type locality*.—Tributary of Trunnels River, St. Mary Parish, Jamaica.

*Distribution*.—Jamaica, Puerto Rico, Cuba, and Guadeloupe.

*Host for all specimens*.—*Macrobrachium faustinum*.

*Habitat*.—Freshwater.

*Description of holotype female*.—Length 10.3 mm, from border of first pereonite to tip of sixth pleonite; maximal width at third pereonite, 7 mm. Distortion angle  $26^\circ$ , outline pyriform (Figs. 1, 2). Head almost as wide as long, front rounded, posterior border deeply inserted into first pereonite, surface smooth. No well defined frontal lamina, indicated by only a narrow line; anterolateral corners of head produced into slight rounded tips. Antennula and antenna bisegmented; antennula ovoid, 4–5 spines on distal tip; antennae smaller than antennulae, basal portion wider than antennulae, distal one subspheric-shape (Fig. 3); both antennae with small dispersed pectinate scales on surface. Maxilliped bisegmented, subovoid, anterolaterally convex, nonsetose palp formed by two digitiform processes (Fig. 4). Three pairs of smooth, lamellar projections on barbula; inner lateral projections lanceolate, outer ones slightly larger and wider, third one smaller than former and beneath them; middle region rounded (Fig. 5); eyes absent. Pereonites dorsally distinct; border of pereonites 1–4 produced into distinct dorsolateral bosses, coxal plates narrow (Fig. 2). Oostegites completely surrounding but not enclosing marsupium; oostegite 1 relatively large, partially covering head and anterior part of brood pouch; anterior segment transversely ovoid and concave, frontal border rounded and slightly undulate; distal segment digitiform, larger axis perpendicular to the former; digitiform process on inner ridge, distal portion smooth, small spines on inner border; reticulated black pigmentation on surface, ex-

cept on distal portion (Fig. 6). Oostegites 2–4 progressively longer; oostegites 3–4 on larger side unpigmented; fifth oostegites longer than others, slightly falcate, ending in blunt tip, densely setose along posterior margin, extending across posterior region of marsupium and overlapping each other. Pereopods with massive basipodite, dactylus hook shape (Fig. 7). Robust high carina on pereopods, either rectangular (P1–P2), convex (P3–P4) or subquadrangular (P5–P7) (Fig. 8). Pigmentated spots on basis of pereopods 1–5 on short side; basis of pereopods 6–7 on short side, and 1–7 on larger side, unpigmented. Pleon 0.3 times body length, five dorsal and laterally separated pleonites; lateral plates lamellar, almost rounded or slightly truncated. Pleotelson bell-shaped, relatively small, bilobated, deep fissure in the middle, lobes unseparated, tips shorter than the fifth lateral plates (Fig. 2). Five pairs of biramous foliate pleopods completely covering ventral surface of pleon, each different in shape and size; exopods on large side enlarged, increasing in length from first to fifth, protruding notably from tips of pleon (Figs. 1, 2, 15); endopods decreasing in size from first to fifth; larger exopods on opposite side slightly rippled (Fig. 9); uropods absent.

*Description of male*.—Length 1.84 mm, width 0.6 mm; body unpigmented. Head twice as wide as long, slightly depressed at middle (Figs. 10, 12, 13); posterior margin almost straight, anterolateral borders rounded. Antennae different in size and shape; antennula three-segmented, bottle-shape, proximal portion globose, upper portion small, button shape, eight obscure small spines on tip. Antenna bisegmented, slightly smaller and thinner than antennula, cylindrical, with short proximal basis; stout short setae on tip of distal article. Both antennae with small pyramidal or rounded pectinate scales on surface (Fig. 11). Maxillipeds absent. No eyes. Pereon wider at second pereonite, 4–7 progressively shorter; tips of pereonites subglobose, reflexed ventrally, small scales on ventral surface; midventral tubercles ab-

Table 1.—Morphological comparative characters for the American species of *Probopyrus* (Females). (Hosts: *M.* = *Macrobrachium*, *P.* = *Palaemonetes*, *Pa.* = *Palaemon*).<sup>a</sup>

Species/host	Characters					
	Body shape	Concavity on short side of body	Body, distal region	Pigmentation on pereopods 2-4	Cephalon: shape of the posterior region	Cephalon: frontal border
<i>P. insularis</i> <i>M. faustinum</i>	Pyriform	Present	Pointed	On short side	Rounded, ovoid, or subtriangular	Convex
<i>P. bithynis</i> / <i>M. ohionis</i> (sic)	Pyriform	Present	Pointed	On short side	Triangular	Right
<i>P. bithynis</i> / <i>M. olfersii</i>						
<i>P. markhami</i> <i>M. americanum</i>	Ovoid or pyriform	Absent	Rounded	On short side	Subpentagonal	Right
<i>P. meeki</i> / <i>M. acanthurus</i>	Pyriform	Slight	Rounded	Absent	Ovoid	Convex
<i>P. pacificensis</i> <i>M. tenellum</i>	Pyriform	Present	Pointed	On short side	Ovoid	Right
<i>P. panamensis</i> <i>M. acanthurus</i>	Pyriform	Present	Pointed	On short side	Ovoid	Convex
<i>P. floridensis</i> <i>P. paludosus</i>	Pyriform or ovoid	Present or absent	Pointed	On short side	Ovoid or triangular	Right or acute
<i>P. pandalicola</i> <i>P. hiltonii</i>	Pyriform	Slight	Rounded	On 2 sides	Rounded	Convex
<i>P. pandalicola</i> / <i>P. pugio</i>	Ovoid	Absent	Rounded	On 2 sides	Rounded or ovoid	Right or convex
<i>P. pandalicola</i> <i>P. vulgaris</i>	Pyriform, ovoid or rounded	Present or absent	Pointed or rounded	On 2 sides	Rounded or triangular	Right or convex
<i>P. ringueletii</i> <i>P. argentinus</i>	Ovoid	Absent	Pointed		Ovoid	Acute
<i>P. palaemonii</i> <i>Pa. pandaliformis</i>	Ovoid	Absent	Pointed or rounded	On 2 sides	Rounded or triangular	Right or convex

<sup>a</sup> Sources: see Table 2.

sent. Isomorphic pereopods, larger posteriorly, uncarinated. Pleon outline subtriangular, slightly narrower than seventh pereonite, distinct pleonites separated laterally; four pairs of sessile ovoid pleopods conspicuous in ventral view; gross pleotelson triangular shape, wide basis and rounded tip (Fig. 10); uropods absent.

*Etymology.*—The specific name refers to the Caribbean islands, where the examined specimens were collected.

*Variation in female specimens.*—In younger specimens the cleft of the pleotelson is open V-shaped, and the tips of the lobes reach to or beyond the tips of the fifth pleonite (Fig. 15). Size and shape of the carina of the pereopods varies according to

its position. In *P. insularis* the shape of the carina is rectangular in P1–P2, convex in P3–P4, or subquadrangular in P5–P7, increasing its size behind.

In adult specimens the palp of the maxilliped usually is prominent and finger-like, sometimes with a pair of distal setae; in other specimens the shape of the maxilliped is subquadrate, rudimentary, reduced to a small, acute, lateral point, or bearing two digital processes directed outward.

*Variation in males.*—The body shape and size in males varies with the state of development (Figs. 12–14). The pleon in *P. insularis* is composed by four or five pleonites, depending upon the state of development, which are differentiated dorsally and

Table 1.—Extended.

Palp of maxilliped & number of setae	Height & Shape of the carina	Characters			
		Pleopods: length	Pleopods: protrusion from border of pleon	Pleotelson	Uropods
Digitiform; 2 setae	Extremely high, subquadrangular	Exopodite large, endopodite small	Protruding far	Fissured, lobes not separated	Absent
	Extremely high, quadrangular	Small	Protruding slightly	Entire, notched	Absent
Pyramidal or ovoid; 4 setae	Extremely high, rounded	Small	Diminished	Notched	Present
	Medium, rounded		Not protruding	Fissured	Rudimentary
Ovoid, 8–10 setae	High, rounded	Small	Protruding far	Entire or slightly notched	Absent
	High, rounded	Small	Not protruding	Slightly notched	Absent
	Medium, rounded	Small or subequal	Protrusion variable	Entire or notched	
Ovoid, 8–10 setae				Notched	
		Small	Not protruding or only slightly	Entire or notched	
	High, quadrangular	Small	Not protruding or far	Entire (right/ rounded) or notched	
Ovoid, undetermined	High, rounded	Exopodite large, endopodite small	Diminished	Notched	Absent
Ovoid, 3 setae		Small	Protruding slightly or not	Bilobated	

laterally, but sometimes the pleonites are differentiated only laterally.

The shape of the pleotelson in males of *P. insularis* can be subtriangular, subovoid, subrounded, irregularly shaped, fused central and laterally with the previous pleonite on one or both sides but invariably bulbous and blunt, directed behind or laterally.

*Description of the epicaridium larva.*—Body length: 0.18 to 0.25 mm; length width ratio from 1.7 to 2.3. Antenna large, six segmented, reaching between the second and sixth pleonites; segments 1–4 large; distal seta on internal face of fourth, fifth and sixth segments thinner than others. Distal segment bordered by three small spines and two large unequal setae (Fig. 16). Maxillipeds not distinguishable. Pereopods sub-

equal and dimorphic; first three pairs robust (Fig. 17); other three thinner (Fig. 18). Posteroventral border of fifth pleonite finely denticulate (Fig. 19); ventral side of sixth pleonite formed of plates. First pleopod with basal plate and a long, thin, curved external ramus ending in three long feathered setae. Posteromedial corner of basipodite of pleopod 1 with large feathered setae (Fig. 20). This seta absent in following three pairs of pleopods, and replaced in fifth the length of the exopodite. Fifth pair unsegmented, basipodite semi-rounded, exopodite ending in three short feathered setae (Fig. 21). Uropods of two equal branches ending in two denticles and one strong median seta (Fig. 22); anal tube small.

Table 2.—Morphological comparative characters for the American species of *Probopyrus* (Males). (Hosts: *M.* = *Macrobrachium*, *P.* = *Palaemonetes*, *Pa.* = *Palaemon*).

Species/host	Characters			Source
	Shape of pleon	Shape of pleotelson		
<i>P. insularis</i> / <i>M. faustinum</i>	Scutelliform or subtriangular	Subtriangular, digitiform, bulky	Present work	Richardson, 1904; 1905
<i>P. bithynis</i> / <i>M. ohionis</i> (sic)	Semicircular or ovoid	Rounded, entire or fissured		
<i>P. bithynis</i> / <i>M. olfersii</i>				
<i>P. markhami</i> / <i>M. americanum</i>	Subtrapezoidal	Rounded	Román-Contreras, 1996	
<i>P. meeki</i> / <i>M. acanthurus</i>	Semicircular	Button rounded	Richardson, 1912	
<i>P. pacificensis</i> / <i>M. tenellum</i>	Semicircular	Button rounded	Román-Contreras, 1993	
<i>P. panamensis</i> / <i>M. acanthurus</i>	Semicircular	Rounded	Richardson, 1912	
<i>P. floridensis</i> / <i>P. paltodosus</i>	Semicircular	Rounded or bare-necked	Richardson, 1904; 1905	
<i>P. pandalicola</i> / <i>P. hiltonii</i>	Semicircular	Rounded	Jiménez and Vargas, 1990	
<i>P. pandalicola</i> / <i>P. pugio</i>	Variable	Rounded	Markham, 1985	
<i>P. pandalicola</i> / <i>P. vulgaris</i>	Semicircular, posterior edge truncate	Rounded or triangular	Packard, 1879; Gissler, 1882; Bonnier, 1900; Richardson, 1905; Markham, 1985	
<i>P. ringueleti</i> / <i>P. argentinus</i>	Slightly rounded	Rounded or truncate	Verdi and Schuldt, 1988	
<i>P. palaemoni</i> / <i>Pa. pandaliformis</i>	Wide, semicircular	Rounded, fissured or bilobulated	Lemos de Castro and Brasil Lima, 1974	

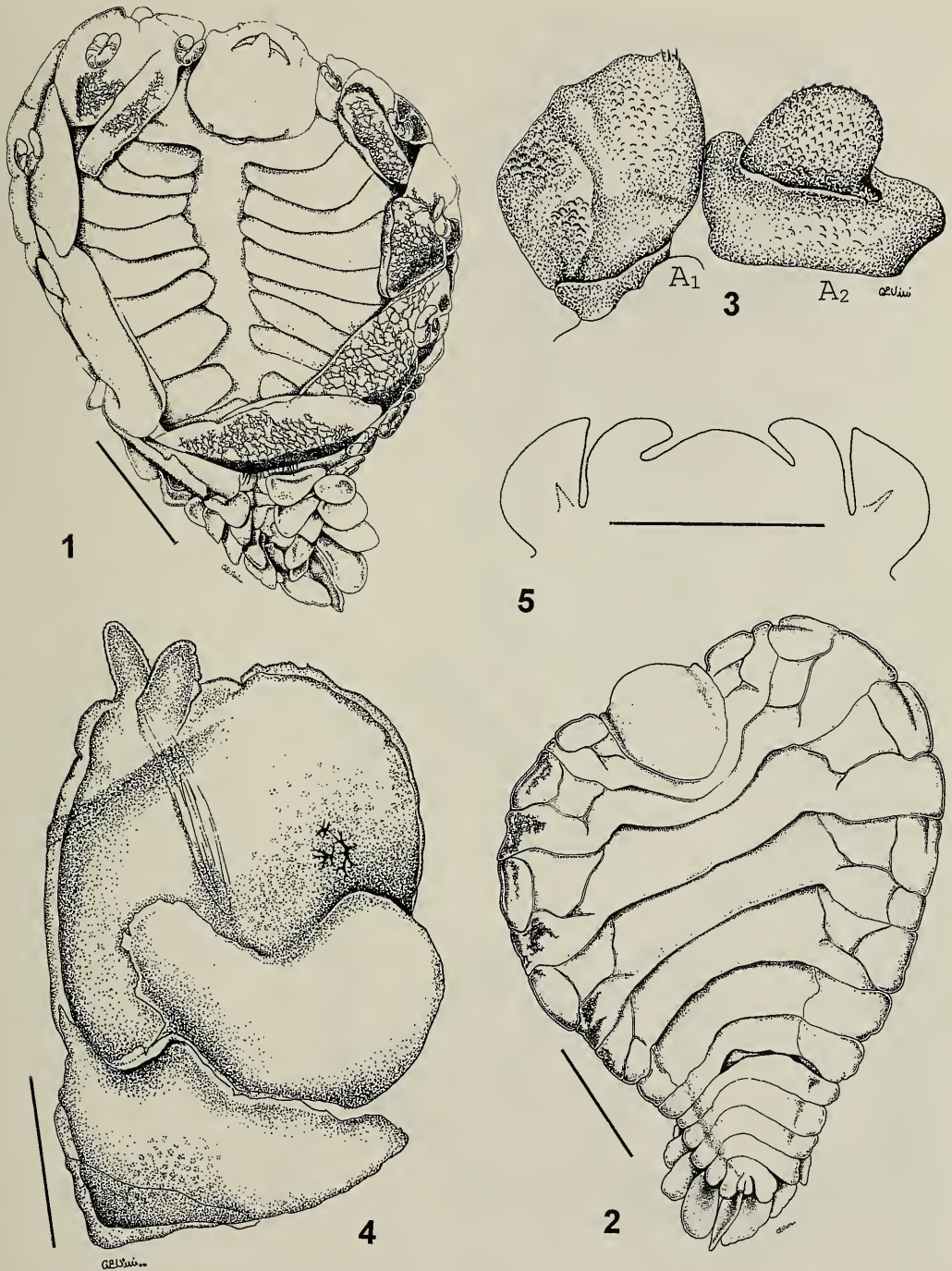
## Discussion

The use of host selectivity, pigmentation patterns, habitat, behavior, morphological structures, and statistical methods to differentiate species in the genus *Probopyrus* have been discussed in a recent paper by Román-Contreras (1993, 1996). The following morphological characters that should be described carefully in to differentiating species have been discussed by Giard & Bonnier (1888), Bonnier (1900), Richardson (1904, 1905, 1912), Chopra (1923), and Román-Contreras (1993, 1996).

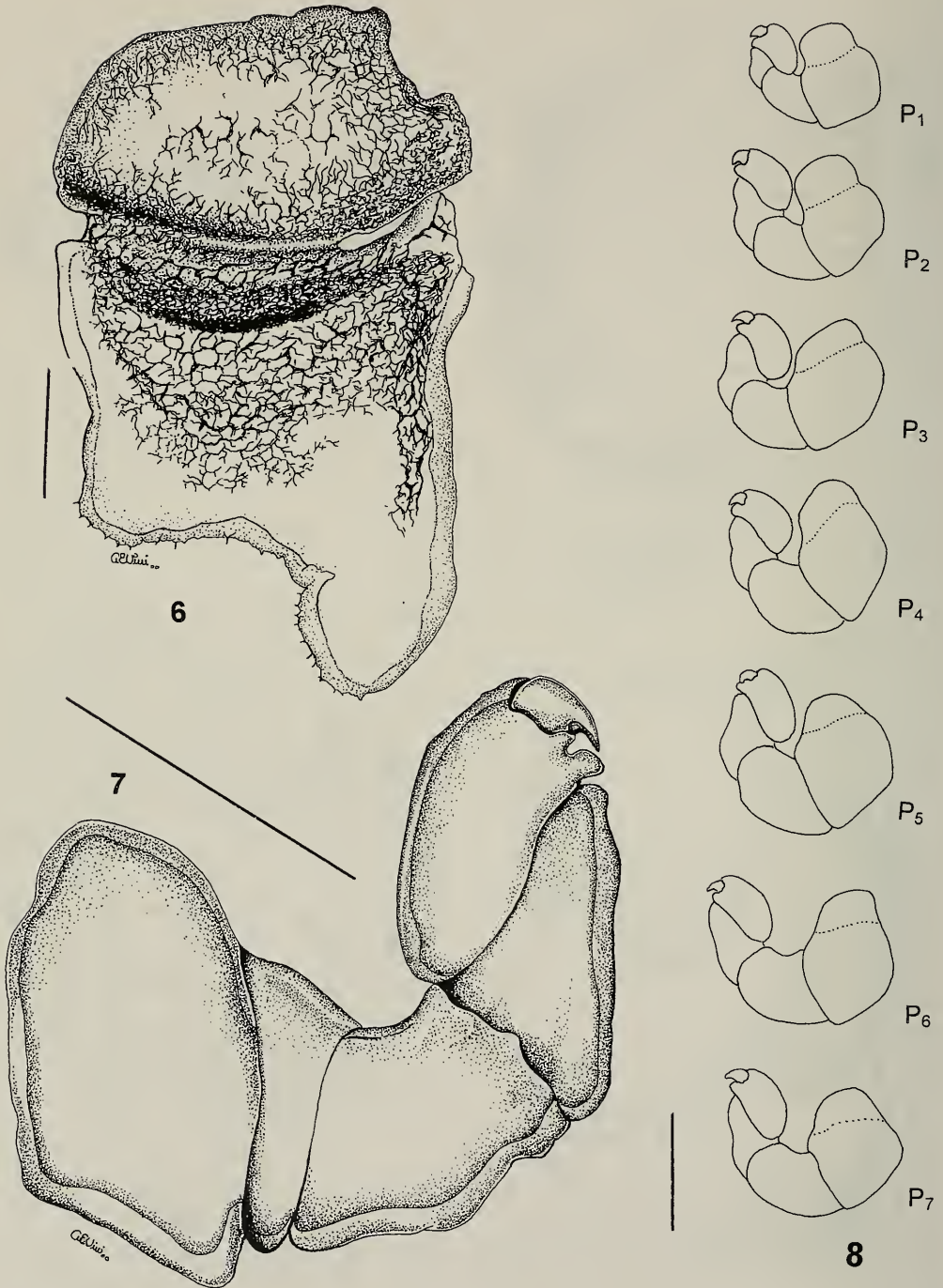
Females of *P. insularis* can be differentiated from other American species of *Probopyrus* by their relatively short and narrow pleotelson. In adult specimens a deep fissure with rounded and unseparated lobes is present; usually the edge of the lobes do not reach the tip of the fifth pleonite. The shape of the female pleotelson of *P. insularis* is similar only to *P. meeki* Richardson, 1912. However, the sixth segment of *P. meeki* has a posterior notch that extends half of its length and forming two posterior unseparated lobes (Richardson, 1912: fig. 1).

The robust carina of the seventh leg of *P. insularis* is comparable to the high and prominent carina of *P. markhami*. All legs of *P. bithynis* Richardson, 1904 have an extremely high carina (Richardson 1904, 1905). The legs of *P. pandalicola* have a high quadrangular-shaped carina, while the carina of *P. floridensis* Richardson, 1904 are rounded (Richardson 1912). Román-Contreras (1993, 1996) noted the rounded carina of *P. pacificensis*.

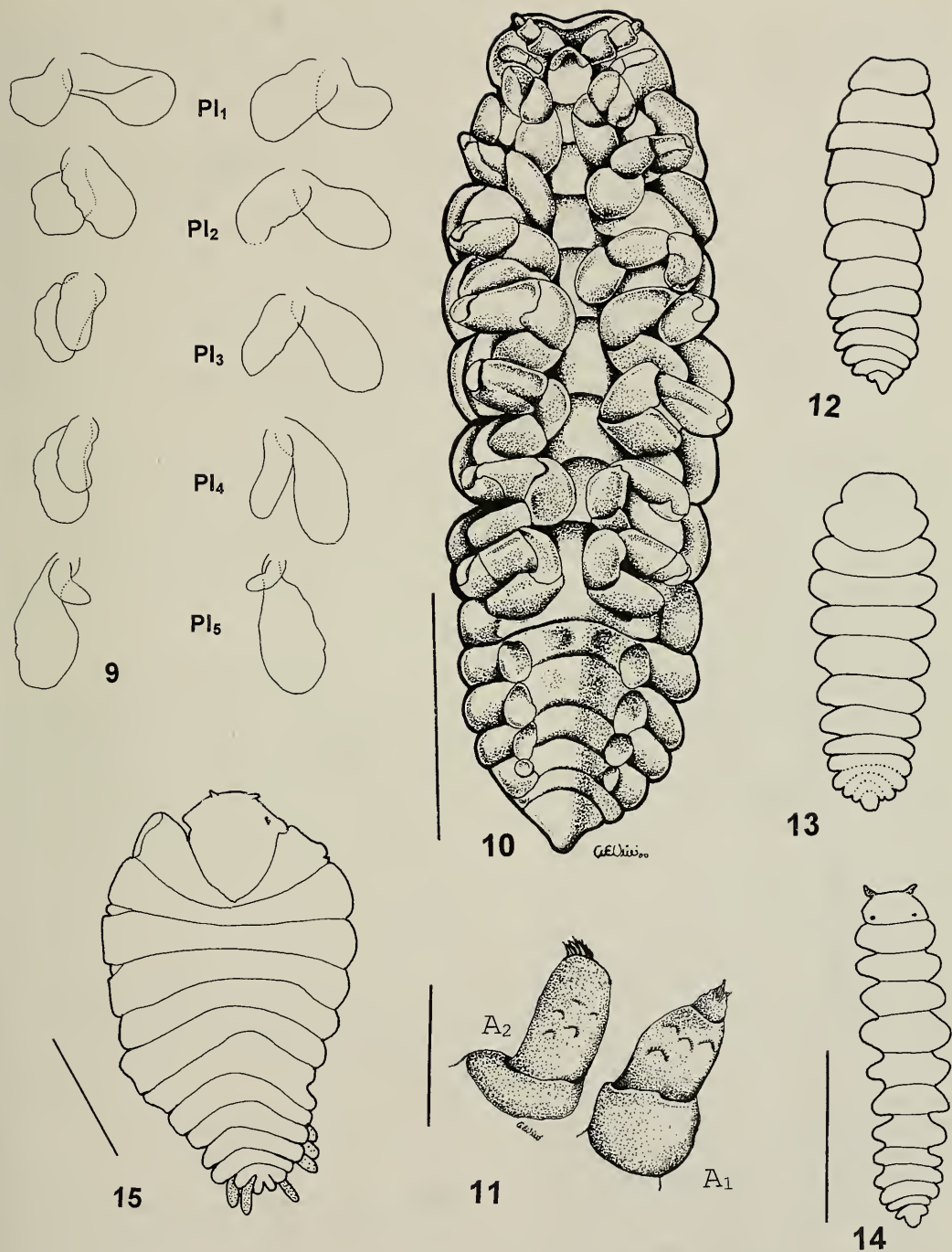
Although the maxilliped palp of *Probopyrus* may vary according to the developmental state of the specimens, the morphology has proven valuable in separating species. The maxilliped palp of adult females of *P. insularis* is finger-like in most specimens (79%); a small percentage (14%) have two setae on the tip or no palp is present; few individuals have a triangular, a rounded, or a rudimentary palp. For *Probopyrus ringueleti* Verdi & Schuldt, 1988,



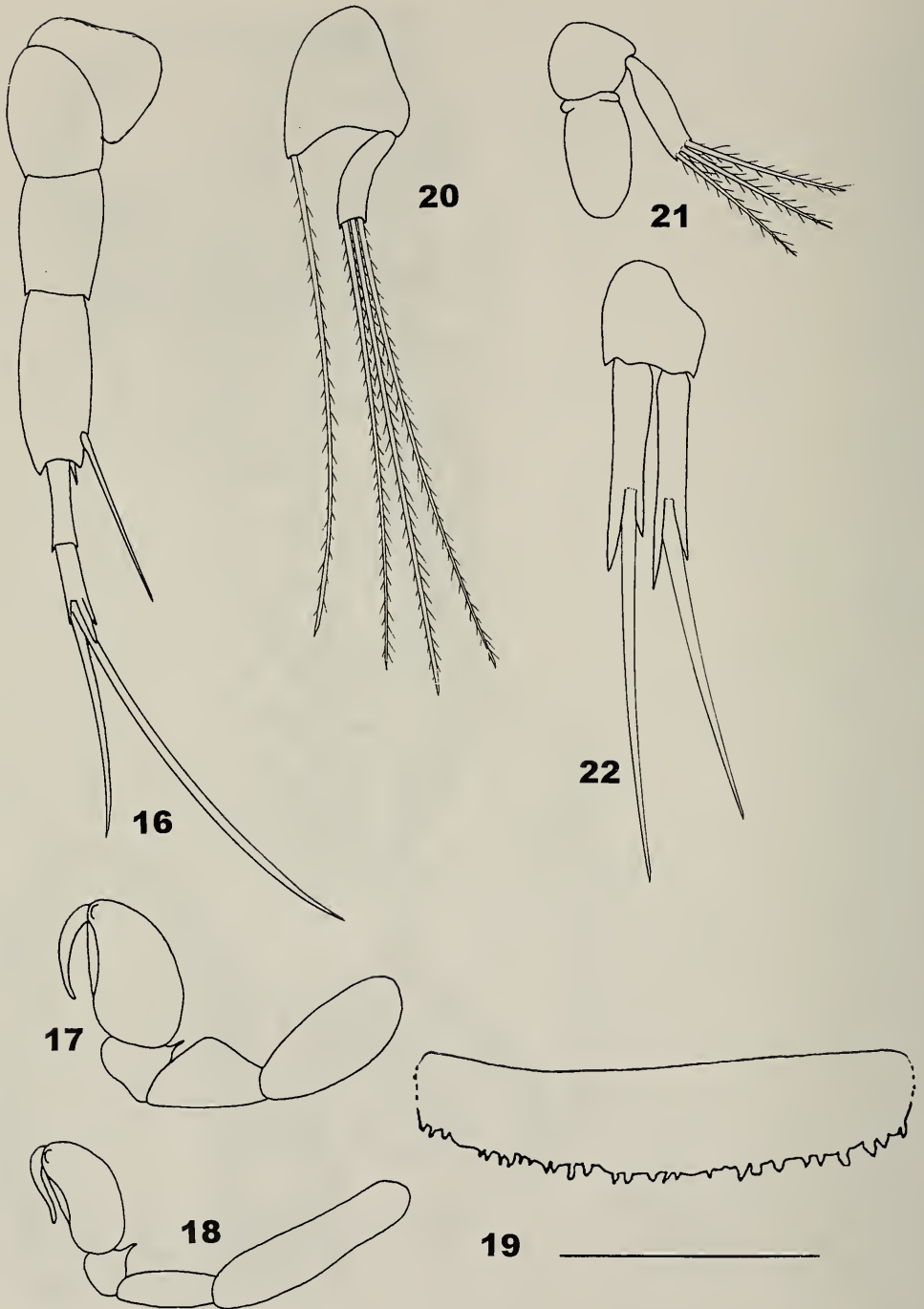
Figs. 1-5. Holotype female of *Probopyrus insularis* sp. nov. 1), in ventral view (oostegite 1 and barbula removed); 2), same in dorsal view; 3), antennula and antenna from a paratype specimen (picture taken with scanning electron microscopy: SEM); 4), maxilliped in dorsal view; 5), barbula of a paratype. Scale bar: 1 and 2 = 2.0 mm; 4 = 0.5 mm; 5 = 1.0 mm.



Figs. 6-8. *Probopyrus insularis* sp. nov. 6), oostegite 1 in dorsal view; 7), pereopod 7 of holotype female; 8), pereopods 1-7 of paratype female. Scale bar: 6 and 15 = 1.0 mm; 7 = 0.5 mm.



Figs. 9–15. *Probopyrus insularis* sp. nov. 9), pleopods 1–5 of paratype female; 10), allotype male in ventral view; 11), antennula and antenna of paratype male (taken with SEM); 12–14), variation of males in dorsal view; 15), young female from Puerto Rico (USNM 235988). Scale bar: 8 and 10 = 0.5 mm; 11 = 0.05 mm; 12–14 = 1.0 mm.



Figs. 16-22. Epicardium larva of *Probopyrus insularis* sp. nov. 16), antenna; 17), pereopod 1; 18), pereopod 4; 19), posterior edge of the fifth pleonite; 20), first pleopod; 21), fifth pleopod; 22), uropods. Scale bar: 0.05 mm.



the palp is rectangular and bears an undetermined number of setae. The palp of *P. pacificensis* is ovoid bearing 8 to 10 setae (Román-Contreras 1993), while the palp of *P. markhami* is pyramidal and bears a reduced number of setae (Román-Contreras 1996).

The pleon of males also has been used to differentiate some species of *Probopyrus*. However, the narrow pleon in males of *P. insularis* is not unique; it is comparable to that of *P. meeki*, and the gross structure of the pleotelson is similar to adult specimens of *P. meeki* as well as *P. markhami*.

In addition to structures of adult females and males, larval morphology of *Probopyrus* has been used to separate species (Dale & Anderson 1982). Although such features may prove to be important, mature larval stages are not always available to taxonomists.

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## A new asellote isopod of the genus *Santia* Sivertsen & Holthuis, 1980 (Crustacea: Isopoda: Asellota: Santiidae) from Japan

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*Abstract.*—*Santia longisetosa*, a new species of the family Santiidae (Isopoda: Asellota) is described from the Pacific coast of Shikoku, Japan. The new species differs from its congeners in having a long robust sensory seta distal-ventrally on each propodus of pereopods 2–7, the nearly straight frontal margin of the head bearing some long setae, and 2 long robust sensory setae distal-laterally on article 2 of antenna 1.

Santiidae is a small family of four genera and 21 species in the suborder Asellota. *Santia* Sivertsen & Holthuis, 1980, is the largest genus in the family and includes 15 species (Wolff 1989, Wolff & Brandt 2000, Shimomura & Mawatari 2000), all from marine benthic habitats. Among them only one species, *Santia katoi* Shimomura & Mawatari, 2000 has been so far described from Japan. Our recent investigation yielded an undescribed species of *Santia* from the subtidal zone of Kochi Prefecture, Shikoku, the second record of the genus from Japan.

### Materials and Methods

Specimens were obtained from 0.5 m depth of the subtidal zone by filtering surface water; specimens were fixed with 5% neutral formalin solution diluted with seawater, and preserved in 70% ethanol. Each isopod was dissected and prepared for observation using a light microscope equipped with Nomarski differential interference contrast (Shimomura & Mawatari 1999). Total length as indicated in “Material examined” was measured from the tip of the head to the end of the pleotelson.

The type specimens are deposited in the Zoological Museum, Division of Biological Sciences, Graduate School of Science, Hok-

kaido University (ZIHU), and in the Toyama Science Museum (TOYA).

### *Santia longisetosa*, new species Figs. 1–4

*Material examined.*—Murotomisaki-cho, Muroto Cape, Kochi Prefecture, Japan, 33°16'N, 134°7'E, 0.5 m, surface water, subtidal, 27 June 2000: holotype, male, 1.0 mm (ZIHU-01963); paratype, ovig. female, 1.1 mm (TOYA Cr-12877); paratypes, 2 females, 1.1 mm (TOYA Cr-12878), 1.3 mm (ZIHU-01966).

*Description.*—Male: Body (Fig. 1A) about 2.4 times as long as maximum width. Head 2.0 times as broad as long, slightly narrower than pereonite 1, with 10 dorsal setae; frontal margin of head nearly straight, with 8 long setae; labrum surpassing head anteriorly; posterior margin of head convex between eyestalks. Preocular lobes narrow, with 1 or 2 apical setae. Eyes dorsal lateral, each with 3 ommatidia. Pereonites 1–4 laterally rounded, each with 4–7 lateral and few dorsal setae; pereonites 5–7 laterally rounded, each with 0–3 lateral and 2 dorsal setae. Pereonites 1, 2 and 4 subequal in length; pereonite 3 slightly shorter than pereonite 2; pereonites 5 to 7 increasing in length. Pereonites 1 and 2 subequal in width; pereonite 3 slightly wid-

er than pereonite 2; pereonite 4 as broad as pereonite 3; pereonite 5 widest; pereonites 5 to 7 decreasing in width. Coxal plates dorsally visible on pereonites 4–7, laterally rounded, each with 2 or 3 lateral setae. Pleonite short and narrow, without dorsal setae. Pleotelson (Figs. 1A, 2A) about 1.1 times as long as broad, with 13 dorsal, 2 posterolateral, 2 apical, and 12 ventral setae. Uropod (Fig. 2B) stout, directed posteriorly, shorter than pleotelson. Protopod wide posteriorly, about  $\frac{2}{3}$  as long as exopod, with 1 mesial and 1 lateral robust sensory setae. Exopod and endopod longer than broad. Exopod about 1.5 times as long as protopod, with 1 ventral, 5 dorsal, 2 lateral, 1 subapical and 4 apical robust sensory setae, with 1 apical simple seta; endopod as long as peduncle, with 2 ventral, 1 dorsal, 2 subapical and 2 apical robust sensory setae, with 3 lateral and 2 subapical plumose setae.

Antenna 1 (Fig. 2C) of 6 articles. Article 1 broadest, with 1 distal-lateral and 1 distal-medial setae; article 2 longest, narrower than article 1, with 1 distal-ventral, 1 distal-dorsal and 1 lateral simple setae, with 1 distal-lateral and 1 distal-medial plumose setae, and distal-lateral with 2 long robust sensory setae; article 3 narrow, with 1 distal-ventral and 1 distal-dorsal setae; article 4 slightly shorter than article 3, without setae; article 5 about 1.7 times as long as article 4, apically with 1 aesthetasc; article 6 narrow and short, apically bearing 1 aesthetasc and 2 short, 1 long setae.

Antenna 2 (Fig. 2E) composed of 6 stout articles and 12 thin flagellar articles. Article 1 with 1 distal-lateral seta; article 2 as broad as article 1, without setae; article 3 longer than article 2, with 3 distal-ventral, 1 dorsal and 1 distal-medial setae; article 4 shorter than article 3, with 2 distal-ventral, 3 distal-lateral and 1 medial setae; article 5 as long as article 6, with 2 ventral, 3 dorsal, 2 lateral and 3 mesial simple setae, and with 1 long robust sensory seta distal-medially and 1 plumose seta laterally; article 6 narrower than article 5, bearing 3 ventral, 4 dorsal, 2

lateral and 2 medial simple setae, and with 1 lateral and 1 medial plumose setae. Flagellum about 2.6 times as long as article 6, each with many setae.

Left mandible (Fig. 2F) lacking palp, bearing 1 short seta arising from its base; incisor with 4 cusps; lacinia mobilis with 3 teeth; setal row with 4 setae; molar process stout, bearing 2 apical setae. Right mandible (Fig. 2G) lacking palp and lacinia mobilis, bearing 1 short seta arising from its base; incisor with 6 cusps; setal row with 4 setae; molar process stout, bearing 2 apical setae.

Maxilla 1 (Fig. 2H) with inner lobe bearing 4 apical setae; outer lobe apically with 5 pectinate setae and 5 simple setae, dorsally with many short setae. Maxilla 2 (Fig. 2I) with inner lobe with 5 apical setae and many dorsal setae; outer 2 lobes each with 4 apical setae.

Maxilliped (Fig. 3A) with moderately broad palp composed of 5 articles; article 1 as broad as article 2, with 1 medial seta; article 2 trapezoidal, about 2.3 times as long as article 1, with 1 lateral and 2 medial setae; article 3 as long as article 2, with 2 lateral and 3 medial setae; article 4 slightly shorter than article 3, with 2 lateral and 4 medial setae; article 5 narrowest, with 1 subapical and 2 apical setae; endite quadrate, bearing 4 dorsal, 6 distal simple setae, with 5 distal pectinate setae and 3 subdistal fan-shaped setae, and with many short setae laterally and 2 coupling hooks medially, epipod lanceolate, moderately broad, narrower than endite, with rounded apex.

Pereopod 1 (Fig. 3B) shorter than pereopods 2–7: basis the longest article, with 2 ventral, 2 dorsal and 1 lateral setae; ischium narrower than basis, bearing 1 ventral, 2 dorsal, 1 lateral and 2 distal setae; merus trapezoidal, with 1 ventral, 3 distal-ventral and 2 distal-dorsal simple setae, with 1 long robust sensory seta distal-dorsally; carpus trapezoidal, broadest, ventrally with 2 long robust sensory setae and 3 simple setae, medially with 1 simple seta and 3 spinulose scales, and with 1 simple seta distal-dorsal-

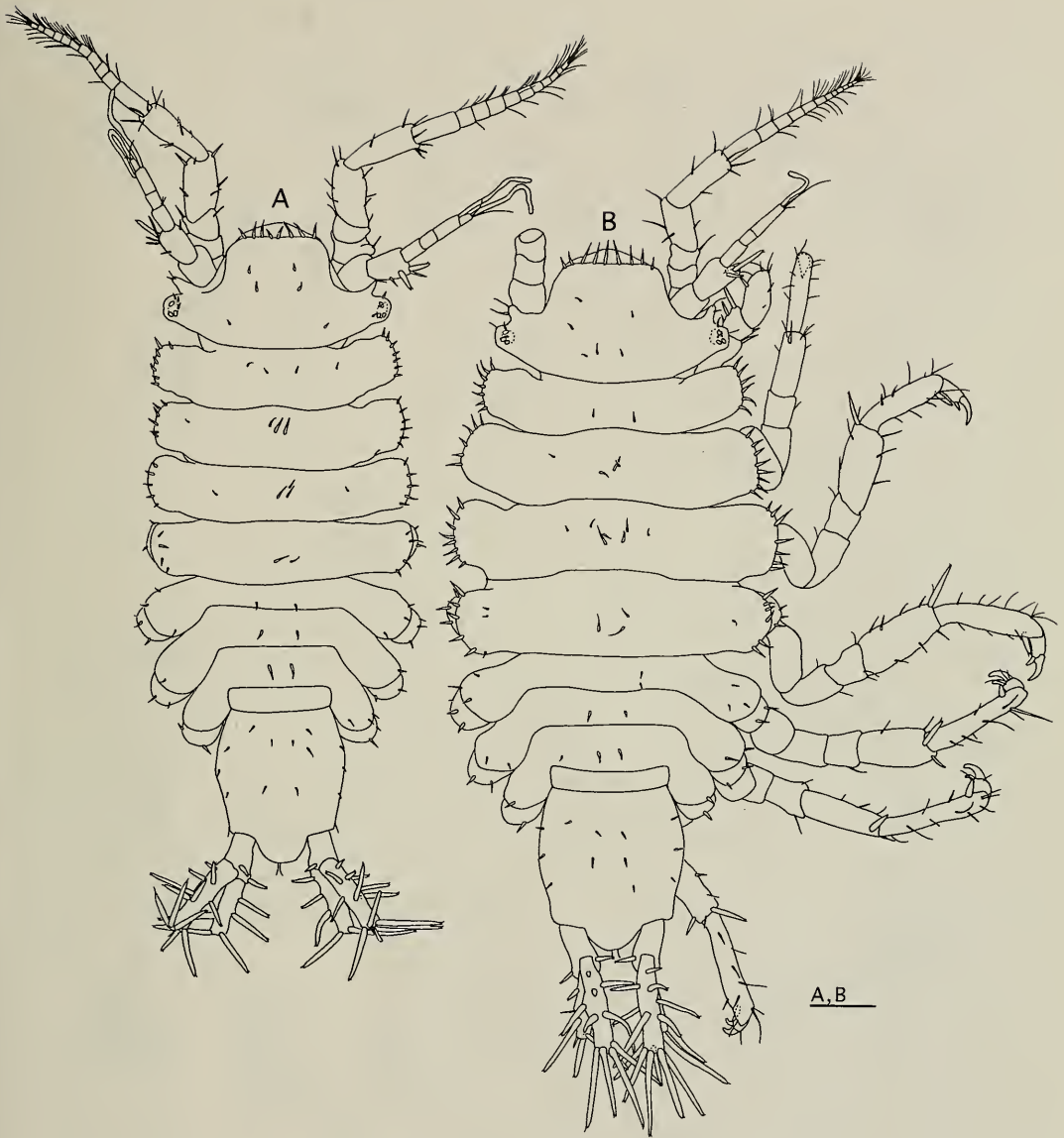


Fig. 1. *Santia longisetosa*, new species. A, holotype male, dorsal; B, paratype female (TOYA Cr-12877), dorsal. Scales = 0.1 mm.

ly; propodus ovate, ventrally with 5 simple setae and 1 robust sensory setae, medially with 1 simple short seta and 7 spinulose scales, and with 5 simple setae dorsally; dactylus shorter than propodus, narrowest of all articles, with 2 distolateral and 3 medially setae, 1 curved unguis, and 1 short accessory spine.

Pereopod 2 (Fig. 3C) as long as pereopod

4: basis with 2 ventral, 2 dorsal and 1 lateral setae; ischium shorter than basis, with 2 ventral, 2 dorsal and 2 medially setae; merus trapezoidal, distal-dorsally with 2 simple and 1 long robust sensory setae, with 2 ventral, 1 distal-lateral and 1 distal-medial simple setae; carpus longer than basis, dorsally with 4 simple, 1 robust sensory and 1 plumose setae, with 3 ventral, 2 lat-

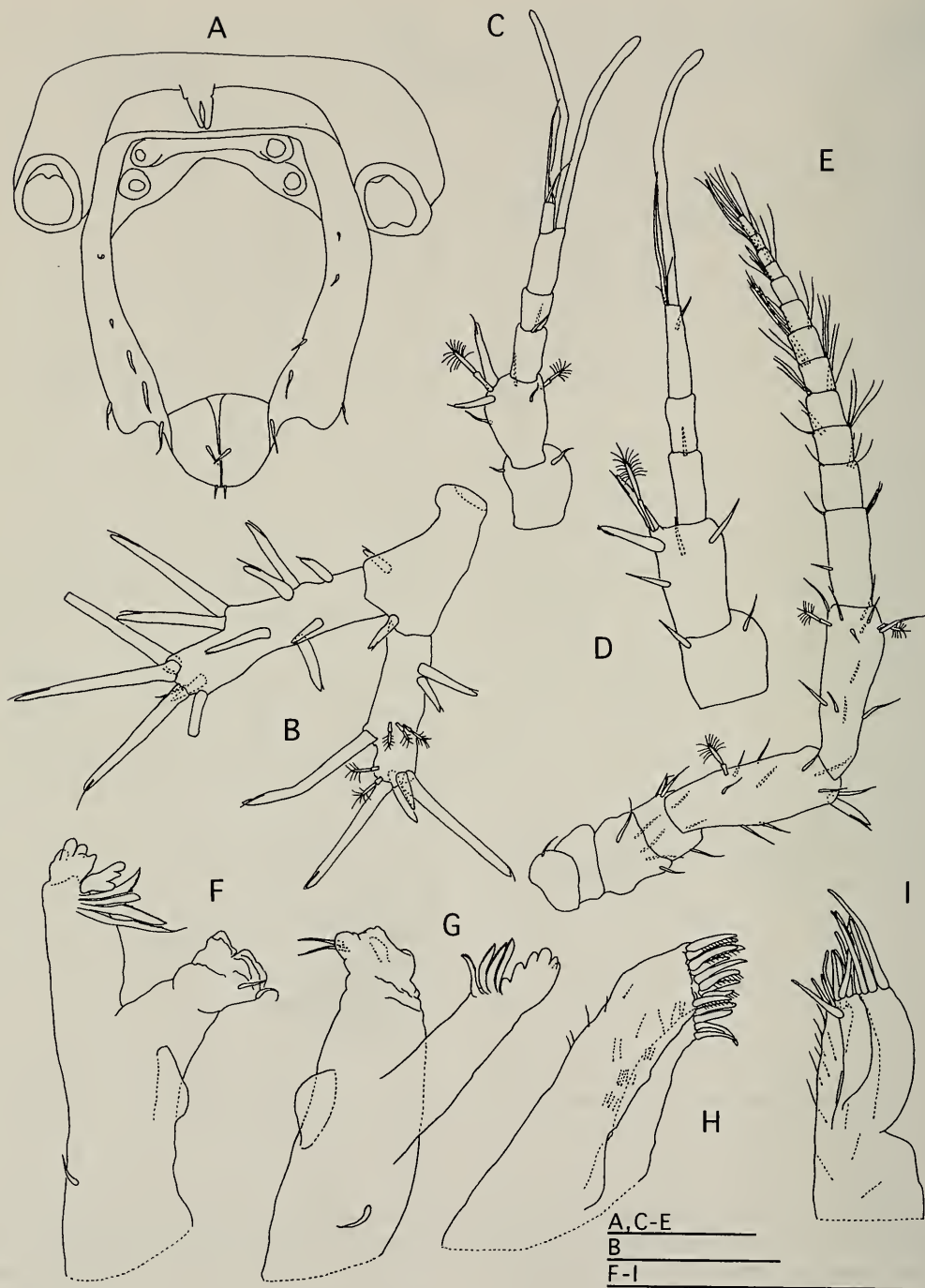


Fig. 2. *Santia longisetosa*, new species. A-C, E-I, holotype male; D, paratype female (ZIHU-01966): A, pereonite 7 and pleon, ventral; B, right uropod, ventral; C, left antenna 1, dorsal; D, left antenna 1, dorsal; E, left antenna 2, dorsal; F, left mandible, dorsal; G, right mandible, dorsal; H, right maxilla 1, ventral; left maxilla 2, ventral. Scales = 0.1 mm.

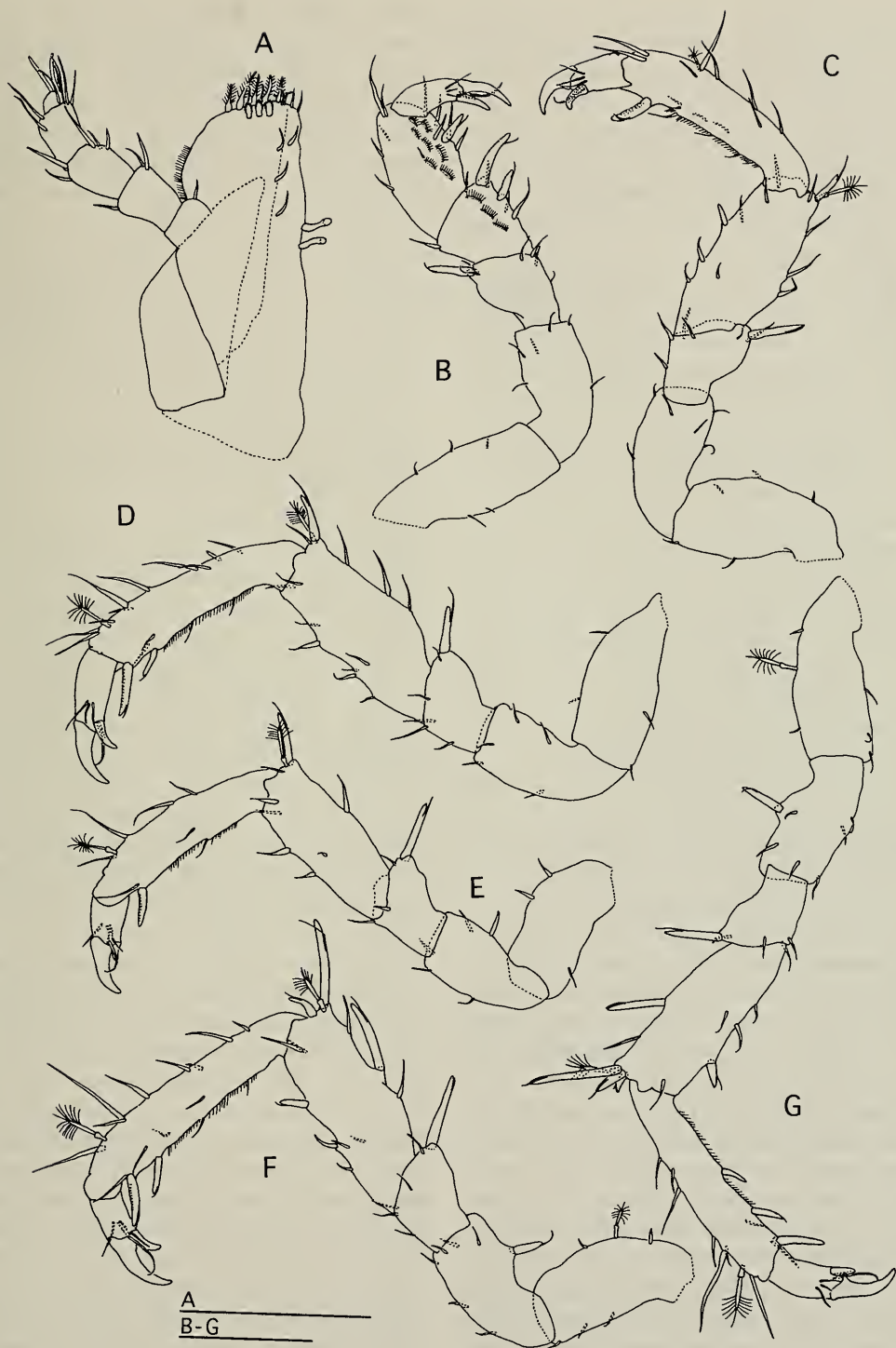


Fig. 3. *Santia longisetosa*, new species. A-G, holotype male: A, left maxilliped, dorsal; B, left pereopod 1, mesial; C, right pereopod 2, mesial; D, right pereopod 3, mesial; E, left pereopod 4, lateral; F, left pereopod 5, lateral; G, right pereopod 6, mesial. Scales = 0.1 mm.

eral and 2 medial simple setae; propodus the longest article, dorsally with 5 simple and 1 plumose setae, with 3 ventral, 3 lateral, 4 mesial simple setae, and with 1 distal-ventrally long robust sensory seta and many ventral short setae; dactylus the narrowest article; with 2 distal-lateral and 3 medial setae, 1 curved unguis, and 1 minute accessory spine.

Pereopod 3 (Fig. 3D) slightly longer than pereopod 2: basis with 2 ventral and 2 dorsal setae; ischium with 2 ventral, 2 dorsal and 1 distal-medial setae; merus distal-dorsally with 1 simple and 1 long robust sensory setae, with 2 ventral, 1 distal-medial and 1 distal-lateral simple setae; carpus dorsally with 4 simple, 1 robust sensory and 1 plumose setae, with 4 ventral, 2 lateral and 2 mesial simple setae; propodus dorsally with 10 simple and 1 plumose setae, with 2 ventral, 1 lateral, 1 mesial simple setae, and with 1 ventral-distal long robust sensory, 1 ventral short robust sensory setae and many ventral short setae; dactylus with 2 distal-lateral and 3 medial setae, 1 curved unguis, and 1 minute accessory spine.

Pereopod 4 (Fig. 3E) slightly shorter than pereopod 3: basis with 1 ventral and 2 dorsal setae; ischium with 2 ventral, 2 dorsal and 1 distal-medial setae; merus distal-dorsal with 1 simple and 1 long robust sensory setae, with 1 distal-ventral and 1 distal-lateral simple setae; carpus dorsally with 1 simple, 1 long robust sensory and 1 plumose setae, with 2 ventral, 3 lateral and 1 mesial simple setae; propodus dorsally with 4 simple and 1 plumose setae, with 2 ventral and 1 lateral simple setae, and with 1 distal-ventral long robust sensory seta and many ventral short setae; dactylus with 2 distal-lateral and 3 medial setae, 1 curved unguis, and 1 minute accessory spine.

Pereopod 5 (Fig. 3F) longer than pereopod 3: basis dorsally with 2 simple and 1 plumose setae, with 3 ventral simple setae; ischium with 1 dorsal robust sensory seta and 3 ventral, 2 lateral and 1 distal-medial simple setae; merus distal-dorsal with 1 simple and 1 long robust sensory setae,

with 2 ventral, 1 distal-medial and 1 distal-lateral simple setae; carpus dorsally with 2 simple, 2 long robust sensory, 1 short robust sensory and 1 plumose setae, with 1 ventral robust sensory seta and 2 ventral, 2 lateral and 2 medial simple setae; propodus dorsally with 7 simple and 1 plumose setae, with 3 ventral, 3 lateral, 2 medial simple setae, and with 1 distal-ventral long robust sensory, 1 ventral short robust sensory setae and many ventral short setae; dactylus with 2 distal-lateral and 3 medial setae, 1 curved unguis, and 1 minute accessory spine.

Pereopod 6 (Fig. 3F) the longest pereopod: basis dorsally with 2 simple and 1 plumose setae, with 3 ventral simple setae; ischium with 1 dorsal robust sensory seta and 3 ventral, 3 medial simple setae; merus distal-dorsal with 1 simple and 1 long robust sensory setae, with 2 ventral and 1 distal-medial simple setae; carpus dorsally with 1 simple, 2 long robust sensory, 2 short robust sensory setae and 1 plumose setae, with 2 ventral robust sensory setae and 2 ventral, 2 medial simple setae; propodus dorsally with 7 simple and 1 plumose setae, with 1 distal-ventral and 1 lateral simple setae, and with 1 distal-ventral long robust sensory, 2 ventral short robust sensory setae and many ventral short setae; dactylus with 2 distal-lateral and 3 medial setae, 1 curved unguis, and 1 minute accessory spine.

Pereopod 7 (Fig. 4A) slightly shorter than pereopod 6: basis dorsally with 1 simple and 2 plumose setae, with 2 ventral simple setae; ischium with 1 dorsal robust sensory seta and 2 ventral, 2 dorsal and 1 distal-lateral simple setae; merus distal-dorsal with 1 simple and 1 long robust sensory setae, with 1 distal-ventral, 1 distal-medial and 1 distal-lateral simple setae; carpus dorsally with 1 simple, 1 long robust sensory, 2 short robust sensory setae and 1 plumose setae, with 1 short ventral robust sensory, 1 distal-lateral short robust sensory setae, and with 2 ventral, 1 lateral and 2 medial simple setae; propodus, dorsally with 7 simple and 1 plumose setae, with 1 distal-ventral, 2 lateral simple setae, and with 1 distal-ventral



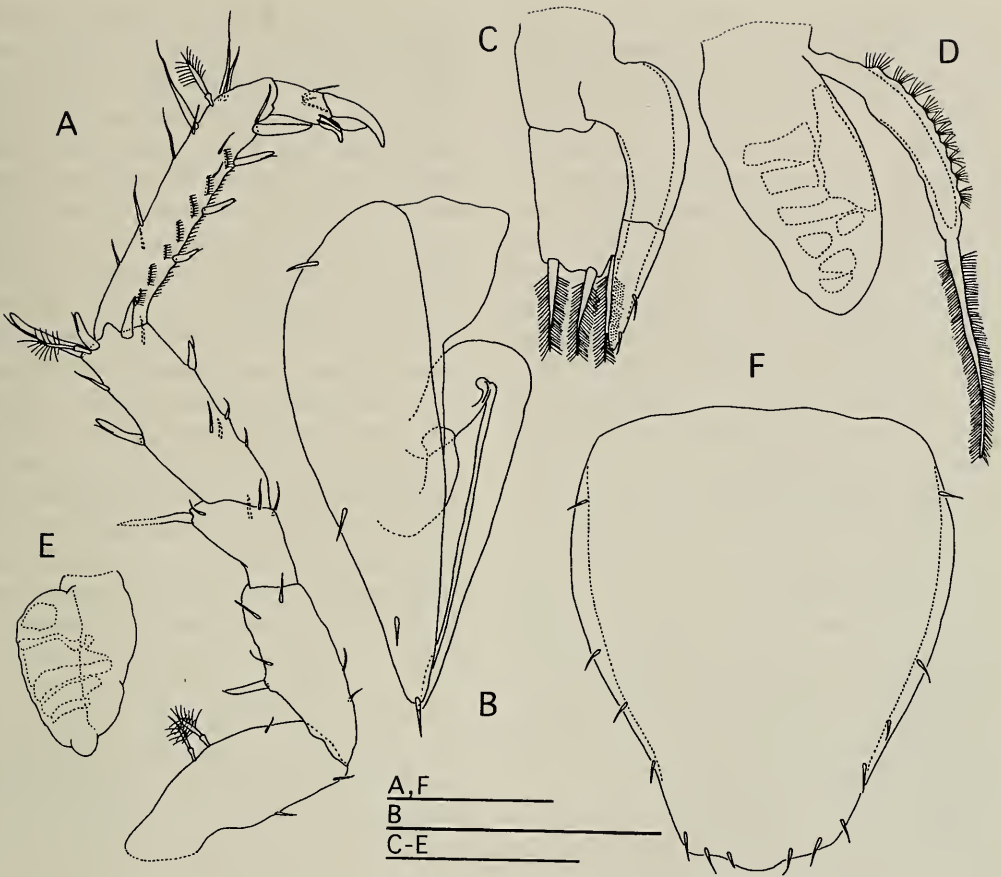


Fig. 4. *Santia longisetosa*, new species. A-E, holotype male; F, paratype female (ZIHU-01966): A, right pereopod 7, lateral; B, left pereopod 2, ventral; C, left pleopod 3, ventral; D, right pleopod 4, dorsal; E, left pleopod 5, dorsal; F, operculum, ventral. Scales = 0.1 mm.

long robust sensory, 3 distal-ventral short robust sensory setae, many ventral short setae and 7 lateral spinulose scales; dactylus with 2 distal-lateral and 3 medial setae, 1 curved unguis, and 1 minute accessory spine.

Pleopod 1 broken. Pleopod 2 (Fig. 4B) with broad protopod, tapering to rounded apex, lateral margin convex, bearing 1 apical and 3 submarginal setae; endopod with slender second article; exopod narrow. Pleopod 3 (Fig. 4C) with endopod bearing 3 stout, plumose setae distally; exopod composed of 2 articles, narrower than endopod; article 2 bearing 2 lateral simple setae. Pleopod 4 (Fig. 4D) with exopod narrow, distally with 1 stout, long plumose seta, lat-

erally with many short setae; endopod ovate and broad, without setae. Pleopod 5 (Fig. 4E) ovate, uniramous, about 1.6 times as long as broad, without setae.

Female: Similar to male in morphology of all pereopodal appendages. Body (Fig. 1B) about 2.1 times as long as maximum width. Head slightly narrower than pereonite 1, with 10 dorsal setae; frontal margin of head nearly straight, with 9 long setae. Pereonites 1-4 laterally rounded, each with 6-8 lateral setae and few dorsal setae; pereonites 5-7 laterally rounded, each with 1-3 lateral setae and few dorsal setae. Pereonite 1 shorter than pereonite 2; pereonites 2 and 3 subequal in length; pereonite 4 longest; pereonites 5 and 6 subequal in length; pereon-

ite 7 longer than pereonite 6. Pereonites 1 to 3 increasing in width; pereonite 3 widest; pereonite 4 slightly narrower than pereonite 3; pereonites 5 to 7 decreasing in width. Coxal plates dorsally visible on pereonites 4–7, each with 1–3 lateral setae. Pleonite short and narrow, without dorsal setae. Antenna 1 (Fig. 2D) composed of 5 articles. Article 1 broadest, with 1 distal-lateral and 1 distal-medial setae; article 2 longest, narrower than article 1, with 1 distal-ventral, 1 lateral and 1 distal-medial simple setae, with 1 distal-lateral plumose seta, and with 2 distal-lateral robust sensory setae; article 3 narrow, with 1 distal-ventral seta; article 4 slightly shorter than article 3, without setae; article 5 about 1.6 times as long as article 4, subapically with 1 short setae, apically with 1 aesthetasc and 2 short, 1 long setae. Operculum (Fig. 4F) about 1.2 times as long as broad, apically with short rounded projection, submarginally with 14 setae.

*Etymology.*—The specific name refers to the long sensory setae on the antenna 1 and on the propodi of the pereopods 2–7.

*Remarks.*—The present new species is assigned to Santiidae Kussakin, 1988, having a set of the following characters: eyes situated on lateral processes, short antenna 1 having 5 or 6 articles, antenna 2 with 4 short proximal, 2 long distal articles and flagellum, subcylindrical truncate mandibular molar process, narrow maxillipedal palp, distally pointed epipod of maxilliped, coxal plates of pereonites 5–7 visible dorsally, prehensile pereopod 1 and ambulatory pereopods 2–7, uropods situated on posterolateral margin of pleotelson, and terminally exposed anus. The following features displayed by the present new species indicate that it belongs to *Santia* Sivertsen & Holthuis, 1980: antenna 1 and 2 in anterior indentations laterally on the head, preocular lobes in front of the eyestalks, pleotelson apically with short rounded projection, pereopod 1 armed with 1 unguis and 1 accessory spine, female operculum longer than broad, and uropods with stout protopod, cylindrical endopod and exopod.

*Santia longisetosa* is distinguishable from its congeners by 2 long robust sensory setae on article 2 of antenna 1 and 1 long robust sensory seta ventrodistally on each propodus of pereopods 2–7. The nearly straight frontal margin of head and the robust long uropods are shared by *Santia longisetosa*, *S. milleri* (Menzies & Glynn, 1968) from Caribbean Sea (type locality), *S. hispida* (Vanhöffen, 1914) from St. Paul Island, the southern Indian Ocean (type locality), Tristan da Cunha (Nordenstam 1933) and the Magellan Strait (Winkler 1993). The present new species is distinguished from *S. milleri* by the following features (those of *S. milleri* in parentheses): article 2 of antenna 1 has 2 long robust sensory setae, propodi of pereopods 2–7 have a long robust sensory seta distal-ventral, pereonite 1 is slightly wider than head (narrower than head), coxal plates lack anterior-lateral stout setae (each with anterior-lateral stout seta), mandibular palp is absent (present), maxillipedal palp is moderately broad (narrow). *Santia hispida* differs from the present new species in having the narrow maxillipedal palp, the mandibular palp, many long stout dorsal and lateral setae on head, pereon and pleon, very long second article of pleopod 1 in male, and a pair of stout setae on operculum in female.

*Santia charcoti* (Richardson, 1906) (Hodgson 1910, Wilson 1980) from the Antarctic has stout uropods, similar to those of *S. longisetosa*. The present new species is however distinguished from the *S. charcoti* by the following features (those of *S. longisetosa* in parentheses): the frontal margin of head is bilobed (unilobed), many long setae are on head, pereon and pleon (some short setae), the pleotelson is short (long), endopod of uropod is curved (straight), protopod of pleopod 1 in male is broad (narrow), and coxal plates of pereonite 7 are dorsally invisible (visible).

The present new species differs from another Japanese species, *S. katoi* Shimomura & Mawatari, 2000 described from Shirahama coast, Wakayama Prefecture in the

following features (those of *S. katoi* in parentheses): the mandible lacks palp (palp present), the frontal margin of head is nearly straight (slightly convex), with 8 or 9 long setae (4 short setae), the head is narrower than pereopod 1 (broader than pereopod 1), the uropod shorter than pleotelson (longer than pleotelson), the article 2 of antenna 1 has 2 long robust sensory setae distolaterally (without sensory setae), and the propodi of pereopods 2–7 are armed with long robust sensory setae ventrodistally (with short robust sensory setae).

The present new species shows a variation in segmentation of antenna 1 as follows: holotype male has 6-articulate antenna 1 consisting of 2 stout, 2 short, 1 long and 1 minute articles, while all paratype females have 5-articulate antenna 1 consisting of 2 stout, 2 short and 1 long articles.

#### Acknowledgments

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## A new genus and species of freshwater crab from Colombia (Crustacea: Decapoda: Pseudothelphusidae)

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*Abstract.*—A new genus, *Achagua*, is established for the new species *A. casanarensis*, and *Eudaniela pestai* (Pretzmann). Consequently, the latter is removed from the genus *Eudaniela* Pretzmann. Species of the new genus are known exclusively from the upper Colombian Orinoco basin and the western region of the Venezuelan coastal cordillera. The new genus is characterized by features of the third maxilliped, the orifice of branchial efferent channel, and the first male gonopod.

During faunistic surveys of the upper Colombian Orinoco basin, specimens belonging to a new species of the family Pseudothelphusidae were collected. The new species resembles *Eudaniela pestai* (Pretzmann, 1965) which according to Rodríguez (1982) and Rodríguez & Pereira (1992), exhibits the least derived first male gonopod morphology and less reduced exognath of the third maxilliped within the tribe Kingsleyini. These two species are sufficiently distinct from others of the tribe in the characteristics of the third maxilliped, orifice of the branchial efferent channel, and first male gonopod, to warrant their assignment to a new genus. *Eudaniela pestai* is distributed in the western region of the Venezuelan coastal cordillera. The new genus and species are described herein. The new genus is considered a basal group from which species of *Eudaniela* Pretzmann, 1971 originated (Rodríguez, pers. comm.).

The terminology used for the morphology of the male first gonopod follows Smalley (1964) and Rodríguez (1982). The abbreviations cl and cb stand for carapace length and carapace breadth, respectively. The color nomenclature used follows Smith (1975). The material is deposited in Museo de Historia Natural, Instituto de

Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN-MHN).

### Systematics

Family Pseudothelphusidae Rathbun, 1893  
Tribe Kingsleyini Bott, 1970  
Genus *Achagua*, new genus

*Diagnosis.*—Third maxilliped with merus of endognath regularly curved; exognath approximately 0.5 times length of ischium; orifice of branchial efferent channel partially closed by spine of jugal angle, and by production of lateral lobe of epistome. First male gonopod straight with wide marginal process; subapical mesial process spine-like; mesial plate quadrate or slightly rounded, apex with mesial and cephalic plates distally overlapping or in parallel arrangement.

*Type species.*—*Achagua casanarensis*, new species.

*Other included species.*—*Eudaniela pestai* (Pretzmann, 1965)

*Etymology.*—The genus is named in honor of the Achagua Indians, who lived in the region where the new genus was discovered. Gender: feminine.

*Achagua casanarensis*, new species

Figs. 1, 2

*Holotype*.—Municipio Aguazul, 26 km SW from Yopal, Casanare Department, Colombia, 290 m alt., 3 Oct 1995, leg F. Fernández: 1 male, cl 32.7 mm, cb 51.6 mm, ICN-MHN-CR 1626.

*Paratype*.—Same locality data as holotype: 1 male, cl 29.3 mm, cb 48.7 mm, ICN-MHN-CR 1862.

*Type locality*.—Municipio Aguazul, 26 km SW from Yopal, Casanare Department, Colombia.

*Diagnosis*.—Marginal process of first male gonopod wide, spatulated distally; with subapical broad-base, and distally acute spine-like mesial process; mesial plate quadrate; apex with mesial and cephalic plates distally overlapping, and basal triangular projection; field of spines narrow and straight, spinules conspicuous, uniform in size, directed distally.

*Description of holotype*.—Carapace (Fig. 1A) with deep, straight cervical groove, ending short distance from lateral margin. Anterolateral margin with depression behind external orbital angle, followed by 15 tubercles on anterior half; posterior lateral margin smooth. Postfrontal lobes small, rounded, without anterior depressions; median groove narrow, shallow, with incision on upper margin of front. Surface of carapace in front of postfrontal lobes flat and inclined anteriorly. Upper border of front crest-like, marked with row of tubercles; lower margin slightly sinuous in frontal view. Surface of front between upper and lower borders high and slightly excavated. Upper and lower orbital margins each with row of tubercles. Surface of carapace covered with small papillae; limits between regions demarcated. Third maxilliped (Fig. 2F) with merus of endognath regularly curved; exognath approximately 0.5 times length of ischium of third maxilliped. Orifice of branchial efferent channel partially closed by spine of jugal angle, and by projection of lateral lobe of epistome (Fig. 1C).

First pereiopods heterochelous, right cheliped larger than left. Merus with 3 crests as follows: upper crest with rows of tubercles, internal lower crest with rows of teeth, and external lower crest with few tubercles. Carpus with 3 tubercles on internal crest, and prominent acute spine distally. Palm of larger cheliped swollen, without external tubercle, fingers gaping when closed, with rows of tubercles on dorsal side (Fig. 1B); smaller cheliped slightly swollen, fingers not gaping when closed.

Walking legs (pereiopods 2–5) thick (Fig. 1A). Dactyli elongated, each about 1.6 times as long as propodi, with papillae and 5 longitudinal rows of large, dark spines diminishing in size proximally. Number of spines and papillae on each dactylus arranged as follows: 1 anterolateral row and 1 anteroventral row each with 6 spines; 1 external row with 6 spines and 1 pair of proximal papillae; 1 posterolateral row and 1 posteroventral row with 4 spines.

First male gonopod (Fig. 2A–E) straight, marginal process wide, spatulated distally; mesial border convex with subapical broad-based, and acute spine-like mesial process, followed by deep depression, ending distally in quadrate mesial plate; lateral border slightly sinuous with notch at basis of spermatoc channel. Apex laterally, with mesial and cephalic plates distally overlapping, and basal triangular projection; field of spines narrow and straight, spinules conspicuous, uniform in size, and directed distally (Fig. 2B, D, E).

*Color*.—In alcohol, the dorsal side of the carapace is gray (near 45, Smoke Gray) with Buff (24) specks. The walking legs are Tawny (38). The chelae are Pale Horn Color (92). The ventral surface is gray (near 45, Smoke Gray) with Cinnamon (39) specks.

*Etymology*.—The specific name refers to Casanare Department, where the specimens were collected.

*Remarks*.—The new species is most similar to *Achagua pestai*. The two can be distinguished by differences in the first male

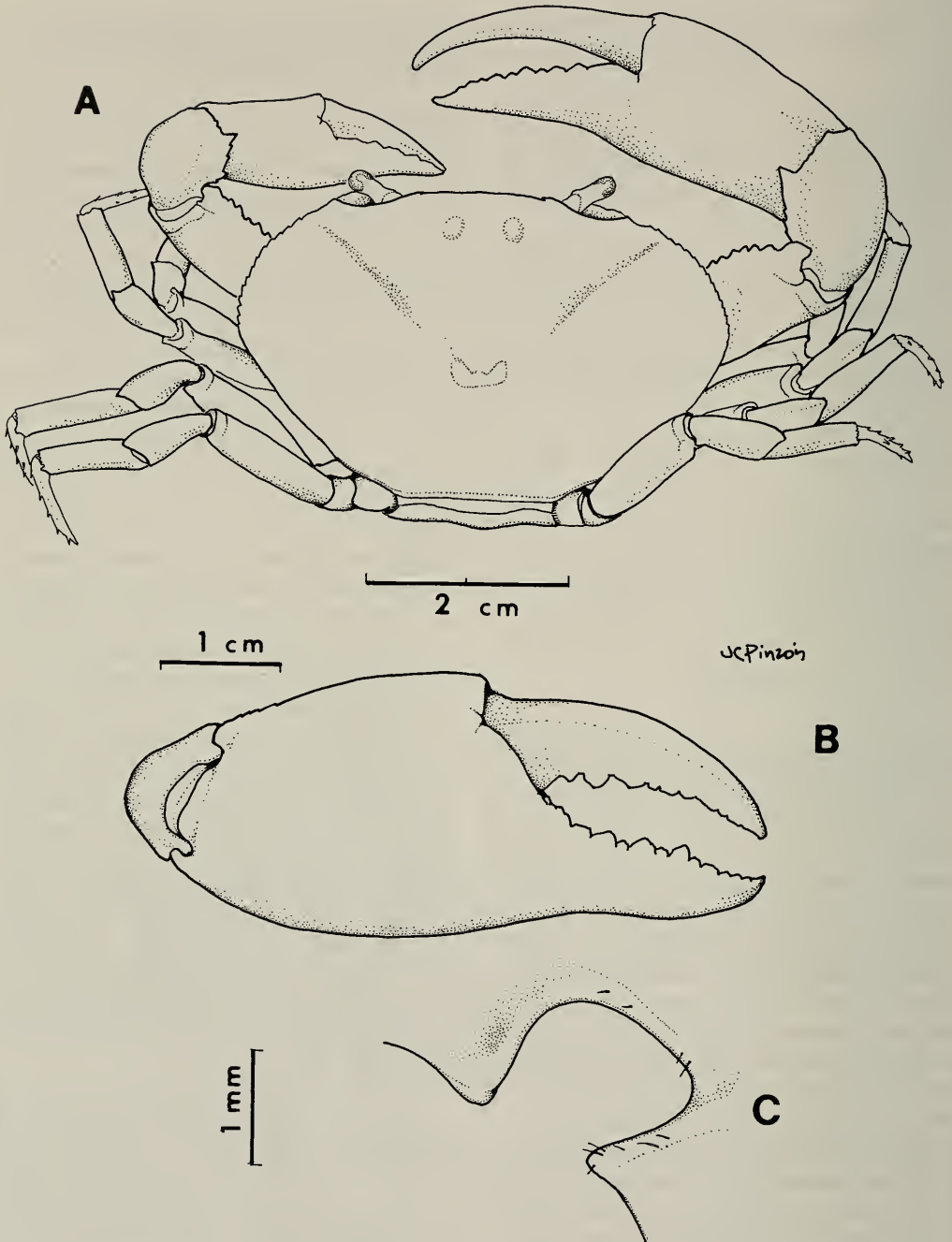


Fig. 1. *Achagua casanarensis*, new species, male holotype, cl 32.7 mm, cb 51.6 mm, ICN-MHN-CR 1626. A, dorsal view; B, chela of large cheliped, external view; C, orifice of branchial efferent channel.

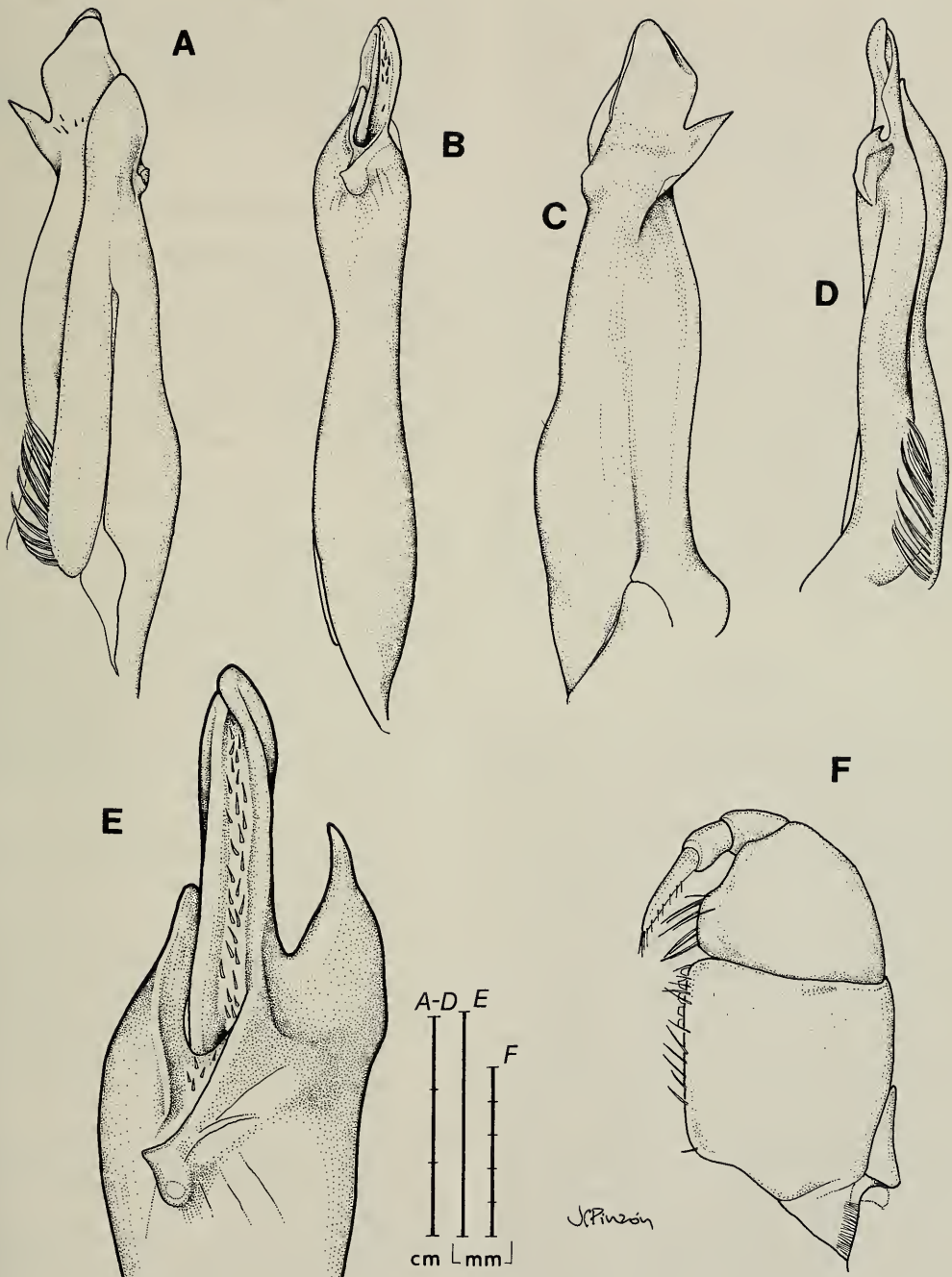


Fig. 2. *Achagua casanarensis*, new species, male holotype, cl 32.7 mm, cb 51.6 mm, ICN-MHN-CR 1626. A, left first gonopod, caudal view; B, same, lateral view; C, same, cephalic view; D, same mesial view; E, apex of same, distal view; F, left third maxilliped, external view.

gonopod. In the new species the mesial plate is quadrate, while in *A. pestai* the mesial plate is slightly rounded; the subapical mesial process is acute distally, followed by a deep depression in *A. casanarensis*, whereas the subapical mesial process is rounded, and there is a shallow depression in *A. pestai*. The marginal process is spatulated distally in the new species, whereas in *A. pestai* the marginal process is rounded distally. In the new species the apex has the mesial and cephalic plates distally overlapping, whereas they are parallel in *A. pestai*; in the new species there is a basal triangular projection in the apex which is absent in *A. pestai*. In *A. casanarensis* the field of spines is straight, and there are only uniform conspicuous spines, whereas in *A. pestai* the field of spines is recurved, with large setae distally, and short spinules near the spermatid channel.

#### Discussion

In a cladistic study of the tribe Kingsleyini, Rodríguez & Pereira (1992) concluded that in *Eudaniela pestai* the exognath of the third maxilliped is less reduced than in other members of the tribe. In addition, the cephalic lobe of the first male gonopod is formed by two separate plates which resemble an ancestral *Strengeriana*-type of gonopod with three independent plates. For these reasons they considered "*Eudaniela pestai* as approaching the ancestral pseudothelphusid condition", a conclusion confirmed by Rodríguez & Campos (1998). More recently, a cladistic analysis of morphological characters was conducted by Sternberg et al. (1999) to resolve the relationships of the *Eudaniela* species complex. The result presented *Eudaniela* as a paraphyletic taxon, and *E. pestai* was positioned basal to the *Eudaniela* species complex, and to other representatives of the tribe Kingsleyini, i.e. the genera *Fredius* Pretzmann, 1967, *Guinotia* Pretzmann, 1965, *Kingsleya* Ortmann, 1897, and *Microthelphusa* Pretzmann, 1968. In this study *E. pestai* is trans-

ferred to the new genus *Achagua*, and with the new species *A. casanarensis* they seem to constitute a basal group from which *Eudaniela* species originated. Thus, *Achagua* likely represents a sister-group to all other Kingsleyini.

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**A new pontoniine shrimp of the genus *Coralliocaris* Stimpson, 1860  
(Crustacea: Decapoda: Palaemonidae) from the Ryukyu Islands**

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*Abstract.*—A new species of coral-associated shrimp *Coralliocaris tridens*, is described from the Ryukyu Islands, southwestern Japan. The new species differs primarily from the eight congeneric species in having three teeth on the cutting edge of the dactylus of the second pereopod.

In 1969, the second author carried out a field trip to Ishigaki Island, the southern Ryukyu Islands, to investigate the coral reef shrimps of the family Palaemonidae. Most of the specimens collected were then identified, but some remained unstudied. Recently, we re-examined the collection, and discovered two unusual specimens belonging to the pontoniine genus *Coralliocaris* Stimpson, 1860. The genus is composed of eight known species which are obligatory associates with scleractinian corals (Chace & Bruce 1993, Bruce 1998, Mitsuhashi 2000). Detailed examination has shown that the two specimens represent an undescribed species described herein.

The type specimens of the new species are deposited at the Kitakyushu Museum and Institute of Natural History, Kitakyushu (KMNH). The carapace length (CL), from the posterior margin of the orbit to the midpoint of the posterodorsal margin of carapace, is an indication of specimen size. The measurements and drawings were made with the aid of a drawing tube mounted on a LEICA MZ8 stereo microscope or Nikon 70021 microscope.

*Coralliocaris tridens*, new species  
Figs. 1–3

*Material examined.*—Holotype: ovigerous ♀ (CL 3.05 mm), KMNH IvR 300002,

Kabira Bay (24°26'N, 124°8'E), Ishigaki Island, Ryukyu Islands, southwestern Japan, from tabular coral (*Acropora* sp.), 28 Jul 1969, coll. T. Fujino. Paratype: 1 sex undet. (CL 2.06 mm), KMNH IvR 300001, same data as holotype.

*Description of holotype.*—Medium-sized shrimp, with typical shape for genus *Coralliocaris*. Body (Fig. 1) moderately depressed dorsoventrally. Rostrum (Figs. 1, 2A) unarmed, rather abruptly narrowed in distal half, just reaching base of intermediate segment of antennular peduncle; midrib well developed, broadened posteriorly; supraorbital eave nearly straight in dorsal view. Carapace (Figs. 1, 2A) glabrous; antennal spine submarginal; anterolateral angle broadly rounded.

Abdomen (Figs. 1, 2A) with pleura of first 3 segments broadly expanded, forming marsupium; third segment feebly produced posterodorsally, partially covering lateral surfaces of fourth and fifth segments; fourth and fifth segments each with posteroventrally rounded pleuron; sixth segment longer than fifth segment, with acute posteroventral tooth; posterolateral process blunt.

Telson (Fig. 3A) elongate, subtriangular, length about 3 times greatest width; dorsal surface with 2 pairs of small spines dorso-laterally, anterior pair situated slightly pos-

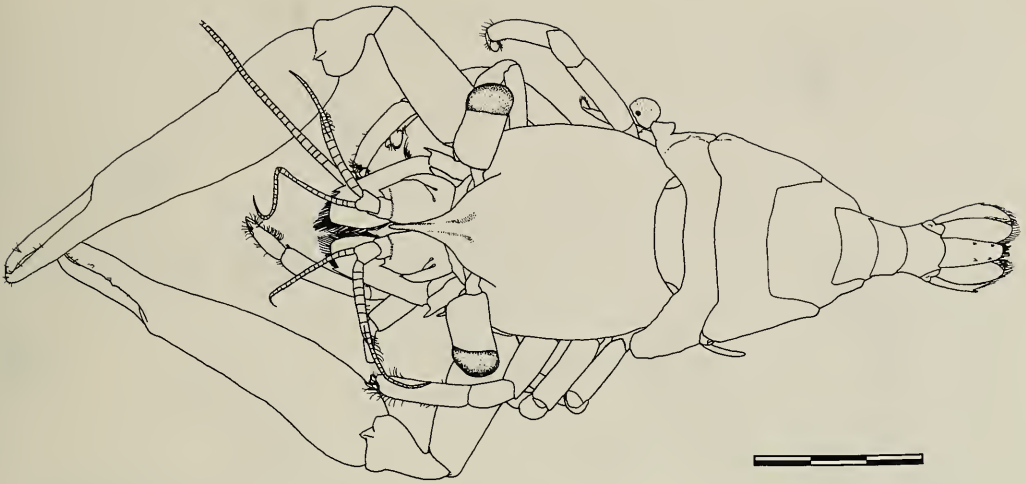


Fig. 1. *Coralliocaris tridens*, new species. Holotype (KMNH IvR 300002) ovigerous female (CL 3.05 mm). Habitus, dorsal. Scale: 3 mm.

terior to midlength of telson, posterior pair situated at about midlength between anterior pair and posterior margin; posterior margin rounded, with 3 pairs of spines, lateral pair shortest; intermediate pair longest, stout; submedian pair somewhat shorter than intermediate; simple fine seta arising from near bases of submedian and intermediate pairs of spines.

Eyes (Figs. 1, 2A) moderately large; eye-stalk subcylindrical, 1.4 times as long as wide; cornea oval, slightly inflated.

Antennular peduncle (Fig. 1) reaching 0.7 of scaphocerite; basal segment broad, greatest width approximately equal to length of medial margin; ventral surface with small tooth at posterior 0.7; outer margin of stylocerite convex along general outline of basal segment, reaching level of distal 0.2 of medial margin. Intermediate segment as long as wide, with row of long plumose setae on medial margin. Distal segment weakly broadened distally; upper flagellum biramous, with proximal fused part composed of 7 articles.

Basicerite of antenna with prominent lateral spine; scaphocerite twice as long as broad, lateral margin straight, armed with stout tooth distally.

Third maxilliped with stout endopod; ba-

sis and ischiomeral segments incompletely fused; ischiomeral segment 3 times as long as basis, unarmed on lateral margin; carpus swollen medially, 1.5 times broader than terminal segment, with numerous, fine plumose setae on medial surface; terminal segment short, teardrop-shaped, with dense plumose setae on dorsal surface; exopod almost reaching distal end of endopod; rounded epipod present; arthrobranch with 6 lamellae.

First pereopod (Fig. 3B, C) slender, exceeding distal margin of scaphocerite by length of chela and half of carpus. Chela about half as long as carpus, gradually tapering distally; fingers half length of palm, each with entire cutting edge; palm with about 10 transverse rows of anteriorly curved, serrate setae on ventral surface. Carpus gradually widened distally, ventrodistally with transverse row of setae. Merus 3 times longer than ischium.

Second pereopods (Fig. 1) subequal in length and shape. Chela large, elongate, somewhat compressed laterally. Dactylus about half length of palm, nearly straight in ventral view, weakly curved and distally hooked in lateral view, lacking longitudinal ridge on lateral face; cutting edge with 3 subtriangular equidistant teeth on proxi-

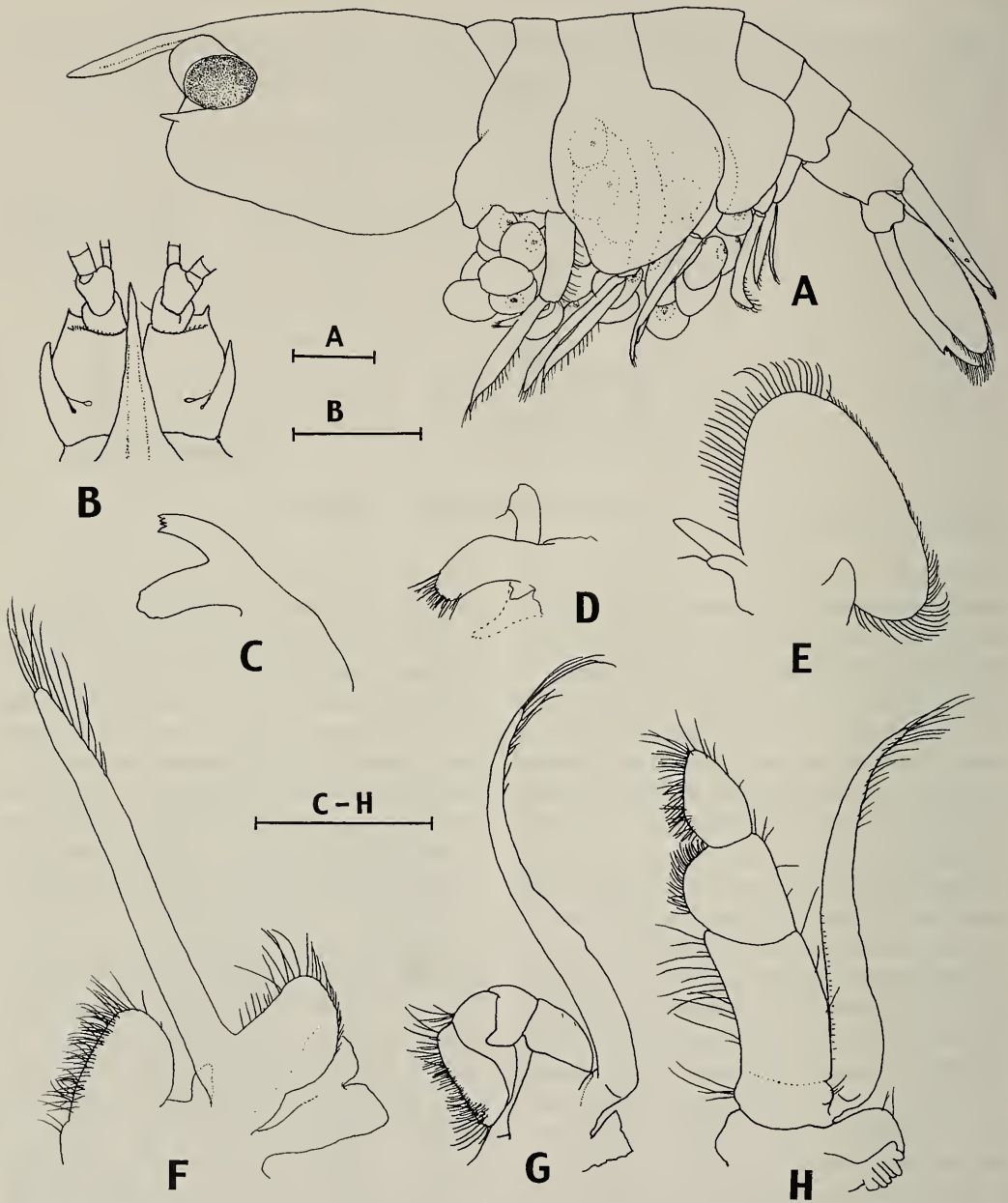


Fig. 2. *Coralliocaris tridens*, new species. A, holotype (KMNH IvR 300002) ovigerous female (CL 3.05 mm); B-H, paratype (KMNH IvR 300001), sex undet. (CL 2.06 mm). A, body, lateral, cephalic and thoracic appendages omitted; B, antennular peduncles and anterior part of rostrum, dorsal; C, left mandible, ventral; D, left maxillula, ventral, lower lacinia missing; E, left maxilla, ventral; F, left first maxilliped, ventral; G, left second maxilliped, ventral, part of epipod missing; H, left third maxilliped, ventral. Scales: 1 mm.

mal half. Fixed finger with 4 teeth, distal 3 similar to dactylar teeth, proximal tooth faintly tridenticulate; 3 shallow concavities fitting to 3 teeth on opposable margin of

dactylus on slightly medial to cutting edge. Palm with weakly concave lateral profile in dorsal view. Carpus short, about 0.3 as long as palm, cup-shaped; distal margin

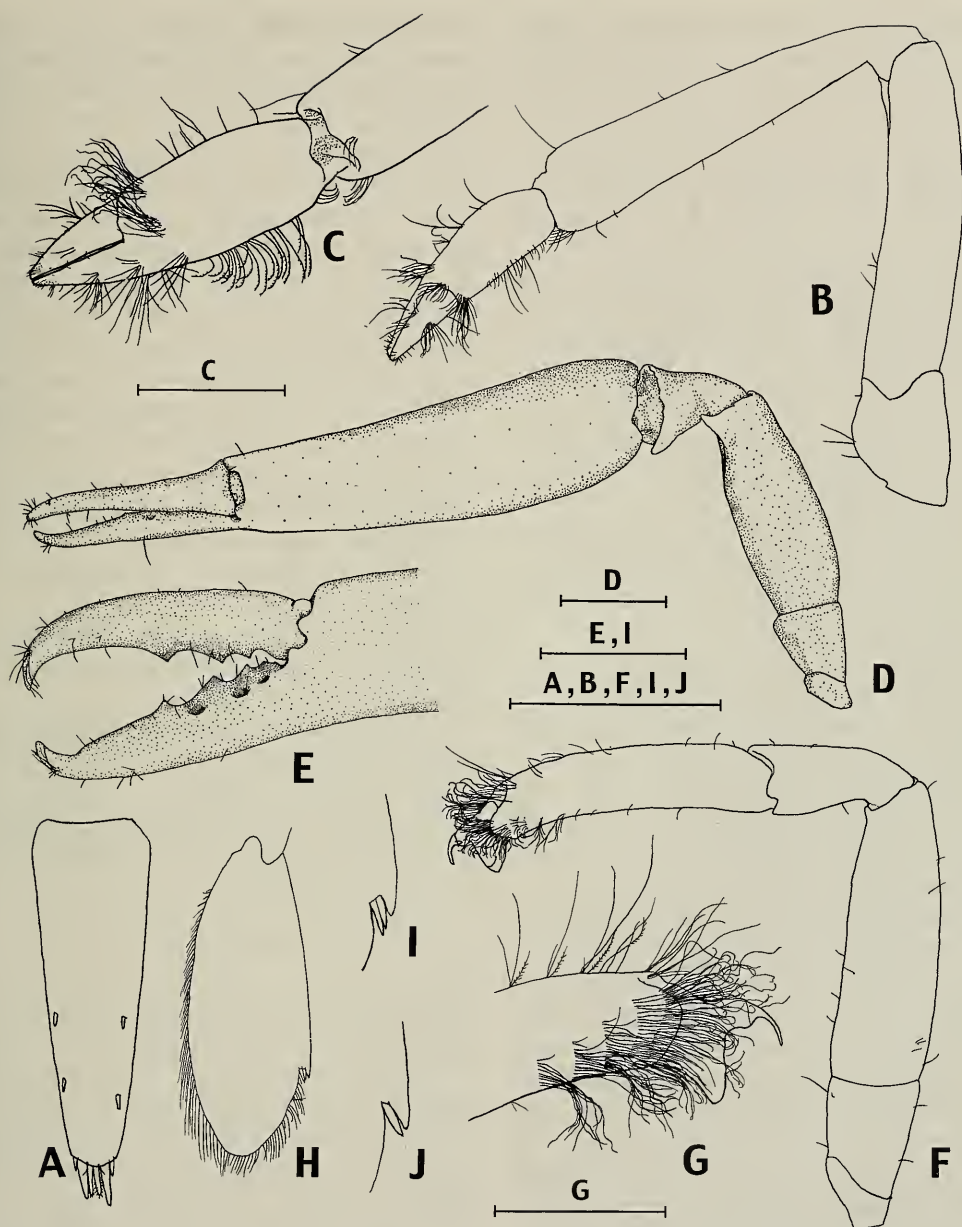


Fig. 3. *Coralliocaris tridens*, new species. A–C, H, I, holotype (KMNH IvR 300002) ovigerous female (CL 3.05 mm); D–G, J, paratype (KMNH IvR 300001), sex undet. (CL 2.06 mm). A, telson, dorsal; B, left first pereiopod, ventral; C, chela of right first pereiopod, lateral; D, left second pereiopod, ventral; E, fingers, same, medial; F, left third pereiopod, lateral; G, same, dactyl and distal part of propodus, medial; H, exopod of right uropod, dorsal; I, J, lateral part of exopod of right uropod, dorsal. Scales: 1 mm, except C and G, 0.5 mm.

with a stout process on ventral part, obscurely denticulate dorsally. Merus about half length of palm and twice as long as carpus, with moderately strong distomedial

tooth. Ischium compressed, about half length of merus.

Third to fifth pereiopods similar, robust. Dactyli short, distally blunt, each with

strong acute unguis on midlength of margin of extensor surface. Propodi 4 times longer than wide, with transverse rows of dense curly setae distally. Carpi short, about half of propodi; meri subequal in length to propodi and about twice as long as carpi, slightly narrowed distally. Ischia about half as long as meri.

Pleopods normal; first pleopod without setae on surface of protopod; endopod subcylindrical, elongate, overreaching half of exopod.

Uropod (Fig. 3H, I) overreaching tip of telson; exopod with acute immovable tooth and 2 movable spines at distal 0.3 of lateral margin on both sides.

About 70 ova at early-eyed stage present, measuring 0.64–0.74 mm × 0.48–0.53 mm.

*Description of paratype.*—Body more slender than holotype.

Rostrum (Fig. 2B) extending to midlength of distal segment of antennular peduncle. Abdominal segments more slender than holotype, with feebly developed pleura. Antennular peduncle (Fig. 2B) with well-developed stylocerite; tip of stylocerite protruding obliquely forward from basal segment leaving v-shaped notch.

Mandible (Fig. 2C) deeply divided in incisor and molar processes, without palp; molar process slender with dense bristles distally; incisor process tapering distally, armed with 4 teeth on distomedial margin, intermediate 2 teeth somewhat smaller than outer teeth. Maxillula (Fig. 2D) with short apical seta on tip of inner lobe of palp; upper lacinia with several stout setae on distal margin. Maxilla (Fig. 2E) with short, simple endite bearing long apical seta; palp slender, feebly tapering, twice as long as endite. First maxilliped (Fig. 2F) with short non-setose palp; basal endite rounded, fringed with setae on medial margin, without distinct notch separating it from coxal endite; coxal endite with a few setae at medial margin; exopod approximately 3 times as long as basal endite, with several plumose setae distally; caridean lobe short, broad. Second maxilliped (Fig. 2G) typical

for genus; dactylar segment with dorsally curved setae on medial margin; propodus not produced anteriorly, with several setae on medial margin. Third maxilliped (Fig. 2H) similar to that of holotype.

First pereopod stouter than in holotype. Chela 0.6 times as long as carpus. Second pereopod (Fig. 3D, E) similar to that of holotype on left side, but smaller on right side, right chela about half as long as left chela. Cutting edge of fixed finger of left chela (Fig. 3E) with most proximal tooth truncate, with 2 faintly developed denticles; dactylus of small right chela with small tooth and fixed finger with 2 small teeth. Third pereopod (Fig. 3F, G) to fifth pereopod slightly more slender than in holotype; propodi with dense setae distally, as in holotype.

Pleopods without specific features; endopod and exopod of first pleopod short, narrow triangular.

Posterior half of left uropod broken; right exopod (Fig. 3J) with immovable tooth and 1 spine on lateral margin.

*Coloration.*—The preserved specimens in spirit are uniformly whitish-cream. Color in life not recorded.

*Etymology.*—The specific name is a combination of the Latin, *tri* (=three) and *dens* (=tooth), in reference to the characteristic three teeth on the cutting edge of the dactylus of the second pereopod.

*Distribution.*—Known so far only from Kabira, Ishigaki Island, Ryukyu Islands.

*Host.*—The host coral is an unidentified species of *Acropora*, like in most of *Coralliocaris* species (Bruce 1972, 1977).

*Remarks.*—The sex of the paratype could not be determined, because the appendix masculina is not differentiated.

*Coralliocaris tridens*, new species, is readily distinguished from the other species of *Coralliocaris* by having three teeth on the cutting edge of dactylus of the second pereopod. The cutting edge of the dactylus of the second pereopod is armed with two teeth in *C. brevirostris* Borradaile, 1898, *C. nudirostris* (Heller, 1861) and *C. venusta*

Kemp, 1922, and with one blunt projection in *C. superba* Dana, 1852 and *C. taiwanensis* Fujino & Miyake, 1972. In *C. graminea* Dana, 1852, *C. viridis* Bruce, 1974 and *C. macrophthalma* (H. Milne Edwards, 1837), the cutting edge of the dactylus of the second pereopod is unarmed, bearing a fossa in which fits a flattened tooth on the opposable margin (Chace & Bruce 1993, Bruce 1998, Mitsuhashi 2000). The armature of the dactylus is constant and without doubt one of the important character to distinguish the species.

*Coralliocaris tridens* is most similar to *C. nudirostris* in having unarmed rostrum, triangular teeth on the cutting edges of fingers of the second pereopods, and straight subdistal part at the cutting edges of the fixed finger of the second pereopod. We fortunately could examine the type specimens of *C. nudirostris* in the collections of the Natural History Museum in Vienna and found that the dactylus of the second pereopod bears a longitudinal ridge on its medial surface, and differs from that of *C. tridens*, in which the medial surface is not ridged and smooth (Fig. 3E).

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**A new genus and a new species of crab of the family Goneplacidae MacCleay, 1838 (Crustacea: Decapoda: Brachyura) from the tropical western Atlantic**

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*Abstract.*—A new monotypic genus, *Nancyplax*, and a new species, *N. vossi*, of the family Goneplacidae MacCleay, are described from the southern Caribbean and northeastern coast of South America. Characters derived from male pleopods 1 and 2, and male abdomen-sternoabdominal cavity, allow *Nancyplax* to be assigned to the Euryplacinae Stimpson. The carapace in *N. vossi*, however, strongly resembles in overall conformation some species in the Carcinoplacinae H. Milne Edwards. In addition, *N. vossi* has a well developed stridulatory organ, a feature shared with only one other euryplacine species, some carcinoplacines, and some species in the Goneplacinae MacCleay. The mosaic habitus of *Nancyplax* precludes resolution of relationships with other euryplacine genera. Morphological similarities of *N. vossi* with species of *Carcinoplax* H. Milne Edwards, *Psopheticus* Wood-Mason, *Psopheticoides* Sakai, and *Tri-zocarcinus* Rathbun, are summarized.

The family Goneplacidae MacCleay, 1838 currently contains numerous problematic genera with xanthoid affinities that defy phylogenetic arrangement. Guinot (1969a, 1969b, 1969c) proposed a subfamilial arrangement which subsequently has been modified by the removal and addition of subfamilies (Manning & Holthuis 1981, Guinot 1986, Ng & Wang 1994, Hendrickx 1998). As a result, the Goneplacidae is now generally divided by carcinologists into six subfamilies: Carcinoplacinae H. Milne Edwards, 1852, Chasmocarcininae Serène, 1964, Euryplacinae Stimpson, 1871, Goneplacinae MacCleay, 1838, Pseudozinae Alcock, 1898, and Troglolacinae

Guinot, 1986. Of these six subfamilies, the Carcinoplacinae, Euryplacinae, and Goneplacinae are considered closely related (Guinot 1969a, 1969b, 1969c). The remaining three subfamilies appear to have no close affinities either among themselves or with other subfamilies of Goneplacidae, but should remain in the family until detailed phylogenetic analyses are conducted.

Although in-depth taxonomic reviews have been completed for goneplacid genera such as *Carcinoplax* H. Milne Edwards, 1852 (see Guinot 1989), and *Psopheticus* Wood-Mason, 1892 (see Guinot 1990), the systematic position and relationships of many taxa remain to be fully evaluated. Ob-

stacles to resolving relationships include vague subfamilial definitions and mosaic taxonomic distributions of character states. Furthermore, new forms which often exhibit puzzling combinations of generic-level features continue to be discovered throughout the world oceans.

In the last 25 years a substantial number of new taxa from the Atlantic and Pacific coasts of the American continents have been added to the Goneplacidae (e.g., Gómez & Ortiz 1975, Hernández Aguilera 1982, Guinot 1984, Garth 1986, Hendrickx 1989, 1998; Vázquez-Bader & Gracia 1991, 1995; Tavares 1996). Recent examination of numerous unstudied specimens deposited in the collections of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, and obtained in the 1960s during deep-sea cruises of the *R/V Pillsbury* to the Atlantic coast of northern South America, revealed the existence of yet another undocumented goneplacid crab of unclear affinities that requires assignment to a new genus and species. Specimens of this same crab were also recently collected in 1995 from the Caribbean coast of Colombia. Herein, a new monotypic genus and new species are described for this goneplacid crab.

#### Material and Methods

Specimens used were collected in 1968 and 1969 during investigations of the marine fauna of the tropical Atlantic on board the *R/V Pillsbury* by the then Institute of Marine Sciences, University of Miami, now Rosenstiel School of Marine and Atmospheric Science (RSMAS); and in 1995 during a joint expedition along the Caribbean coast of Colombia on board the research vessel *B/I Ancón*, conducted by staff from the Colombian Navy's Centro de Investigaciones Oceanográficas e Hidrográficas, Cartagena (CIOH), Instituto de Investigaciones Marinas y Costeras, Santa Marta (INVEMAR), and National Museum of Natural History, Smithsonian Institution,

Washington, DC (USNM). Sampling methods used on the *R/V Pillsbury* can be found in Voss (1966), and on the *B/I Ancón* in Lemaitre & Campos (2000). The holotype has been deposited in the USNM, with paratypes in the reference collection of INVEMAR, and the Invertebrate Museum of RSMAS (UMML). In general, the descriptive terminology used follows Guinot (1969a, 1969b, 1969c, 1989, 1990). The term "press-button" is used as defined by Guinot & Bouchard (1998) for the abdominal locking mechanism. For the stridulating organ, the terms "pars stridens" and "plectrum" are used in accordance with Guinot-Dumortier & Dumortier (1960) and Guinot (1990). In the "Material examined" section, measurements listed are in millimeters (mm), given in the order: total carapace length (CL)  $\times$  carapace width (CW); and abbreviations are as follows: ovig, ovigerous; P, *R/V Pillsbury*; sta, station.

#### *Nancyplax*, new genus

*Diagnosis*.—Carapace roughly hexagonal in adults, distinctly broader than long; dorsal surface convex, with depression on each side of juncture between gastric and cardiac regions. Branchial region with rounded, low mesial protuberance and prominent, granular metabranchial tubercle. Exorbital angle indistinct, consisting of a low, rounded lobe; anterolateral teeth absent except for epibranchial tooth. Epibranchial (lateral) spine pronounced, sharp. Front straight, gently deflexed, double-margined. Orbits oblique; medial angle of infraorbital margin with well-developed occlusive lobe. Antennules folding transversely. Suture separating subhepatic and pterygostomial regions flanked on pterygostomial region by longitudinal ridge with row of small tubercles. Stridulating mechanism present, well developed.

Lateral margins of buccal frame strongly divergent anteriorly. No endostomial ridges present. Posterior margin of epistome with deep medial notch and 2 incisions on either

side extending to anterior margin. Intercalary apophysis between basal antennal article and pterygostomial border well developed and subrectangular in outline. Third maxillipeds not completely covering buccal frame; merus with mesial margin convex, distolateral angle forming rounded lobe, distal margin concave.

Thoracic sternum width between lateral margins of fifth episternites about 1.30 times greater than total length. Sternite 1 separated from sternite 2 by indistinct sulcus. Anterior border of sternite 3 much wider than posterior margin of sternite 2. Sternites 3 and 4 demarcated by shallow remnants of sulcus confined to lateral regions. Sulci separating sternites 4 and 5, 5 and 6, and 6 and 7, interrupted medially. Sulcus delimiting sternites 7 and 8 complete. Median septum of endosternite 8 externally visible as median, longitudinal sulcus. Press-button knobs on fifth sternite distinct, adjacent to sternite 4. Episternites 4 through 7 developed and broadly lobate posteriorly. Sternoabdominal cavity deep, triangular in outline. Episternite 7 covering small portion of male seminal duct aperture on coxa of pereopod 5 and part of short seminal groove on sternite 8.

Abdomen in both sexes with second segment leaving small portion of episternite 8 visible. Male abdomen triangular in overall outline, with 6 free articulating segments and telson; third segment overlapping part of coxae of fifth pereopods and completely covering gonopores located at base of coxae; telson triangular, with distal margin rounded.

Male with pleopod 1 sinuous, much broader at base than at apex, tapering to very slender tip, spinose; euryplacine in organization (cf. Guinot 1969b). Pleopod 2 short; apical lobe reduced and separated from subterminal segment by incomplete fissure.

*Type species.*—*Nancyplax vossi*, new species, by present designation.

*Gender.*—Feminine.

*Etymology.*—The name of the genus is in

honor of Mrs. Nancy Voss, Research Professor at the Rosenstiel School of Marine and Atmospheric Science, University of Miami. The genus name is formed by combining her first name with the Greek suffix *plax*, meaning flat (although morphologically inappropriate here for the only species in the genus) and commonly used in naming genera of the Goneplacidae. Mrs. N. Voss has for many years vigorously promoted the study of the invaluable tropical deep-sea collections housed in her institution.

*Remarks.*—*Nancyplax*, new genus, can be placed in the Euryplacinae with relative confidence. This placement is based first on the structure of male pleopods 1 and 2. Unlike the pleopods 1 seen in the Carcinoplacinae and Goneplacinae, euryplacine pleopods 1 are somewhat broad at the base, almost uniformly tapering to a very slender apex with patches of distinct spines on the surface (Guinot 1969b). This particular pleopod 1 morphology is probably a defining characteristic of the Euryplacinae. In contrast, pleopods 1 of carcinoplacines and goneplacines are considerably stouter along the distal half of the terminal segment, and the apex may or may not possess one or more distal lobes (Guinot 1969b, 1989, 1990). Second, pleopod 2 is short in *Nancyplax* with a rudimentary apical lobe as it is in all other euryplacine taxa (Guinot 1969b); carcinoplacines and goneplacines both have long second pleopods with well defined flagella, and a specific apical conformation (Guinot 1969b, 1989, 1990). Third, *Nancyplax* exhibits a male abdomen outline and sternoabdominal cavity organization that is very close to those seen in euryplacines such as species of *Trizocarcinus* Rathbun, 1914, e.g., *T. dentatus* (Rathbun, 1893). These characters permit *Nancyplax* to be excluded from either the Carcinoplacinae or Goneplacinae.

The carapace in the single species of *Nancyplax* is nevertheless unlike that of any other euryplacine. In terms of overall shape the carapace strongly resembles those seen

in some species of *Psopheticus* and *Carcinoplax*, especially *C. longispinosa* Chen, 1984. However, *Psopheticus* species have in common with *Nancyplax vossi* the presence of a stridulatory organ (Guinot-Dumortier & Dumortier 1960, Guinot 1990), whereas this organ is absent from members of *Carcinoplax*. Within the Euryplacinae, *Trizocarcinus dentatus* also has a well developed stridulatory organ, and the pterygostomial ridges are identical in form to those of the single species of *Nancyplax*, although the two species have different carapace outlines. Species of the goneplacine *Ommatocarcinus* White, 1852 and the carcinoplacine *Bathyplax* A. Milne-Edwards, 1880, likewise possess a *Nancyplax*-like stridulatory organ, but here again carapace morphology is not equivalent among the three genera. Given the patchy taxonomic distribution of the stridulatory organ in goneplacids, and the disparate carapace shapes observed in some genera such as *Carcinoplax* (see Guinot 1989), it would appear that characters from the carapace cannot be used to argue against placing *Nancyplax* in the Euryplacinae.

The morphology of *Nancyplax* exemplifies many of the problems inherent in goneplacid systematics. To partially reiterate, this new genus can be said to have a mosaic habitus. The male pleopods, male abdomen outline, and sternoabdominal cavity conformation are euryplacine. The shapes of the male telson and third maxilliped merus are very close to those in *Trizocarcinus dentatus*. *Nancyplax* has the same type of stridulatory organ as seen in *T. dentatus* and some carcinoplacines. *Nancyplax* and *Carcinoplax longispinosa* have almost equivalent carapace anatomies except for the stridulatory ridges. The lack of defined grooves on episternite 8 for the seminal ducts suggests that *Nancyplax* is not as derived as many other carcinoplacines, euryplacines, and goneplacines (Guinot 1969b). For these reasons, it is unclear whether *Nancyplax* is a basal euryplacine or alternatively, a highly modified taxon.

*Nancyplax vossi*, new species

Figs. 1–5

*Material examined*.—Holotype: ♂ 10.7 × 15.7 mm, off Venezuela, sta P-752, 11°06.3'N, 68°14.6'W, 95–132 m, 26 July 1968, USNM 308995.

Paratypes: 1 ♂ 13.9 × 20.2 mm, USNM 308996; 2 ovig ♀ 8.6 × 12.7 mm, 10.6 × 15.2 mm, UMML 32.8776; off Venezuela, sta P-752, 11°06.3'N, 68°14.6'W, 95–132 m, 26 Jul 1968.—2 ♂ 4.5 × 5.8 mm, 14.3 × 20.1 mm, USNM 308993; 1 ♂ 13.0 × 19.4 mm, INVEMAR-CRU 2926; SW Isla Rosario, Islas del Rosario, Colombia, "Expedición CIOH-INVEMAR-Smithsonian", sta T18, 10°11.97'N, 75°53.41'W, 150–155 m, 7 Aug 1995.—2 ♂ 7.9 × 11.7 mm, 9.2 × 13.4 mm, off SE coast of Trinidad, sta P-837, 10°09.8'N, 60°34.3'W, 55 m, 30 Jun 1969, UMML 32.9079.—4 ♂ 6.0 × 7.6 mm, 7.5 × 10.4 mm, 7.8 × 10.7 mm, 8.5 × 12.1 mm, 1 ♀ 6.0 × 8.0 mm, off SE coast of Trinidad, sta P-836, 9°56.5'N, 60°46'W, 57–59 m, 30 Jun 1969, UMML 32.9078.—1 ♂ 12.1 × 17.2 mm, 1 ♀ 11.9 × 17.5 mm, USNM 308994; 1 ♂ 11.0 × 15.7 mm, 2 ♀ 10.7 × 16.0 mm, 11.3 × 16.0 mm, UMML 32.8775; off Surinam, sta P-671, 7°07'N, 55°08'W, 64 m, 11 Jul 1968.

*Diagnosis*.—Carapace about 0.65 to 0.75 as long as broad, smooth, glabrous; regions weakly demarcated. Front straight, at most about 0.40 as long as CW; frontal lobes divided by weak median cleft. Anterolateral margins with strong epibranchial (lateral) spine. Pterygostomial region with well developed stridulating ridge. Male chelae glabrous; female chelae with dense fringe of setae on dorsal and ventral margins. Dactyls of pereopods 2–5 each with 3 longitudinal fringes of setae dorsally and 1 fringe ventrally. Male pleopod 1 very slender distally, with medial shoulder densely spinose, and minute well-spaced spines on distal third.

*Description*.—Carapace (Figs. 1, 3a) subhexagonal, about 0.65 to 0.75 as long as broad; dorsal surface convex, superficially smooth and glabrous, microscopically with



Fig. 1. *Nancyplax vossi*, new species, paratype male 14.3 × 20.1 mm, SW of Isla Rosario, Islas del Rosario, Colombia, sta T18, USNM 308993: dorsal view.

numerous punctae medially on gastric, cardiac and intestinal regions, and numerous minute granules on hepatic and branchial regions. Regions indistinctly demarcated; gastric and hepatic regions evenly convex; with distinct depression on each side of juncture between gastric and cardiac regions; branchial regions each with low, rounded protuberance medially, and distinct, granular metabranchial tubercle. Front (Figs. 2a, 3b) straight, about 0.30 (adults) to 0.40 (young) times as long as CW; separated on each side from preorbital lobe by small notch; with double margin consisting of lower and upper, pseudofrontal margins, lower margin extending slightly beyond pseudofrontal; pseudofrontal margins divided into lobes by weak medial cleft (weaker

on lower margin); lateral, inferior lobe produced and extending ventrally to third antennal segment near articulation between the second and third segments. Anterolateral margins broadly rounded, lacking any indication of teeth or spines except for prominent, strong epibranchial (lateral) corneous-tipped spine directed slightly forward in dorsal view and slightly upward in frontal view (Figs. 1, 2a). Epibranchial (lateral) spine in adults nearly as long as orbital length. Posterolateral and posterior margins broadly rounded. Subhepatic region minutely granulose. Pterygostomian region (Fig. 2a) smooth, with well developed, raised stridulating ridge (pars stridens) with numerous transverse striae bordering suture between pterygostomian and subhepatic re-

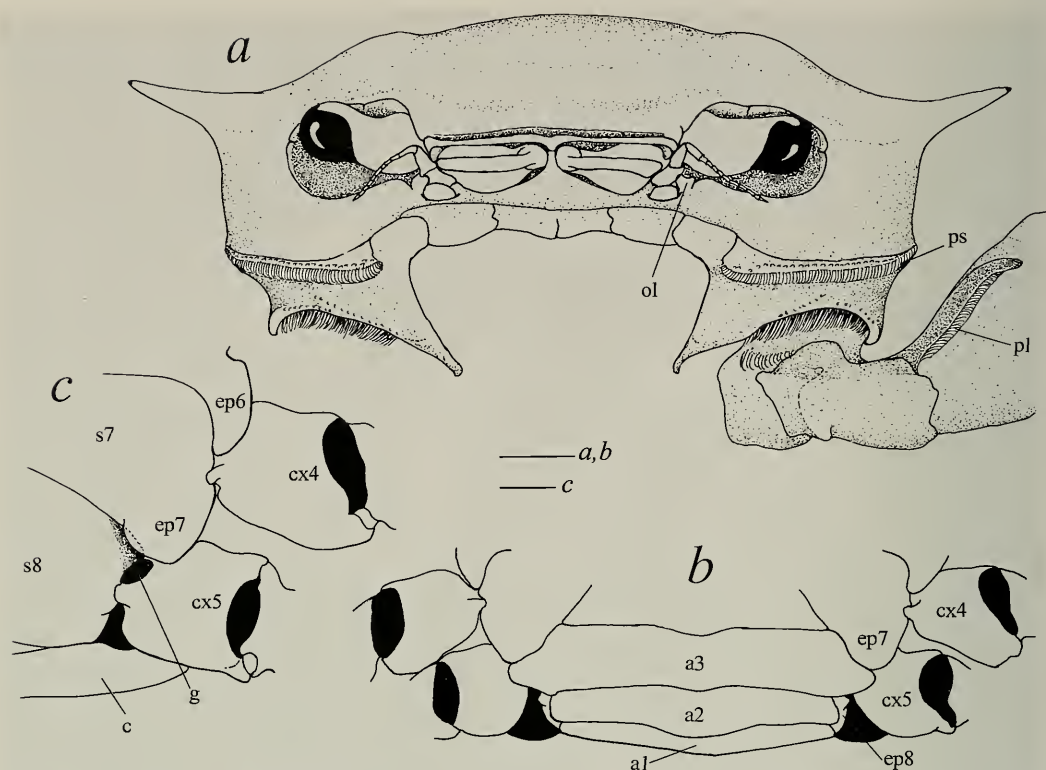


Fig. 2. *Nancylplx vossi*, new species, a, c, male 13.9 × 20.2 mm, sta P-752, off Venezuela, USNM 308996; b, male 14.3 × 20.1 mm, SW of Isla Rosario, Islas del Rosario, Colombia, sta T18, USNM 308993. a, carapace and cephalic appendages, including basal segments and part of merus of left cheliped, frontal view; b, abdominal segments 1 to 3, coxae 4 and 5, and episternite 7, and visible part of episternite 8, ventral view; c, sternites 7 and 8, episternites 6 and 7, coxae 4 and 5, left side (abdomen removed), ventral view. Abbreviations: a1-3, abdominal segments 1-3; c, posterior margin of carapace; cx4,5, coxae of pereopods 4 and 5; ep6-8, episternites 6 to 8; g, gonopore; ol, occlusive lobe; pl, plectrum; ps, par striated; s7,8, sternites 7 and 8. Solid black indicates membranes. Scales equals 2 mm (a, b), and 1 mm (c).

gions. Ventral, pterygostomial border of carapace flanking coxae of pereopods 1 concave, lined with setae on inner margin.

Orbits (Figs. 2a, 3a, b), about 0.50 (adults) to 0.60 (young) as long as front, margins minutely granulate, with small, blunt pre and postorbital lobes; supraorbital margin with 2 short sutures and fringe of well-spaced setae; infraorbital margin exposed in dorsal view, with short suture just below postorbital lobe and subrectangular occlusive lobe. Eyestalks short, completely fitting in orbits when retracted; cornea slightly dilated; peduncles sparsely setose.

Antennules folding transversely into deep fossae, segments similar in length;

basal segment considerably inflated and occupying nearly entire antennular fossae, penultimate and ultimate segments slender. Antennae with first segment immovable, short, semicircular and enclosing urinary opening; second to fourth segments movable, longer than broad; flagellum overreaching antennules when fully extended.

Third maxillipeds (Fig. 3c) with bases separated by triangular tip of thoracic sternum. Ischium longer than broad; outer surface with median longitudinal furrow; mesial margin with row of teeth and fringe of setae. Merus about as long as broad; distolateral angle produced into lobe with minutely granular outer surface and marginal

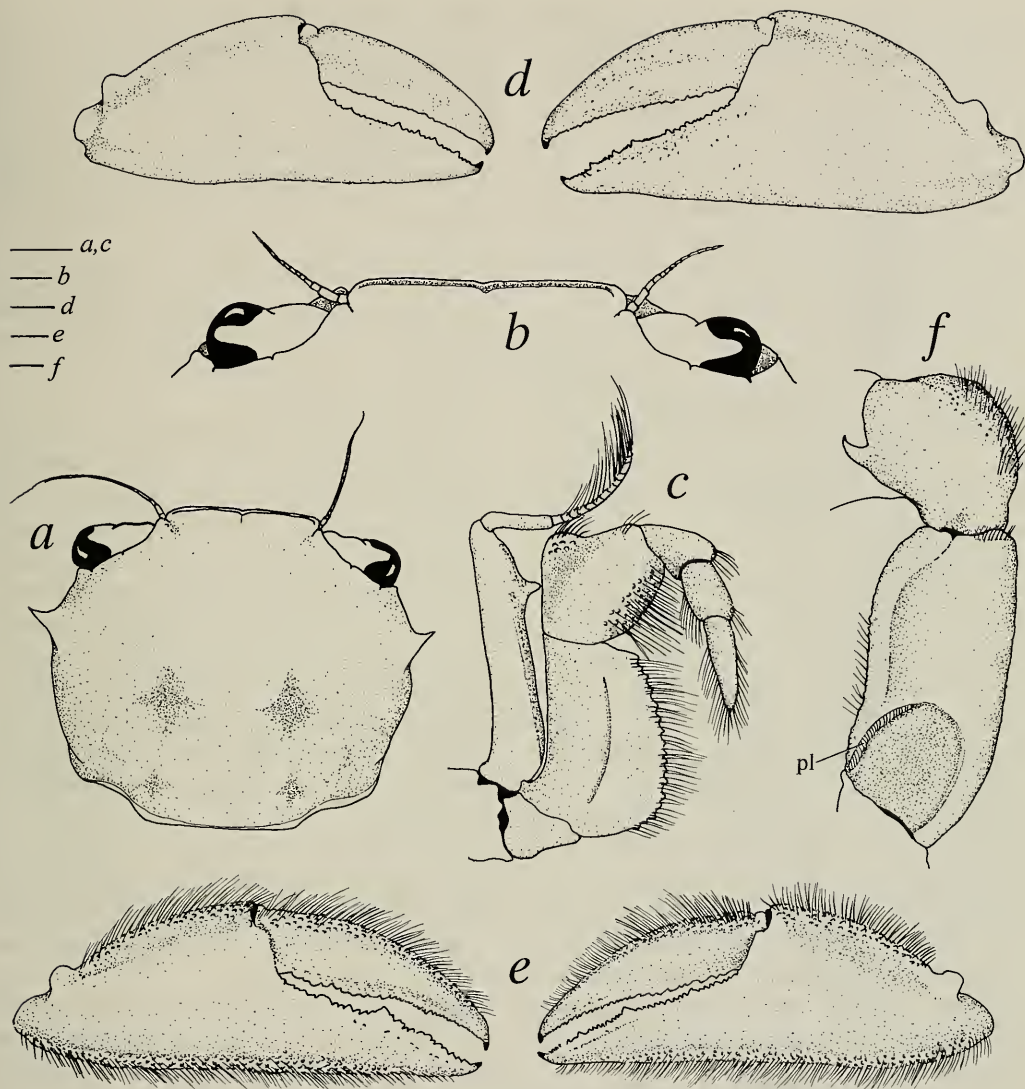


Fig. 3. *Nancyplax vossi*, new species. a, young male 4.5 × 5.8 mm. SW of Isla Rosario, Islas del Rosario, Colombia, sta T18, USNM 308993; b, d, f, male 13.9 × 20.2 mm, sta P-752, off Venezuela, USNM 308996; c, male 14.3 × 20.1 mm, sta T18, USNM 308993; e, female 9.5 × 13.4 mm, sta T18, USNM 308993. a, carapace, eyes and antennae, dorsal view; b, frontal region, eyes and antennae, dorsal view; c, third right maxilliped, outer view; d, left and right chelae male, outer view; e, left and right chelae of female, outer view; f, merus and carpus of right cheliped, dorsal view. Abbreviation: pl, plectrum. Scales equal 1 mm (a–c, e, f), and 2 mm (d).

setae; outer mesial surface minutely granular, setose. Palp about as long as ischium, marginally setose. Exopod with basal segment reaching to tip of distolateral angle of merus; mesial surface minutely granular.

Chelipeds sexually dimorphic. Male chelae (Fig. 3d) slightly unequal in size right

from left, mostly glabrous. Dactyl about as long as palm. Fingers not leaving gap when closed, each terminating in inwardly curved corneous claw; outer surface minutely punctate; cutting edges consisting of row of small sharp or blunt calcareous teeth interspersed with larger calcareous teeth. Palm

glabrous; dorsal margin broadly curved, ventral margin nearly straight. Carpus (Fig. 3f) with outer surface sparsely granulose, setose; inner margin armed proximally with strong spine curving inward distally and terminating in corneous tip. Merus (Fig. 3f) granulose except on dorsal face and plectrum; with sparse row of setae on dorsomesial margin; inner, proximal margin with stridulating ridge (pectrum).

Female chelipeds subequal, differing from those of male as follows: chelae (Fig. 3e) densely setose on dorsal and ventral margins; dactyl about 1.40 times as long as palm; fixed fingers and palm with dorsal and ventral surfaces granulose; carpus with outer face densely setose.

Pereopods 2–5 (Fig. 4) slender; segments with lateral and mesial faces glabrous. Pereopods 2–4 subequal in length, about 1.60 times as long as CW; with granules on ventral surfaces of meri. Pereopod 5 shortest, about 1.30 times as long as CW, lacking granules on ventral surface of merus. Dactyl slightly longer than propodus, terminating in short corneous claw; with 3 dense fringes of setae dorsally, and 1 fringe ventrally. Propodus with dense fringe of setae dorsally and ventrally. Carpi of pereopods 2–4 each with granules and dense fringe of setae on dorsal surface; carpus of pereopod 5 lacking granules, with fringe of setae dorsally. Meri with sparse fringe of setae dorsally.

Thoracic sternum (Fig. 5a) and abdomen with surfaces punctate. Male abdomen (Fig. 2b, 5b) with short setae marginally on segments 1–6 and telson. First segment short, narrow. Second segment twice as long as first. First and second segments not reaching coxae of pereopods 5. Third segment broadest, overlapping part of coxae of fifth pereopods. Fourth and fifth segments subequal in length. Sixth segment subequal to telson in length. Telson bluntly triangular.

Male pleopod 1 (Fig. 5c, d) reaching beyond suture separating sternites 4 and 5 when in situ; medial shoulder with dense cluster of spines on ventrolateral face,

spines diminishing in number, size and sharpness distally; distal third with minute, broad-based and often blunt spines. Pleopod 2 (Fig. 5e, f) slightly curved inwardly, terminating in subtriangular tip with about 3 short stiff setae basally on inner angle. Gonopores (Fig. 2c) located proximally on coxae.

Female abdomen with first and second segments as in male, leaving small portion of sternite 8 visible on each side. Gonopores large, transversely ovate.

*Color*.—Unknown.

*Etymology*.—This species is named in recognition of Mrs. Nancy Voss' late husband, Dr. Gilbert L. Voss, RSMAS, who was Chief Scientist on many of the cruises of the *R/V Pillsbury*. He was also instrumental in making possible the most intense and successful deep-sea sampling program ever conducted in the tropical Atlantic Ocean. The immense number of specimens obtained during that program continue to be studied, and have considerably enriched our knowledge of the fauna from this region of the world.

*Distribution*.—Caribbean Sea, off Colombia and Venezuela; Lesser Antilles, off southeast coast of Trinidad; and northeastern coast of South America, off Surinam. Depth: 55 to 155 m.

*Similarities*.—Given the morphological complexities and frequent overlap of characters among goneplacid taxa, it is useful to point out similarities observed between *Nancyplax vossi*, new species, and species of other genera in the family. The carapace of *N. vossi* superficially resembles those of *Carcinoplax* species, notably *C. barnardi* Capart, 1951 and *C. longispinosa* Chen, 1984. Also, the dense setation of the carpus-propodus-dactyl of *N. vossi* (Fig. 4) is similar to that seen in *C. angusta* Rathbun, 1914 (cf. Guinot 1989: 310, fig. 39B). However, *N. vossi* differs from all *Carcinoplax* species in that the latter lack a stridulatory organ. In addition, the morphology of the male pleopods 1 and 2 is quite different in *N. vossi* and *Carcinoplax* species.



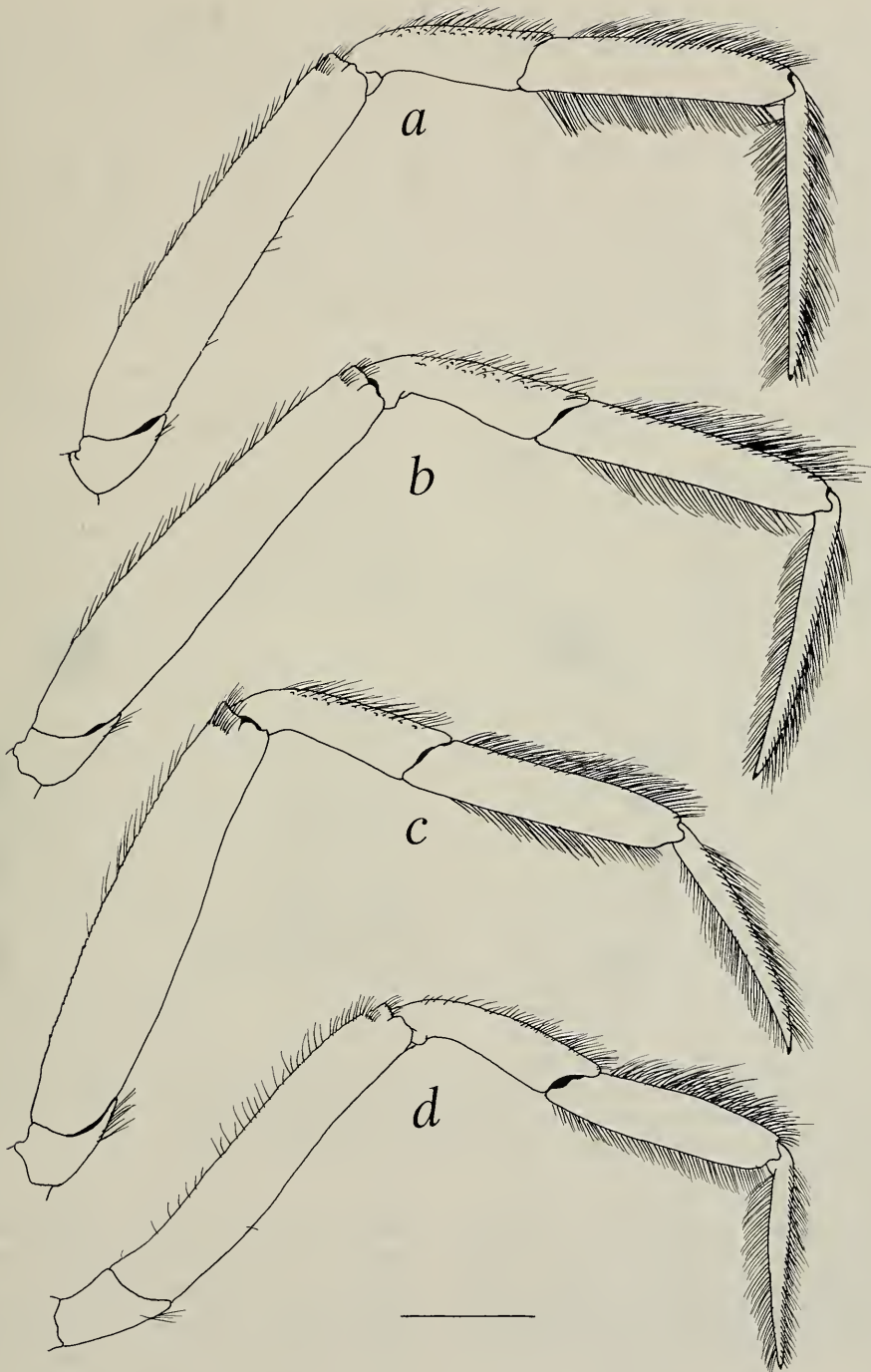


Fig. 4. *Nancyplax vossi*, new species, male 13.9 × 20.2 mm, sta P-752, off Venezuela, USNM 308996. a–d, second to fifth right pereopods, lateral view: a, second; b, third; c, fourth; d, fifth. Scale equals 3 mm.

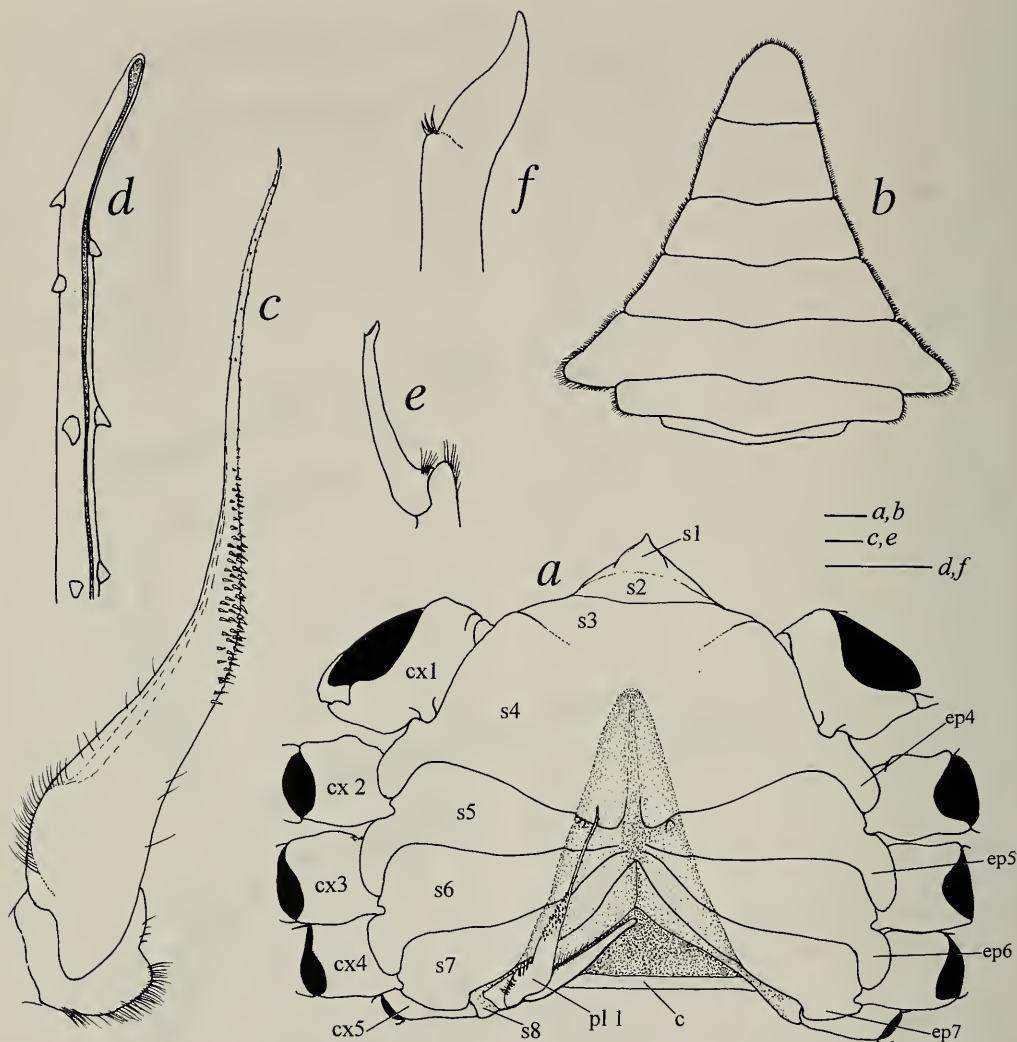


Fig. 5. *Nancyplax vossi*, new species, male 13.9 × 20.2 mm, sta P-752, off Venezuela, USNM 308996. a, coxae, sternum with abdomen removed leaving right first pleopod. Abbreviations: c, posterior margin of carapace; cx1-5, coxae of pereopods 1-5; ep4-7, episternites 4 to 7; pl 1, pleopod 1; s1-8, sternites 1-8. Solid black indicates membranes. Scales equal 1 mm (a, b), 0.25 mm (c, e), and 0.1 mm (d, f).

In the new species, pleopod 1 is very slender distally, and pleopod 2 is short and stubby (Fig. 5c-f), whereas in *Carcinoplax* species pleopod 1 is quite thick distally, and pleopod 2 is long and thin (cf. Guinot 1989).

*Psopheticus* species have a stridulatory organ very similar to that of *N. vossi*, but otherwise differ markedly. The carapace of *N. vossi* has a long lateral spine (Fig. 1, 2a), whereas in *Psopheticus* species the lateral

spine is short (cf. Guinot 1990). Pereopods 2 to 5 in *N. vossi* have the meri unarmed, and the carpi-propodi-dactyls are densely setose (Fig. 4), whereas these pereopods are armed with spines and lack dense setation in *Psopheticus* species (cf. Guinot 1990). In addition, male pleopods 1 and 2 in *N. vossi* and *Psopheticus* species differ significantly in morphology.

The male pleopods 1 and 2, abdomen, and sternoabdominal structure of *Nancy-*

*plax vossi* (Fig. 5c–f) are very similar to those of *Trizocarcinus dentatus* (Rathbun, 1893) and *T. tacitus* Chace, 1940 (cf. Guinot 1969b: 516, figs. 48–51). Male pleopods 1 and 2 of *N. vossi* also resemble those of *Psopheticoides sanguineus* Sakai, 1969, the only representative of the genus *Psopheticoides* Sakai, 1969. However, *N. vossi* differs substantially from these species in carapace shape, and armature and proportions of pereopods.

A variety of stridulatory organs have been described in the Brachyura (Guinot, Dumortier & Dumortier 1960, 1961; Guinot 1990). The stridulating organ in *Nancyplax vossi* appears to be of the simple kind (cf. Guinot 1990) in which the striate plectrum on the merus of the cheliped is rubbed against the striate pars stridens on the pterigostomial region.

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## The systematic position of the genus *Basityto* Mlikovsky, 1998 (Aves: Gruiformes: Gruidae)

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*Abstract.*—The genus *Basityto* Mlikovsky, 1998 was described as a giant Barn Owl and placed in the subfamily Tytoninae, family Strigidae. However its morphological characteristics correspond to a crane and it is here transferred to the recent genus *Balearica*, family Gruidae. Other fossil Balearicinae have been placed in the genus *Probalearica* Lambrecht, 1933, type-species *Probalearica problematica* (Milne-Edwards, 1869). The lectotype of this species, here designated, is a partial rostrum which is now known as belonging to *Palaelodus ambiguus* (Phoenicopteriformes: Palaelodidae). The genus *Probalearica* Lambrecht, 1933 is a junior synonym of *Palaelodus* Milne-Edwards, 1863, and the species *Probalearica problematica* a junior synonym of *Palaelodus ambiguus* Milne-Edwards, 1869. The systematic position of the other elements attributed to *Probalearica problematica*, and of the other species attributed to the genus *Probalearica*, needs to be revised. *Balearica rummeli*, from the Early Miocene of Germany, is so far the oldest known occurrence of the recent genus *Balearica*.

In 1998 Mlikovsky described a new genus and a new species of Barn Owl, *Basityto rummeli*, in the subfamily Tytoninae which he places in the family Strigidae, contrary to the most widespread opinion (Sibley & Ahlquist 1990). The new species was founded on an uncatalogued left humerus in the private collection of Michael Rummel, from the Grafenmühle 21 locality, in Bavaria, Germany, the age of which is Early Miocene, Agenian or Orleanian, mammal biozone MN 2 or MN 3 (Mein 1990). I personally examined this holotype, which is now catalogued as n° 3/21-0001 in Rummel's collection. A cast of the specimen is deposited in the collection of the Université Claude Bernard - Lyon 1, with the number FSL 330816. This humerus does not belong to a member of the Tytonidae but is very similar to that of the recent genus *Balearica*, in the Gruidae. Anatomical terminology follows Baumel & Witmer (1993) and, when necessary, Howard

(1929). Institutional abbreviations: MNHN Paris, Muséum national d'Histoire naturelle de Paris; MHN Lyon, Muséum d'Histoire naturelle de Lyon; UCB Lyon, Université Claude Bernard - Lyon 1.

Order Gruiformes

Family Gruidae

Genus *Balearica* Brisson, 1760

*Balearica rummeli* (Mlikovsky, 1998),  
new combination

Figs. 1-3

*Condition of the holotype.*—The proximal part of the humerus of *Basityto* has been imperfectly restored with plaster on the caudal face, so that this part is much more proximally straightened than it would normally be, although on the cranial face, there is a proper contact between the two pieces bone. If in the photograph the part corresponding to the plaster were removed, the true appearance would not be restored

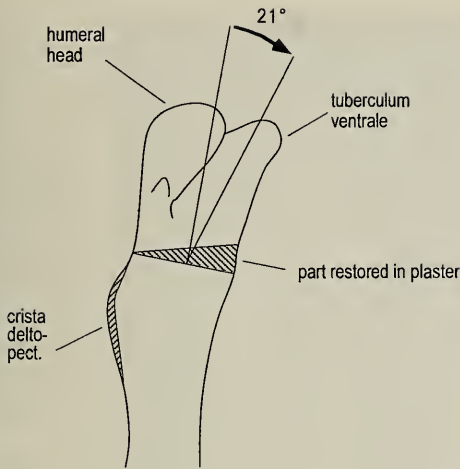


Fig. 1. *Balearica rummeli*, diagram of the humerus, in dorsal view, showing that the plaster on the caudal face has given the bone a more straightened aspect.

because it would still be necessary to rotate the proximal part about  $21^\circ$  caudally (Fig. 1), which would give a rather different aspect. The tuberculum ventrale then seems much less proximally elevated in relation to the humeral head, and the head forms a slight ledge above the incisura capituli and the surface of the caudal face. Because of this artificially straightened aspect, the humerus of *Basityto* does not seem completely similar to that in the Gruidae but looks a little like that of *Xenerodiops mycter* (Rasmussen et al. 1987).

**Comparison with Tytonidae and Gruidae, subfamily Balearicinae.**—The genus *Balearica* (crowned cranes) shows osteological characteristics that are different from those of the other genera of the family Gruidae, which confirms its allocation to a distinct subfamily (Peters 1963, Feduccia & Voorhies 1992). Archibald & Meine (1996) consider that the genus comprises two species, *Balearica pavonina* (Linnaeus, 1758) and *Balearica regulorum* (Bennett, 1834) although the latter is sometimes considered a subspecies of *B. pavonina*. These two taxa have practically the same osteological dimensions (Feduccia & Voorhies 1992). Comparison of the humerus of *Basityto* with that of Tytonidae and Balearicinae

shows that it is not a barn owl but a crowned crane.

On the caudal face of the proximal part, in *Basityto*, as in *Balearica*, the caput humeri is globular and proximally raised, while in the Tytonidae it is transversely (i.e., dorso-ventrally) elongated. In *Basityto*, as in *Balearica*, the incisura capituli is wide and almost oriented along the longitudinal axis of the bone, while in the Tytonidae it is narrower and obliquely oriented. In the Gruidae (Gruinae and *Balearica*) there is a smooth ridge that crosses the incisura capituli, from the middle of the caput humeri to the crus dorsale of the pneumatic fossa. This smooth ridge is more globular in the Gruinae and more elongate in the Balearicinae. This ridge is also present in *Basityto*, while it is absent in the Tytonidae. The tuberculum dorsale is very conspicuously projecting in *Balearica* and it is an important characteristic differentiating the Balearicinae from the Gruinae. It is also strongly projecting in *Basityto*, while it is only slightly projecting in the Tytonidae. On the cranial face, in the Tytonidae, there is a depression situated between the intumescencia humeri and the delto-pectoral crest that is proximo-distally elongated. The intumescencia is bordered on its dorsal side by a distinct ledge (see Mourer-Chauviré 1987, fig. 1). This depression is absent in *Balearica* and in *Basityto*. In *Balearica* the intumescencia humeri shows a bulge distally, on the ventral side but, this part of the bone is missing in *Basityto* (Figs. 2, 3).

On the caudal face of the proximal part of the shaft, *Basityto* shows a very elongate impression of *M. latissimus dorsi* in the sagittal plane of the bone. This impression begins proximally with a tubercle and then becomes a thin, elongate impression, that is continued distally by a shallow groove. Both the tubercle and the muscular impression exist in *Balearica* and in *Basityto* whereas in the Tytonidae the impression of *M. latissimus dorsi* has a completely different shape and is situated on the dorsal side of the shaft. The shallow groove is not al-

ways very pronounced in *Balearica*, and it also exists in the Gruinae (e.g., *Grus* and *Anthropoides*).

The distal extremity in the Tytonidae is strongly ventrally elongated, whereas it is proportionally less elongated in *Basityto* and in *Balearica*. On the cranial surface, the condylus ventralis is globular in *Basityto* and in *Balearica*, but more elongate in the Tytonidae. The ectepicondylar prominence is situated more proximally in *Basityto* and in *Balearica* than in the Tytonidae. The incisura intercondylaris is deeper in *Basityto* and in *Balearica* than in the Tytonidae. In *Basityto*, as in the Gruidae, there is a muscular attachment, situated on the cranial face of the epicondylus ventralis, distally to the attachment of the anterior articular ligament. This muscular attachment has the shape of a small, deep circular depression. In the Tytonidae this muscular attachment is situated more ventrally, on the ventral face of the epicondylus ventralis (Fig. 3). On the caudal surface, in *Basityto* as in the Gruidae, the fossa olecrani is almost invisible and there are two well marked grooves (internal and external tricipital grooves of Howard 1929), while in the Tytonidae the fossa olecrani is well delimited and there is only one visible sulcus, on the ventral side.

*Comparison with recent Gruidae.*—Feduccia & Voorhies (1992) have indicated that the humerus of *Balearica* differs from that of Gruinae by the following characteristics: humerus with pneumatic fossa less excavated and with pneumatic foramen smaller; crista delto-pectoralis not extended down shaft as in Gruinae and intumescencia humeri relatively less extensive. It can be added that the tuberculum dorsale is much more proximally projecting, and that the distal end is more ventrally elongated in *Balearica* than in Gruinae.

In *Basityto*, because of the break, it is not possible to see the exact shape of the pneumatic fossa, but it seems that it was shallow. The other characteristics of the Balearicinae are also found in *Basityto*. Compared to *Anthropoides virgo*, the humerus

of which is almost the same size, in *Balearica* the crista delto-pectoralis is proximo-distally shorter, less extended in the cranio-caudal direction, and is inserted more on the cranial surface, while in *A. virgo* it is inserted along the dorso-cranial angle of the shaft. In these characteristics, *B. rummeli* corresponds perfectly to *Balearica*. In *Balearica* the condylus dorsalis tapers at its proximal end, and sometimes shows a slight distalward curvature. This characteristic does not appear in *Basityto*, where the end of the condyle seems more rounded, but is slightly incomplete (Fig. 3).

According to these morphological characteristics, I propose that the genus *Basityto* be placed in synonymy with the genus *Balearica*. The species *Balearica rummeli* differs from the recent species *B. regulorum* and *B. pavonina* by its smaller size.

Measurements of the humerus (mm), after Mlikovsky 1998: estimated total length, 175; proximal width as preserved, 35; depth of head, 10.6; proximal depth from tuberculum ventrale to intumescencia humeri, 17.2; length from proximal part of caput humeri to distal end of crista delto-pectoralis, 52.5; width and depth of shaft at midpoint, 13.1 and 11.2; distal width, ca. 26.5; distal depth, 14.6; length from ectepicondylar prominence to the distal surface of condylus dorsalis, 13.0. In *B. pavonina* the humerus length varies from 189.2 to 228.9 mm ( $n = 10$ ), and in *B. regulorum* from 186.4 to 211.1 mm ( $n = 10$ ) (Feduccia & Voorhies 1992). The dimensions of *B. rummeli* are about 90% of the mean dimensions of the recent crowned cranes.

*Comparison with fossil Balearicinae.*—Genus *Probalearica* Lambrecht, 1933: The genus *Probalearica* was created by Lambrecht (1933) for the species *Grus problematica* Milne-Edwards, 1869, described from an incomplete os premaxillare (MNHN, Av 8728 from Saint-Gérard-le-Puy (Early Miocene, mammal zone MN 2a) and two sterna from Gannat (Late Oligocene, reference-level MP 30). Cracraft (1973) incorrectly considered the anterior





Fig. 2. Humeri in caudal view. a, *Baelearica rummeli* (Mlikovsky), left humerus, holotype, Michael Rummel collection, n° 3/21.0001. b, *Tyto alba*, recent, left humerus, Collection UCB, Lyon, n° 245-3. c, *Baelearica pavonina*, recent, right humerus, Collection UCB, Lyon, n° I-73. a and c, natural size, b 1.5 × natural size.



Fig. 3. Humeri in cranial view. a, *Balearica rummeli* (Mlikovsky), left humerus, holotype, Michael Rummel collection, n° 3/21.0001. b, *Tyto alba*, recent, left humerus, Collection UCB, Lyon, n° 245-3. c, *Balearica pavonina*, recent, right humerus, Collection UCB, Lyon, n° I-73. a and c, natural size, b 1.5 × natural size.

part of rostrum to be the holotype, whereas it is actually one of three syntypes. I therefore designate the partial rostrum as the lectotype.

Cheneval & Escuillié (1992) have demonstrated that this premaxillare does not belong in the Gruidae but is a part of the skull, previously unknown, of *Palaeolodus ambiguus*, in the Phoenicopteriformes. The genus *Probalearica* thus becomes a synonym of the genus *Palaeolodus* Milne-Edwards, 1863, and the species *Probalearica problematica* becomes a synonym of *Palaeolodus ambiguus* Milne-Edwards, 1863.

The sternum illustrated in Milne-Edwards, 1867–1871, pl. 76, fig. 4, was one of the other syntypes of the species "*Grus*" *problematica*, and is in the collection of the Paris MNHN, n° Av 8729, and needs re-study. The other syntypical sternum (Milne-Edwards, 1867–1871, pl. 76, fig. 3) is missing at the present time (Cheneval & Escuillié 1992). These two sterna were from birds the same size as the recent crowned cranes, whereas *Balearica rummeli* is slightly smaller.

Three other species were later placed in the genus *Probalearica*, *P. crataegensis*, *P. moldavica*, and *P. mongolica*. The generic allocation of these species must be revised.

"*Probalearica*" *crataegensis* Brodkorb, 1963: This species, from the early Miocene of Florida is represented only by the distal part of a tibiotarsus (Brodkorb 1963). In *Balearica* the tibiotarsus widens medially in the distalmost part of the bone, at the level of the medial condyle, while in the Gruinae, the widening is more progressive and begins more proximally. In the Gruidae, there is a strong tubercle at the distal part of the supratendinal bridge, on its lateral side, close to the distal opening of the canalis extensorius. In *Balearica*, on the cranial face, the lateral condyle is short and does not extend very far proximally, while in the Gruinae, it is longer and extends up to the level of this tubercle. In *Balearica* the sulcus extensorius is wide and occupies a large part of the cranial face of the distal end,

while in the Gruidae it is narrower and occupies only the medial part of the cranial face. In *Balearica*, the supratendinal bridge is wide medio-laterally and extends on the lateral side to the tuberositas retinaculi extensoris, while in the Gruinae it is much narrower in the medio-lateral direction. In distal view, in the Gruinae, the condylus medialis is more medially projecting than in the Balearicinae. In lateral view in the Gruinae, the distal outline of the lateral condyle forms an indentation that is much less pronounced in the Balearicinae.

The distal part of tibiotarsus of "*P.*" *crataegensis* differs from that of *Balearica* because it does not show a conspicuous widening at the level of the condylus medialis, the condylus medialis in distal view does not show pronounced projecting in the medial direction, and the indentation of the distal outline of the lateral condyle is absent. The species may be referable to the genus *Palaeogrus*.

*Aramornis longurio* Wetmore, 1926: The genus *Aramornis*, from the earliest middle Miocene of Nebraska, was described by Wetmore (1926) from the distal part of tarsometatarsus and placed in the family Aramidae. Olson (1985) has indicated that it is a *Balearica*-like crane and Becker (1987) has classified it in the subfamily Balearicinae. There is a large amount of new, unstudied crane material, from Oligocene and Miocene localities in North America which should make it possible to clarify the systematic position of "*P.*" *crataegensis* and *A. longurio* (Olson 1985, and pers. comm.). The size of *A. longurio* is 67% of the mean size of the recent *Balearica*, and "*P.*" *crataegensis* is 76%. These two species are thus smaller than *B. rummeli*, the humerus of which is 90% smaller than the mean size of the recent forms.

"*Probalearica*" *moldavica* Kurochkin & Ganya, 1972: This species, from the Sarmatian of Moldavia, was described from an incomplete distal portion of tibiotarsus. Its age corresponds to the beginning of the late Miocene, MN 9 ? (Mlikovsky 1996). This

specimen does not show much resemblance to the Gruidae. The condylus medialis is only slightly displaced medially. On the cranial face, the condylus lateralis is very proximo-distally elongated. The presence of a tubercle on the supratendinal bridge is not mentioned in the description. The distal width is inferior to the distal depth, which is not the case in the recent Gruidae. Its size is similar to that of the recent *Balearica*, so it is larger than *B. rummeli*.

"*Probalearica*" *mongolica* Kurochkin, 1985: This species, from the middle Pliocene of Mongolia, was described from the distal part of tibiotarsus, an incomplete distal portion of tarsometatarsus, and a quadrate. The tibiotarsus actually shows similarities with the genus *Balearica*. On the tarsometatarsus, the three trochleae are broken, but it can be seen that trochlea metatarsi II is more elongate distally, compared to trochlea metatarsi III, than in the Gruinae, and this characteristic corresponds to the Balearicinae. Its size is large, comparable to that of the Common Crane, *Grus grus*, and thus is larger than *B. rummeli*.

*Balearica exigua* Feduccia & Voorhies, 1992: This species, known from most of the skeleton, was described from the early late Miocene of Nebraska. It is characterized by its small size, which is about 75 to 80% of that of the recent *Balearica*, and thus it is smaller than *B. rummeli*. The humerus differs strongly from that of *B. rummeli* by its very robust shaft, by the very strong proximal projection of the tuberculum dorsale, and by the fact that the distal part shows almost no ventral widening.

*Comparison with Palaeogrus excelsa* (Milne-Edwards, 1869).—This species is known from the Early Miocene of the Saint-Gérard-le-Puy area, MN 2a (Milne-Edwards 1867–1871), and is also present in the middle Miocene of Sansan, MN 6 (Cheneval 2000). It is only mentioned here as a matter of interest because it shows a mosaic of the morphological characteristics of the Balearicinae and the Gruinae. There is a large amount of new, unstudied material in

the collections of MNHN Paris, MNH Lyon, and UCB Lyon. The proximal part of the humerus, which has not yet been described or illustrated, has the morphological characteristics of the Gruinae and differs from the Balearicinae. Its size is large, comparable or even slightly superior to that of the recent Common Crane, and thus is larger than *B. rummeli*.

*Conclusions.*—*Balearica rummeli*, the Crowned Crane of Grafenmühle, Bavaria, is as yet the oldest known occurrence of the recent genus *Balearica*, but there is a large amount of new, unstudied material, in Europe as well as in North America, that may provide an earlier appearance. The Balearicinae were widespread in the whole Northern Hemisphere and lived there at least until the middle Pliocene of Mongolia, while at the present time they only survive in tropical Africa, south of the Sahara.

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**A new species of tufted-tailed rat, genus *Eliurus* (Muridae: Nesomyinae), from western Madagascar, with notes on the distribution of *E. myoxinus***

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*Abstract.*—A new species of *Eliurus*, *E. antsingy* (Muridae: Nesomyinae), is described from western Madagascar, only the second one of the genus so far known from this vast and biologically underexplored region of the island. The distribution of *E. myoxinus*, the other species known from western Madagascar, is also amplified on the basis of new collections that have been made over the past decade as interest in small mammals of this region is rekindling.

*Résumé.*—Une nouvelle espèce d'*Eliurus*, *E. antsingy* (Muridae: Nesomyinae), est décrite pour la région Ouest de Madagascar. Ce n'est que la deuxième espèce du genre connu pour cette vaste région encore biologiquement sous-explorée de Madagascar. La distribution de *E. myoxinus*, l'autre espèce connue pour l'ouest de Madagascar, est aussi étendue grâce aux nouvelles collectes qui ont été faites au cours de la dernière décennie car l'intérêt porté aux petits mammifères est rallumé.

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Among Madagascar's nine endemic rodent genera, *Eliurus*, the so-called tufted-tailed rats, is the most speciose with nine currently recognized species (Carleton 1994, Carleton & Goodman 1998). Eight of these nine species inhabit portions of the great humid forest biome (sensu Humbert 1955) of eastern Madagascar, occurring within both lowland and montane rainforest associations (for example, Carleton 1994, Goodman & Carleton 1996, 1998; Goodman et al. 1999). Only one, *E. myoxinus*, the type species of the genus, is known to occupy Madagascar's dryer western and southern landscapes, such as dry deciduous forest and xerophilous scrub formations (Carleton 1994, Goodman et al. 1999). Although some of the disparity in species richness between east and west probably reflects actually lower biodiversity, some may

be plausibly attributed to the historical insufficiency of biological survey of small mammals in Madagascar's drier environments (see Carleton & Schmidt 1990). For example, recent research and collecting in western forests have uncovered four new species of *Microcebus* or mouse-lemurs and resurrected two others from synonymy (Zimmerman et al. 1998, Rasoloarison et al. 2000). This revision and discovery bring to seven the number of *Microcebus* species now recognized from a region that was only a few years ago thought to hold one.

In this paper, we describe a second species of *Eliurus* from western Madagascar. In addition, we report new localities that significantly amplify the known geographic distribution of *E. myoxinus* and provide western records of two forms apparently related to eastern species.

## Materials and Methods

Specimens examined consist principally of study skins with associated skulls from the following collections, their museum acronyms as adopted throughout the report contained in parentheses: The Natural History Museum (BMNH, formerly British Museum of Natural History), London; Field Museum of Natural History (FMNH), Chicago; Muséum National d'Histoire Naturelle (MNHN), Paris; Département de Biologie Animale, Université d'Antananarivo (UA), Antananarivo; National Museum of Natural History (USNM, formerly U.S. National Museum), Smithsonian Institution, Washington, D.C. Coordinates used to compose range maps are those given by collectors for recent collections (see Appendix 1) or those estimated by Carleton & Schmidt (1990) for older ones.

A maximum of 7 external and 18 craniodental variables was recorded in millimeters (mm) for each specimen examined. The external variables, most as given by the collector, include: total length of body and tail (TOTL); head and body length (HBL); length of tail vertebrae (TL); hindfoot length (HFL, usually without claw for recent collections); dry hindfoot length (DHFL, with claw as measured by Carleton); ear length (EL); and weight in grams (WT). The 16 cranial and two dental variables (all measured by Carleton) are: breadth of the braincase (BBC); breadth across both incisive foramina (BIF); breadth of the bony palate across the first upper molars (BM1s); breadth across the occipital condyles (BOC); breadth of the rostrum (BR); breadth of the zygomatic plate (BZP); depth of the auditory bullae (DAB); interorbital breadth (IOB); length of bony palate (LBP); length of diastema (LD); length of incisive foramen (LIF); coronal length of maxillary toothrow (LM1-3); length of rostrum (LR); occipitonasal length (ONL); posterior breadth of the bony palate (PPB); postpalatal length (PPL); width of the first upper molar (WM1); zygomatic

breadth (ZB). These were recorded to the nearest 0.1 mm, using handheld calipers accurate to 0.03 mm and following the anatomical landmarks defined and illustrated in Carleton (1994). Morphological terms for the muroid skull generally follow Hershkovitz (1962), Carleton (1980), and Voss (1988).

Due to the small sample sizes encountered for most western samples of *Eliurus*, specimens from localities over a general region were grouped as operational taxonomic units (OTUs), as defined below. To better gauge the significance of interlocality variation among *E. myoxinus*, four samples of a broadly distributed eastern species, *E. tanala*, were included from throughout its range. Catalog numbers, full locality data, and museum sources of all specimens analyzed are provided in Appendix 1. We use the following abbreviations for various types of Malagasy protected areas: PN, Parc National; RF, Réserve Forestière; RNI, Réserve Naturelle Intégrale; RS, Réserve Spéciale.

*Eliurus myoxinus*.—OTU (1),  $n = 17$ , from 5 mi E Bevilany, Petriky Forest, and Parcel II, PN d'Andohahela. OTU (2),  $n = 13$ , from PN de Isalo, 35 mi E Toliara, Forêt de Vohibasia, Forêt de Vohimena, and Forêt de Zombitse. OTU (3),  $n = 9$ , from Forêt d'Analabe, Beroboka, Kirindy Forest, Morondava, and Tsilambana. OTU (4),  $n = 12$ , from Forêt d'Analavelona. OTU (5),  $n = 11$ , from RF de l'Ankarafantsika.

*Eliurus* new species.—OTU (6),  $n = 2$ , from Bekopaka. OTU (7),  $n = 3$ , from the RNI de Namoroka.

*Eliurus tanala*.—OTU (8),  $n = 18$ , from PN de Ranomafana and vicinity. OTU (9),  $n = 14$ , from PN d'Andringitra. OTU (10),  $n = 17$ , from RS d'Analamazaotra and vicinity. OTU (11),  $n = 6$ , from RS d'Anjanaharibe-Sud.

Standard descriptive statistics (mean, range, standard deviation) and multivariate analyses were calculated based on specimens of adult age classes (young, full, and old) defined on grades of dental wear. Ju-



Fig. 1. Dorsal, ventral, and left lateral views (about  $1.75\times$ ) of adult crania and mandibles of western species of *Eliurus*: left, *E. myoxinus* (BMNH 47.1603; ONL = 36.7 mm) from 5 mi E Bevilany; right, *E. antsingy* (MNHN 1966.220, holotype; ONL = 41.9 mm) from Bekopaka. (In order to illustrate conformation of a complete mandible, that of MNHN 1966.2222 was substituted for the partially broken left mandible of the holotype.)

veniles and subadults, identified by their complete or partial gray coats and newly erupted or little worn third molars, were excluded. Sample statistics for external dimensions were employed in tabular comparisons as a general index of size differences among populations and species, but were not considered in multivariate summaries. Derivation of canonical variates and principal components was computed using only the 18 craniodental measurements, all of which had been first transformed to natural logarithms. Loadings are expressed as Pearson product-moment correlation coefficients of the principal components or canonical variates with logs of the original skull variables. All analytical procedures

were conducted using Systat (version 9.01, 1999).

*Eliurus antsingy*, new species

Fig. 1, Table 1

*Holotype*.—Muséum National Histoire Naturelle number 1966.2220, an adult male prepared as skin and skull (original number 86), collected 1 July 1964 by J. M. Klein.

The round skin is roughly prepared but intact, the hind feet unconventionally folded forward under the ventrum. It bears two tags affixed to the right hind foot, the collector's original skin label and a later one identifying the collection of the MNHN, Paris. The skull is mostly intact, with minor



breakage of the posterior hard palate and pterygoid processes; the halves of the lower jaw are separated, and both dentaries are missing the tips of the coronoid and angular processes. The habitat is sparingly noted on original tags as "en forêt."

No external measurements are found on the original labels. Approximate dimensions, inferred by measurement of the dry museum skin, are: total length, 300+ mm; tail length, 140+ mm; and hind foot length, 30+ mm.

*Type locality*.—Madagascar, Toliara Province, Antsingy Forest, near Bekopaka, about 19°07.5'S, 44°49.0'E.

Original tags read only "Bekopaka, Antsingy." *Tsingy* is a type of geological formation, with a characteristic vegetational community, that commences about 3 km to the east of the village of Bekopaka and is enclosed within a reserve that has been recently reclassified as the Parc National de Bemaraha. Formerly much of the forest in this region was within a protected area, variously called the RNI de l'Antsingy or the RNI de Bemaraha; only the southern half has recently been regazetted as the PN de Bemaraha.

In discussions with M. Dokobe, who collaborated with J. M. Klein during the mission to Bemaraha in July 1964, Goodman learned that the site where the MNHN specimens were collected is located to the east of the former Bekopaka aviation field (pers. comm. in Antsalova, Feb 2001). Dokobe confirmed that the animals were trapped in typical tsingy forest, near the trail connecting Bekopaka and Andriandriambe, and we estimate the coordinates of the type locality to be approximately 19°07.5'S, 44°49.0'E.

*Diagnosis*.—A species of *Eliurus* characterized by large size (ONL = 40–44 mm), correspondingly robust molars (LM1-3 = 5.5–6.0 mm), relatively long incisive foramina (LIF/LD = 56%), and large auditory bullae. Tail tuft composed of dark hairs to the tip, not bicolored. Alveolus of lower incisor short, not terminating laterally as a capsular process.

Table 1.—Comparison of selected external and craniodental measurements of specimens of *Eliurus antsingy* from the type locality, Bekopaka, and the Réserve Naturelle Intégrale de Namoroka.

Variable	Bekopaka		RNI de Namoroka (n = 3, 4)
	MNHN 1966.2220	MNHN 1966.2222	
TL	—	—	161.7 ± 10.2 150.0–169.0
HFL	—	—	30.6 ± 0.9 29.0–31.0
ONL	41.9	44.1	40.5 ± 0.8 39.8–41.4
ZB	20.8	21.8	19.1 ± 0.4 18.6–19.4
BBC	16.3	15.8	15.3 ± 0.2 15.0–15.5
IOB	5.9	6.1	6.0 ± 0.1 5.9–6.1
LR	14.8	15.1	13.4 ± 0.6 12.9–14.0
BR	7.4	7.5	7.0 ± 0.2 6.7–7.1
PPL	14.7	15.1	14.5 ± 0.2 14.3–14.7
LBP	7.8	7.7	7.4 ± 0.1 7.3–7.5
LIF	6.7	6.8	6.3 ± 0.1 6.2–6.4
BIF	3.1	2.8	2.6 ± 0.1 2.5–2.7
LD	11.7	12.4	11.2 ± 0.5 10.9–11.8
BM1s	8.0	8.3	7.5 ± 0.2 7.3–7.6
PPB	6.1	6.0	5.5 ± 0.2 5.3–5.7
DAB	6.0	6.4	5.6 ± 0.05 5.5–5.6
BZP	3.5	4.3	3.8 ± 0.1 3.7–3.9
BOC	9.5	9.6	9.0 ± 0.2 8.8–9.2
LM1-3	6.00	5.65	5.69 ± 0.14 5.51–5.85
WM1	1.65	1.58	1.49 ± 0.03 1.45–1.53

*Referred specimens*.—MNHN 1966.2222, an adult female from Bekopaka, also noted as from Antsingy; collected 1 July 1964 by J. M. Klein and prepared as skin and skull (original number 85). FMNH 167563–167566, all young to fully adult females from the RNI de Namoroka, collect-

ed June 1999 by M. Anselme Toto Volahy and each prepared as skull with whole carcass in fluid. M. Toto Volahy trapped mammals in two different sites within the reserve, both in dry deciduous forest. Unfortunately, the collector's field tags for the specimens listed were lost and it is not possible to associate them with the original data.

*Distribution.*—Known only from the type locality and the RNI de Namoroka, western Madagascar.

*Description.*—Fur texture relatively soft and fine. Cover hairs of dorsal pelage bicolored or tricolored: basal three-quarters a medium plumbeous gray and the distal one-quarter pale buff, some hairs faintly tipped with a third band of dusky brown. Cover hairs 9–11 mm in length over middle rump. Guard hairs medium brown, only slightly longer than cover hairs. General effect of upperparts a dark drab brown to brownish-gray. In specimens from Bekopaka, cover hairs of chest, abdomen, and inguinum bicolored, basal half pale gray and distal half cream to bright white; hairs over chin and throat monocolored white in both specimens, a tract of creamy white hairs extending over the midventer of MNHN 1966.2222; general effect of underparts a medium gray. All specimens from Namoroka with entire venter plain white to pale buff, their underparts contrasting sharply with dorsum; one individual (FMNH 167564) with intense buff to pale ochraceous over thorax, grading to buffy white over the abdomen. Tops of forefeet and hindfeet covered with silvery white hairs, concentrating to form a loose tuft at base of claws that extends to or slightly beyond their tip.

Hindfeet comparatively broad, toes appearing short proportional to the length of the tarsus-metatarsus; HFL, as measured on the dry (toes slightly curled) and fluid specimens, about 29–31 mm, shorter than hind foot of *E. tanala*. Plantar pads six and arranged as per genus, but size large, extremely bulbous and packed very close to-

gether; hypothenar pad as big as an interdigital. Pinnae rounded and relatively small (about 20 mm as measured on the fluid preserved specimens), in proportion resembling those of *E. majori*; color dusky brown externally and clothed with fine brown hairs, paler brown internally and sparsely covered with fine white hairs. One pair each of axillary, abdominal, and inguinal mammae present, total = six (as confirmed on MNHN 1966.2222).

Tail tuft or brush well developed, noticeably evident over distal 40–50% of caudal length, hairs over fullest section about 12 mm long. Tuft dark to tip, composed of pale brown to dusky hairs; tuft of holotype with some fine white hairs randomly intermixed, but not forming a contradistinctive wholly white tip as observed in *E. tanala*. Tail of MNHN 1966.2222 and FMNH 167566 apparently naturally broken at midsection, terminating as a whorl of dark brown and some white hairs. Caudal epidermis medium gray all around near the base of the tail, becoming slightly to heavily mottled, dorsally and ventrally, toward the tip. Scutellation finely textured.

Cranium large in size, approximating that of *E. ellermani* or the largest *E. tanala*, with the incisors, zygoma, rostrum and mandible correspondingly stout in appearance. Dorsal profile of skull appreciably arched, sloping gradually toward the rostrum and more steeply toward the occiput, not so flat as in *E. tanala* of similar size. Rostrum moderately long (LR/ONL = 35%), proportions typical for the genus; zygomatic arches bowed laterally over their midsection, not so parallel-sided as in *E. myoxinus*; braincase relatively wide, rounded and smoothly contoured. Incisive foramina bluntly pointed on their anterior and posterior ends, relatively long and broad for the genus, their diastemal expanse (LIF/LD = 56%) in proportion resembling examples of *E. majori* and *E. penicillatus*. Posterior palatine foramina a single pair of small ovate holes, the palatine bones lacking extensive supernumerary foramina or slitlike vacuities.

Posterior edge of bony palate about even with end of third molars, lacking medial spine; anterior rim of mesopterygoid fossa nearly straight to gently curved. Alisphenoid strut present on both sides in all specimens. Subsquamosal fenestra patent but small, exposing little or none of the brain cavity; hamular process of the squamosal short and stout. Auditory bullae absolutely the largest in the genus, relatively as large as those of *E. myoxinus*.

Enamel face of upper and lower incisors pale yellow-orange in color. Alveolus of lower incisor relatively short, terminating at the level of the coronoid process and appreciably below the sigmoid notch; mandible without prominent capsular process. Molar toothrows long (LM1-3 = 5.6–6.0), about the size of *E. tanala*, absolutely and relatively shorter than those of *E. majori* and *E. penicillatus*; upper and lower third molars smaller than second.

Other external, cranial, and dental features as described for the genus (Carleton 1994, Carleton & Goodman 1998).

*Comparisons.*—A combination of large physical size, long and wide incisive foramina, and relatively inflated auditory bullae easily distinguishes *Eliurus antsingy* from most members of the genus. For most cranial variables measured, only individuals of *E. ellermani* and some examples of *E. tanala* attain the same large dimensions. Crania of those species, however, possess noticeably smaller auditory bullae, shorter and narrower incisive foramina, a more fenestrated hard palate, and a longer rostrum; further, they exhibit a flatter dorsal profile compared to the distinctly arched shape of *E. antsingy*. The pinnae and hind feet of *E. ellermani* and *E. tanala* are also absolutely longer.

Several characteristics of *E. antsingy* recall examples of *E. majori* and *E. penicillatus*. Like those species, its pinnae appear small and rounded for the size of the animal. Further, the alveolar tract of the lower incisor is somewhat short and does not produce a conspicuous lateral bulge where it

terminates within the mandibular ramus; and the incisive foramina are comparatively long and wide, spanning over 50% of the diasternal length. Unlike *E. majori* and *E. penicillatus*, however, the molar rows of *E. antsingy* resemble most other *Eliurus* in their shorter proportional length, lower crown height, and smaller third molars.

Both *E. antsingy* and its western congener *E. myoxinus* possess relatively large ectotympanic bullae (large, that is, for the size variation observed within *Eliurus*), but the former is not simply an enlarged version of the latter (Fig. 1; Tables 1, 3). The cranium of *E. antsingy* lacks the stocky, squarish appearance of *E. myoxinus*, a contrast imparted by its longer rostrum, comparatively narrow interorbital constriction, and more laterally bowed zygoma. The two differ in configuration of the incisive foramina (long, wide in *E. antsingy* versus short, narrow in *E. myoxinus*) and development of the capsular process (absent in *E. antsingy* versus a moderate bulge in *E. myoxinus*). The pelage of *E. antsingy* is more drably colored than the soft, pale browns of *E. myoxinus*, and its tail tuft is neither as well developed in length of individual caudal hairs nor in extent of tail vertebrae covered as compared with *E. myoxinus*.

Visual impressions of differences in skull size and shape are generally borne out in multivariate analysis of the 18 continuous variables recorded for *E. antsingy* and representative samples of *E. myoxinus* and *E. tanala* (Fig. 2, Table 2). The separation of *E. antsingy* from *E. myoxinus* along the first canonical variate principally reflects its larger cranial size (correlations mostly large and positive); on this axis, the five intact specimens of *E. antsingy* do not stand apart from those of *E. tanala*. Between-group variation summarized by the second canonical variate involves fewer influential variables with only moderate correlations—notably, inflation of the auditory bullae (DAB) and expansiveness of the incisive foramina (BIF, LIF), and to a lesser extent certain indices of cranial breadth (BBC,

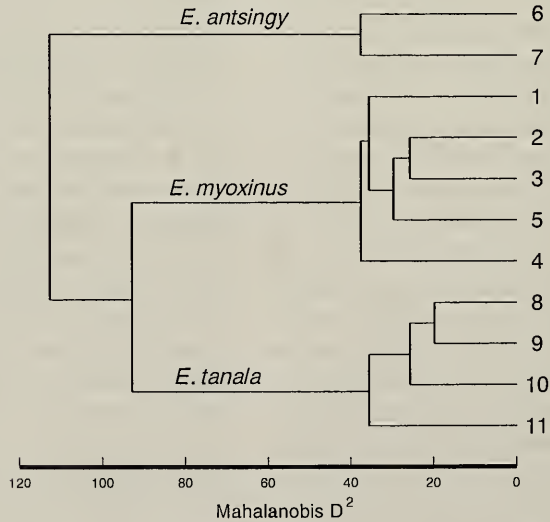
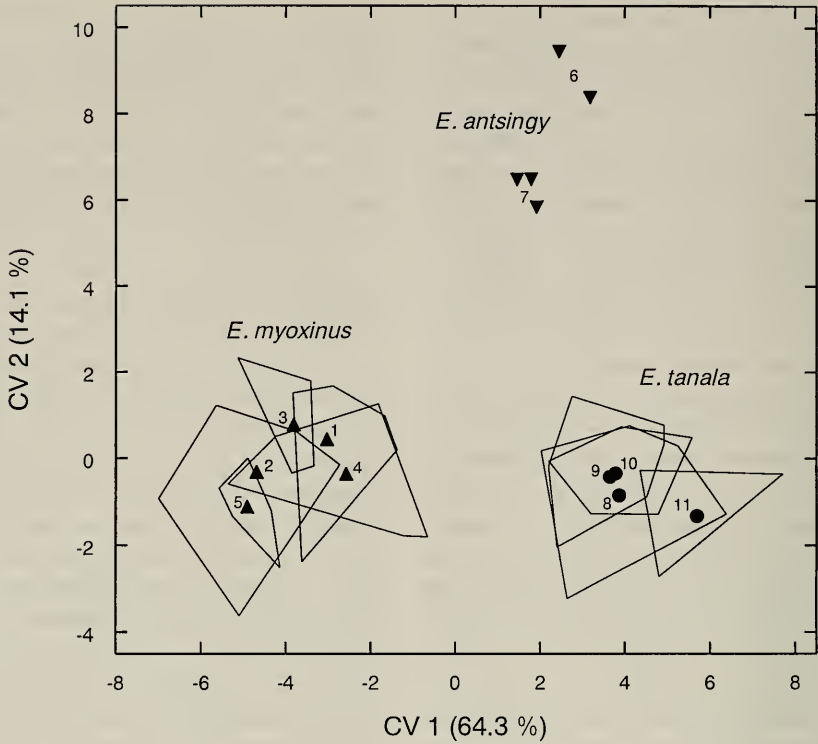


Fig. 2. Results of discriminant function analysis performed on 18 log-transformed craniodental variables, as measured on 122 specimens representing 11 OTUs of *Eliurus* (see Materials and Methods). Top, Projection of individual scores onto the first two canonical variables extracted; polygons for *E. myoxinus* and *E. tanala* enclose the maximal dispersions of specimen scores around a group's centroid, whereas individual scores are themselves plotted for the two samples of *E. antsingy*. Bottom, Phenogram produced from clustering (UPGMA) of Mahalanobis' distances among centroids of the 11 OTUs. See Table 2.

Table 2.—Results of discriminant function analysis of 11 OTUs representing intact specimens of *Eliurus myoxinus* ( $n = 50$ ), *E. antsingy* ( $n = 5$ ), and *E. tanala* ( $n = 44$ ) (see Fig. 2).

Variable	Correlations	
	CV1	CV2
ONL	0.93	0.17
ZB	0.80	0.19
BBC	0.49	0.28
IOB	0.71	0.18
LR	0.95	0.04
BR	0.77	0.09
PPL	0.74	0.20
LBP	0.91	-0.23
LIF	0.70	0.44
BIF	0.34	0.50
LD	0.93	-0.04
BM1s	0.92	0.07
PPB	0.60	0.33
DAB	0.06	0.59
BZP	0.72	0.07
BOC	0.85	0.32
LM1-3	0.91	0.14
WM1	0.87	0.10
Canonical correlation	0.97	0.89
Eigenvalue	16.5	3.2
% Variance	64.3	14.1

BOC, PPB). In each instance, the specimens of *E. antsingy* are exceptional for their relatively greater development, especially as compared with the similarly sized *E. tanala*.

*Remarks.*—Acquisition of additional specimens of *E. antsingy* is needed to bring taxonomic illumination to the differences remarked between the two examples from Bekopaka, the type locality, and those from the RNI de Namoroka. The latter animals are consistently smaller in size (Table 1), and their ventral pelage is wholly white to pale buff in marked contrast to the gray colored ventrum of the holotype from Bekopaka. The tone of the entirely white venters in the Namoroka series resembles the swath of white observed on the abdomen of MNHN 1966.2222 from Bekopaka, and similar variation in ventral pelage coloration has been noted among populations of *E. tanala* and *E. webbi* (Carleton 1994,

Carleton & Goodman 1998). Moreover, while acknowledging that existing sample sizes of *E. antsingy* are smaller than desirable, the amount of morphometric divergence revealed between the Bekopaka and Namoroka specimens approximates that found among larger geographic samples of widely ranging species, such as *E. myoxinus* and *E. tanala* (Fig. 2). In view of their other similarities in cranial shape and qualitative features of the skull and skin, we provisionally refer the Namoroka specimens to the new species and urge the need for continued study to clarify the interpopulational variation noted.

Little is known about the natural history of *E. antsingy*. The two specimens collected by Klein near Bekopaka were obtained in traps placed on the ground in typical *tsingy* forest habitat (M. Dokobe, pers. comm.).

The sites within the PN de Bemaraha and the RNI de Namoroka are separated by about 300 km (by air). The principal exposed geological formation within the PN de Bemaraha is derived from Mesozoic limestone, and the forest cover across this zone is relatively intact. Thus, we suspect that *E. antsingy* probably occurs throughout much of the Bemaraha complex. To the north of this zone, a break occurs in the Mesozoic limestone formation, which reappears as a series of isolated geological islands all the way north to and including Namoroka (Du Puy & Moat 1998). Within the intermediate zone there are two protected areas—the RS de Maningozy, which rests on sandstone and unconsolidated sands, and the RS de Kasijy, a portion of which occurs on Mesozoic limestone. Further survey work is needed to document whether *E. antsingy* inhabits these intermediate zones.

At the type locality of Bekopaka, Klein collected a third specimen (MNHN 1966.2221) of *Eliurus* together with the two examples of *E. antsingy* described above. The fact that the individual was collected at a later date (13 September 1964) and on a different trip ("Mission no. 7") suggests

that Klein captured it in a different area or microhabitat. The animal is not representative of either *E. myoxinus* or *E. antsingy*. Overall size is large (ONL = 44.3, LM1-3 = 5.85), resembling the dimensions of *E. antsingy* and the most robust samples of *E. tanala* (e.g., those from the northern highlands; Carleton & Goodman 1998). Approximate external dimensions, as measured on the dry skin (no field recorded data) are: total length, ca. 340 mm; tail length, ca. 160 mm; hind foot length, 34+ mm; and ear length, 22+ mm. The upperparts are a pale, grayish-brown; the underparts are entirely creamy white, from the chin to the inguinal region, and contrast sharply with the brown dorsum. The tail tuft is about 70 mm long and consists of two colors arranged in three bands: proximal (ca. 30 mm) and terminal (ca. 10 mm) sections of light brown caudal hairs, separated by a middle segment of purely white hairs (ca. 30 mm). Collection of additional specimens is needed to determine whether this three-banded tuft pattern is typical of the population. A short, terminal dark section is observed, albeit rarely, among samples of *E. tanala*, which otherwise possess a bicolored tuft composed of dark hairs proximally and white hairs towards the tip. The pale brown pinnae seem proportionally the largest in the genus, particularly in comparison to the specimens of *E. antsingy*, but the wrinkled condition of the dried pinnae disallows objective confirmation of our impression.

In addition to generous size and relatively stout construction, the cranium of MNHN 1966.2221 exhibits other traits suggestive of *E. tanala* or *E. ellermani* from eastern Madagascar. The rostrum is comparatively long with short and narrow incisive foramina, sharply pointed on both ends. Small supernumerary foramina occur behind the principal pair of posterior palatal foramina, although these are not coalesced as elongate vacuities as found in many *E. tanala*. The subsquamosal fenestra is occluded, the hamular process thus undefined

except at its posteroventral tip where it abuts the mastoid chamber. The capsular projection of the lower incisor is well developed and terminates just below the ventral rim of the sigmoid notch. Principal component analysis of the same craniodental variables disclosed the same array of specimen clusters as obtained in the canonical variates plot, with MNHN 1966.2221 positioned at the very periphery of the *E. tanala* constellation (not illustrated; % total variance explained on PC I and PC II = 71.0 and 6.7, respectively).

*Etymology*.—The species name is derived from the Malagasy words *tsingy*, which refers to the spectacular pinnacle-like limestone formation (karst) that occurs to the east of Bekopaka (in the Bemaraha reserve complex) and in the RNI de Namoroka, and *an*, a common prefix which means place of.

Additional Distributional Records of *E. myoxinus* Milne Edwards, 1885

As understood by Carleton in 1994, the geographic range of *E. myoxinus* was confined to southern and southwestern Madagascar, principally along or near the coast from the vicinity of Petriky Forest, extreme southeastern Madagascar, to the Forêt d'Analabe, a place just south of the mouth of the Tsiribihina River. The few localities then known (six) represented dry deciduous forest or xerophilous scrub, and none was recorded above 245 m. Subsequent reports have altered this distributional picture of *E. myoxinus* (e.g., Goodman & Ganzhorn 1994, Goodman & Rasoloarison 1997, Goodman et al. 1999), in particular amplifying its distribution in the southwestern interior between the Mangoky and Onilahy rivers (Fig. 3). These localities, and others listed in Appendix 1, have appreciably broadened the known altitudinal span of the species in the southwest, now documented from near sea level to 1250 m (Forêt d'Analavelona). In addition, they have revealed the greater ecological tolerance of

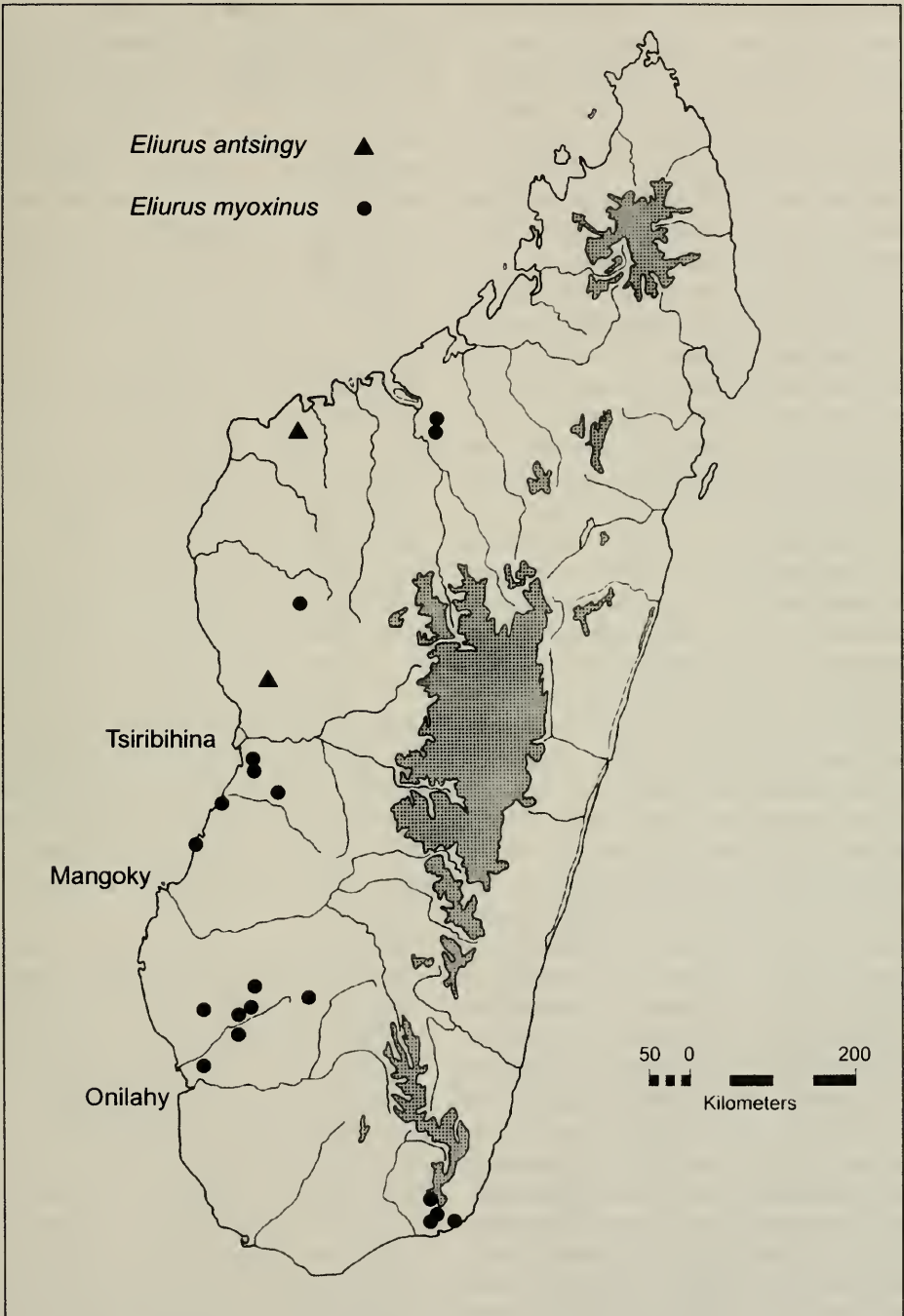


Fig. 3. Geographic occurrence of the species *Eliurus antsingy* and *E. myoxinus*, the two species so far documented as indigenous to western Madagascar. Names refer to the three western rivers discussed in the text, and shaded areas indicate highlands above 1200 m.

the species. Certain habitats above the western coastal piedmont and in inland zones of moderate elevation (e.g., Vohibasia and Analavelona) are floristically transitional between eastern humid forest and western dry deciduous forest (Du Puy et al. 1994, Jenkins & Goodman 1999) and suggest accommodation to more mesic conditions than previously recorded for the species.

A recent mission to the summital zone of the Analavelona Massif (Nov 2000) uncovered a remarkable density of *Eliurus myoxinus*, the single nesomyine rodent living in pristine forest at 1250 m. During five nights of trapping, 500 trap-nights were accrued and only two species of rodents were captured: 91 individuals of *E. myoxinus* and 116 individuals of the introduced *Rattus rattus*. The abundance of this nesomyine species suggests little or no suppression of its population size in the presence of non-native *Rattus*, a finding that contrasts with the diminished catch usually recorded for native rodents in eastern humid forests where *Rattus* is equally plentiful (Goodman 1995). Long-term ecological study is needed to track population fluctuations and determine whether western *Eliurus* are less affected by high densities of *Rattus*.

The habitat in the summital zone of Analavelona is mid-altitude montane sclerophyllous forest as defined by Koechlin et al. (1974). At this elevation in eastern forest, high levels of small mammal diversity have been regularly encountered, with up to six nesomyine species and including as many as three sympatric *Eliurus* (e.g., Goodman & Carleton 1998). The Analavelona Forest exhibits floristic and faunistic affinities to eastern humid forests (Koechlin et al. 1974, Raxworthy & Nussbaum 1997), in particular the Central Domain (sensu Humbert 1955), and appears to represent a mesic relict from a recent geological period when the climate over parts of southwestern Madagascar was distinctly wetter (Burney 1993, Goodman & Rakotozafy 1997). On the basis of the highly successful capture rates of *Eliurus* at the site, 91 of 207 ro-

dent trapped and all referable to *E. myoxinus*, the sympatric occurrence of a congener seems unlikely. In spite of the biogeographic affinities demonstrated between the Analavelona Forest and eastern humid forests for certain organisms, such past links cannot be conjectured based on the rodent community as presently understood. However, evidence for past east-west biotic connections is found in the nearby PN de Isalo, where a form related to eastern *E. majori* has been identified (Jansa & al. 1999).

We here report additional geographic occurrences of *E. myoxinus* that considerably extend its range northwards to the region of the RF de l'Ankarafantsika (16°20.3'S), Mahajanga Province, a distance of about 480 km from the species' previous northernmost locality (Forêt d'Analabe, 19°58'S). Specimens of *E. myoxinus* were first collected in January 1991 (Ampijoroa, 70 m) and later in February 1997 (5 km SSW Ampijoroa, 160 m). The natural wooded habitat in this reserve consists of dry deciduous forest, and the site of the 1997 collections was distinctly degraded due to human activities. Within the reserve and its vicinity, *E. myoxinus* occurs in sympatry with *Macrotarsomys bastardi* and *M. ingens*.

The northern samples of *E. myoxinus* average slightly but consistently smaller in most dimensions of the skull compared with southern populations (Table 3). Still in aspects of cranial shape, the series from Ankarafantsika exhibits the blocky construction characteristic of *E. myoxinus*, such as the parallel-sided zygoma, rectangular braincase, and relatively wide interorbital region. The dorsal pelage, however, is generally more saturated and darker in shade than the sandy brown typical of *E. myoxinus*, though the texture is similarly fine and the length relatively short. The tail tuft is long and bushy, as is characteristic of the species, but the caudal hairs are not quite so long, perhaps a reflection only of its smaller body size. The pelage of one animal (UADBA 9936) in the series is inordinately



Table 3.—Comparison of selected external and craniodental measurements for the holotype (MNHN 1886.1120) and two population samples of *Eliurus myoxinus* (sample statistics include the mean  $\pm$  1 SD and the observed range).

Variable	MNHN 1886.1120	Analavelona (n = 12)	Ankarafantsika (n = 8–11)
HBL	—	127.7 $\pm$ 6.4 117–136	123.6 $\pm$ 8.7 109–130
TL	—	145.5 $\pm$ 12.8 125.0–167.0	132.7 $\pm$ 9.5 115–142
HFL	—	25.4 $\pm$ 0.8 24.0–26.0	23.7 $\pm$ 0.5 23.0–24.0
EL	—	23.7 $\pm$ 0.8 23.0–25.0	20.0 $\pm$ 1.9 18.0–23.0
WT	—	65.5 $\pm$ 8.3 51–75	59.4 $\pm$ 13.3 36–79
ONL	34.2	36.1 $\pm$ 1.2 34.0–37.8	34.5 $\pm$ 0.8 33.0–35.3
ZB	17.6	17.8 $\pm$ 0.8 16.7–19.0	17.6 $\pm$ 0.4 17.1–18.2
BBC	13.6	14.0 $\pm$ 0.4 13.1–14.5	13.7 $\pm$ 0.2 13.5–14.0
IOB	5.5	5.6 $\pm$ 0.1 5.2–5.7	5.4 $\pm$ 0.1 5.3–5.6
LR	11.4	12.4 $\pm$ 0.7 10.7–13.3	11.4 $\pm$ 0.2 11.2–11.7
BR	6.6	6.7 $\pm$ 0.2 6.3–7.0	6.4 $\pm$ 0.3 6.1–7.0
PPL	—	13.2 $\pm$ 0.7 11.8–14.0	12.7 $\pm$ 0.4 12.0–13.1
LBP	7.1	7.6 $\pm$ 0.5 6.7–8.3	7.0 $\pm$ 0.3 6.6–7.7
LIF	5.4	5.0 $\pm$ 0.3 4.5–5.7	4.9 $\pm$ 0.2 4.6–5.1
BIF	2.0	2.2 $\pm$ 0.1 1.9–2.5	2.3 $\pm$ 0.1 2.2–2.4
LD	10.1	10.3 $\pm$ 0.6 9.1–11.0	10.0 $\pm$ 0.3 9.5–10.4
BM1s	6.7	7.1 $\pm$ 0.3 6.5–7.5	6.6 $\pm$ 0.2 6.4–6.9
DAB	5.0	5.5 $\pm$ 0.3 5.2–5.9	5.1 $\pm$ 0.1 5.0–5.3
BZP	3.1	3.3 $\pm$ 0.1 3.0–3.6	3.4 $\pm$ 0.2 3.1–3.7
BOC	—	7.9 $\pm$ 0.3 7.3–8.3	7.7 $\pm$ 0.3 7.1–8.1
LM1-3	4.90	5.19 $\pm$ 0.25 4.74–5.55	4.72 $\pm$ 0.10 4.57–4.90
WM1	1.27	1.41 $\pm$ 0.07 1.30–1.52	1.28 $\pm$ 0.07 1.18–1.38

“bleached,” its dorsum appearing uniformly tan or light tawny.

Although the Ankarafantsika series is nearer the small end of size variation within the species, multivariate analyses emphasize the basic craniodental conformity of the sample to others of *E. myoxinus* (Fig. 2). The amount of inter-sample differentiation among all OTUs of *E. myoxinus*, including that from Ankarafantsika, resembles the pattern of variation shown by samples of a broadly distributed eastern species, *E. tanala*. Recent molecular work on nesomyine rodents has included samples across the range of *E. myoxinus* (including, from north to south, Ankarafantsika, Kirindy, Isalo, Zombitse, and Andohahela [parcel II]—see Appendix 1), and the amount of sequence divergence and resulting cladogram are consistent with the hypothesis that these various populations represent a single species (Jansa 1998, Jansa & al. 1999).

Two other noteworthy examples of *E. myoxinus* have been recently (Nov-Dec 1999) captured at a second northern locale, the Forêt d'Ankazotshifototra (1150 m) in the RS d'Ambohijanahary. This site (18°15.7'S) lies geographically intermediate to Forêt d'Analabe and the RF de l'Ankarafantsika and suggests that future biological survey will disclose a broad distribution of the species throughout western landscapes. The Forêt d'Ankazotshifototra is situated at the very western edge of the Central Highlands, lying to the north and east of the Bemaraha reserve complex, and consists of humid forest of the Central Domain (sensu Humbert 1955). Faunistically, the Forêt d'Ankazotshifototra is a mixture of eastern and western elements. Within the RS d'Ambohijanahary, *E. myoxinus* was taken sympatrically with two individuals (FMNH 167546, 167555) of an *E. majori*-like form. They are appreciably smaller than typical *E. majori* with stronger contrast of the dorsal-ventral pelage color. While further study is required to properly assess the status and relationship of this form, its trenchant features recall species

(*E. majori* and *E. penicillatus*) that were previously known only from eastern Madagascar.

### Discussion

The unique combination of morphological features exhibited by *E. antsingy* provides insufficient basis for meaningful comment on the new species' closest relatives. We do suspect that, although presumably western in its distributional setting like *E. myoxinus*, *E. antsingy* is not specially related to this more widely known western form. Firmer understanding of their level of relationship within the radiation of *Eliurus* must await the acquisition of additional specimens, recourse to other sources of taxonomic information, and broader intrageneric comparisons. Other geographic parallels are known within Madagascar's small mammal fauna. For example, molecular evidence suggests that the species of mouse lemur known from the Bemaraha area, *Microcebus myoxinus*, is one of the sister taxa to the eastern *M. rufus* group rather than the widespread *M. murinus* group (Yoder et al. 2000).

As currently understood, the taxonomic diversity of Madagascar's indigenous rodents is concentrated along the eastern one-third of the island as compared to its spacious western landscapes (Table 4). Seven genera representing seventeen species have been documented to date in the east versus four genera representing eight species in the west. Such a contrast in species richness could be plausibly attributed to the circumstantial interplay of the island's physical geology and regional climatic patterns, and attendant opportunities for the stratification of plant communities, greater ecological complexity, and geographic isolation that follow.

However, while recent biological inventories have substantially bolstered our knowledge of nesomyine distributions in eastern Madagascar (Goodman & Carleton 1996, 1998, Goodman et al. 1996, 1999,

Table 4.—Tabulation of nesomyine species known from eastern versus western landscapes of Madagascar.

Eastern	Western
<i>Brachytarsomys albicauda</i>	<i>Eliurus antsingy</i> *
<i>B. villosa</i> **	<i>E. aff. majori</i>
<i>Brachyuromys betsileoensis</i>	<i>E. myoxinus</i>
<i>B. ramirohitra</i>	<i>E. aff. tanala</i>
<i>Eliurus ellermani</i> *	<i>Hypogeomys antimena</i>
<i>E. grandidieri</i> *	<i>Macrotarsomys bastardi</i>
<i>E. majori</i> **	<i>M. ingens</i>
<i>E. minor</i>	<i>Nesomys lambertoni</i> **
<i>E. penicillatus</i> **	
<i>E. petteri</i> *	
<i>E. tanala</i> **	
<i>E. webbi</i> **	
<i>Gymnuromys roberti</i>	
<i>Monticolomys* koopmani</i> *	
<i>Nesomys audeberti</i> **	
<i>N. rufus</i>	
<i>Voalavo* gymnocaudus</i> *	

\* = Described as new since 1994.

\*\* = Resurrected from junior synonymy since 1994.

Carleton & Goodman 2000), vouchered documentation of nesomyine occurrences in the west has only started to fill in the significant geographic gaps identified by Carleton & Schmidt (1990). Until now, *Eliurus myoxinus*, described by Milne Edwards in 1885, has remained the only species of that genus recorded from western environments; over just the past six years, three eastern species of *Eliurus* have been newly described and another four recently resurrected from junior synonymy as valid (Carleton 1994, Carleton & Goodman 1998). The diagnosis of *E. antsingy*, reported herein, and the presence of autochthonous genera like *Hypogeomys* and *Macrotarsomys*, together suggest the rich potential for future discoveries among the island's western habitats. The recovery of additional species from Ambohijanahary and Bekopaka that appear to have affinity to forms of eastern *Eliurus*, like the recent report of an *E. majori*-like form from Isalo (Jansa & al. 1999), further attest our imperfect knowledge of nesomyine distributions in western Madagascar. In view of the many regions that still lack thorough site

survey, any meaningful conclusion on the degree of east-west biodiversity contrasts must await this firmer foundation of field inventory and systematic study.

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## Appendix 1

Listed below are specimens of *Eliurus* that formed the basis for the morphological comparisons, sample statistics, morphometric analyses, and mapped distributions presented above.

*Eliurus myoxinus*.—Fianarantsoa Province: Parc National de Isalo, 3.8 km NW Ranohira, along Namaza River, 800 m; 22°32.4'S, 45°22.8'E (FMNH 166079–166081). Mahajanga Province: Forest Station, Ampijoroa, 70 m, 16°15'S, 46°48'E (DR 165; USNM 576754–576756); Réserve Forestière de l'Ankarafantsika, 5 km SSW Ampijoroa, 160 m, 16°20.3'S, 46°47.6'E (UADBA 9935–9943); Réserve Spéciale d'Ambohijanahary, Forêt d'Ankazotsihitafototra, 1150 m; 18°15.7'S, 45°25.2'E (FMNH 167545, 167547). Toiliara Province: Forêt d'Analabe, 60 km N Morondava (MNHN 1980.290, 1982.988); Forêt d'Analavelona, 12 km NW Andranoheza, 1050 m, 22°40.7'S, 44°11.5'E (FMNH 161578–161589); Réserve Naturelle Intégrale d'Andohahela, parcel II, 7.5 km ENE Hazofotsy, 120 m, 24°49.0'S, 46°36.6'E (FMNH 156630); Beroboka, 40 mi N Morondava (BMNH 47.1608, 47.1609, 1987.50); 5 mi E Bevilany, Ambovombe-Fort Dauphin road, the hills, 800 ft (BMNH 47.1600–47.1607, 66.2746); Kirindy Forest, 60 km NE Morondava, 20°04'S, 44°49'E (FMNH 154632, 154633); Lamboromakandro, Forêt de Sakaraha (MNHN 1961.220); Morondava (MNHN 1973.516); Petriky Forest, 5–7 km SE Manambara, 20 m, 25°04'S, 46°53'E (USNM 578679–578687); Tsilambana (MNHN 1886.1120, holotype); 35 mi E Tulear (BMNH 47.1610, 47.1611, 47.1611a); Forêt de Vohibasia, 59 km NE Sakaraha, 780 m, 22°27.5'S, 44°50.5'E (FMNH 156183, 156191); Forêt de Vohimena, 35 km SE Sakaraha (FMNH 156192–156194); Forêt de Zombitsy, 870 m, 22°51'S, 44°43'E (FMNH 151951, 151952).

*Eliurus tanala*.—Antsiranana Province: Réserve

Spéciale d'Anjanaharibe-Sud, 6.5 km SSW Befingitra, 875 m, 14°45.3'S, 49°30.3'E (FMNH 154049); Réserve Spéciale d'Anjanaharibe-Sud, 9.2 km WSW Befingitra, 1260 m, 14°44.7'S, 49°27.7'E (FMNH 154050, 154051, 154249, 154250; UA-SMG 6979). Fianarantsoa Province: Ambodiamontana, 7 km W of Ranomafana, 950 m, 21°16'S, 47°26'E (USNM 448981–448990, 448997, 449250); 3 km NNW Vohiparara, 1225 m, 21°13'S, 47°22'E (USNM 449251–449255); 1 km NW Andrambovato, 875 m, 21°30'S, 47°25'E (USNM 449256); Réserve Naturelle Intégrale d'Andringitra, 38 km S Ambalavao, ridge east of Volotsangana River, 1625 m, 22°11'S, 46°58'E (FMNH

151691, 151692, 151744, 151880, 151881); Réserve Naturelle Intégrale d'Andringitra, 40 km S Ambalavao, along Volotsangana River, 1210 m, 22°13'S, 46°58'E (FMNH 151690, 151743, 151873, 151874, 151897); Réserve Naturelle Intégrale d'Andringitra, 43 km S Ambalavao, junction of Sahanivoraky and Sahavato rivers, 810 m, 22°13'S, 47°00'E (FMNH 151687, 151688, 151869, 151870). Toamasina Province: 10 mi NW Lohariandava, 1500 ft (BMNH 47.1573); Périnet, near Moramanga, 3000 ft (BMNH 47.1557, 47.1560–47.1562, 47.1564–47.1568, 47.1571, 47.1572; MNHN 1961.176); 1 km E Périnet (USNM 341826); 2 km E Périnet (USNM 328828, 328829); 13 km E Périnet (USNM 341827).

## The lophialetid ceratomorph *Eoletes* (Mammalia) from the Eocene of the Zaysan Basin, Kazakstan

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*Abstract.*—The “hyrachyid” ceratomorph *Subhyrachyus tshakpaktasensis* Gabuniya, was named for a nearly complete skull from the Zaysan Basin of eastern Kazakstan. This skull is from the Eocene (Arshantan) Chakpaktas Formation at the Mozhevelnik locality on the Kalmakpay River. Re-examination of the skull indicates it belongs to the lophialetid genus *Eoletes* Biryukov, based on the following diagnostic features: shallow nasal incision only retracted to above the canine, long and shallow maxillary fossa, anterior edge of orbit above M2, no modifications of rostrum as in *Lophialetes*, short postcanine diastema, complete u-shaped lophoid loops on P3-4, and relatively lophodont cheek teeth. The features that distinguish *E. tshakpaktasensis* from *E. gracilis* Biryukov, (type species of *Eoletes*) and Chinese *E. xianensis* Zhang & Qi, are minor (upper cheek teeth relatively wider and more prominent premolar ectoloph ribs in *E. tshakpaktasensis*), but we retain all species as valid pending a larger sample with which to document better dental variability in *Eoletes*. *E. tshakpaktasensis* is the first record of *Eoletes* from the Zaysan Basin and extends the temporal range of the genus from the Irдинmanhan back to the Arshantan.

The Zaysan Basin of eastern Kazakstan (Fig. 1) yields an extensive fossil record of Eocene mammals that represent the Arshantan, Irдинmanhan, and Ergilian land-mammal “ages” (1ma) (e.g., Russell & Zhai 1987, Lucas et al. 2000, Lucas 2001). New discoveries in the Zaysan Basin continue to augment our knowledge of Asian Eocene mammals. Gabuniya (1999) described a new perissodactyl genus and species, *Subhyrachyus tshakpaktasensis*, from the oldest Eocene strata known in the Zaysan Basin. As the name indicates, Gabuniya considered this new taxon to be a member of the ceratomorph family Hyrachyidae and concluded that it was part of an Asian diversification of hyrachyids distinct from the well-docu-

mented North American forms, discussed by Wood (1934) and Radinsky (1965, 1967). However, reexamination of the holotype and only specimen of *Subhyrachyus tshakpaktasensis* indicates that it should be reassigned to the lophialetid genus *Eoletes*. Here we document this reassignment and briefly discuss its implications.

*Abbreviations used.*—When used in dental notations, uppercase letters denote upper (premaxillary and maxillary) teeth, and lowercase letters denote lower (dentary) teeth. Institutional abbreviations are: IPGAN = Institute of Paleobiology, Georgian Academy of Sciences, Tbilisi; KAN = Institute of Zoology, Academy of Sciences of the Republic of Kazakstan, Almaty.



Fig. 1. Map of Kazakhstan showing location of Zaysan Basin.

Systematic Paleontology

Family Lophialetidae Matthew & Granger, 1925

Genus *Eoletes* Biryukov, 1974

*Eoletes tshakpaktasensis* (Gabuniya, 1999) Figs. 2-3

*Subhyrachyus tshakpaktasensis* Gabuniya, 1999:561, figs. 1-3.

*Holotype*.—IPGAN Z402, nearly complete skull with right P3-M3 and left P2-M3 (Gabuniya, 1999, figs. 1-3) (Figs. 2-3).

*Type locality and horizon*.—Mozhevel-

nik locality on the Kalmakpay River, Zaysan Basin, Kazakhstan (UTM Zone 45, 383463E, 5256668N, datum WGS84).

*Referred specimen*.—Only known from the holotype.

*Description*.—Gabuniya (1999) provided a detailed and accurate description of IPGAN Z402, obviating the need for extensive description here. Instead, we list the salient features critical to determining the systematic position of this fossil below.

The nasal incision is very shallow, only retracted to above the canine:

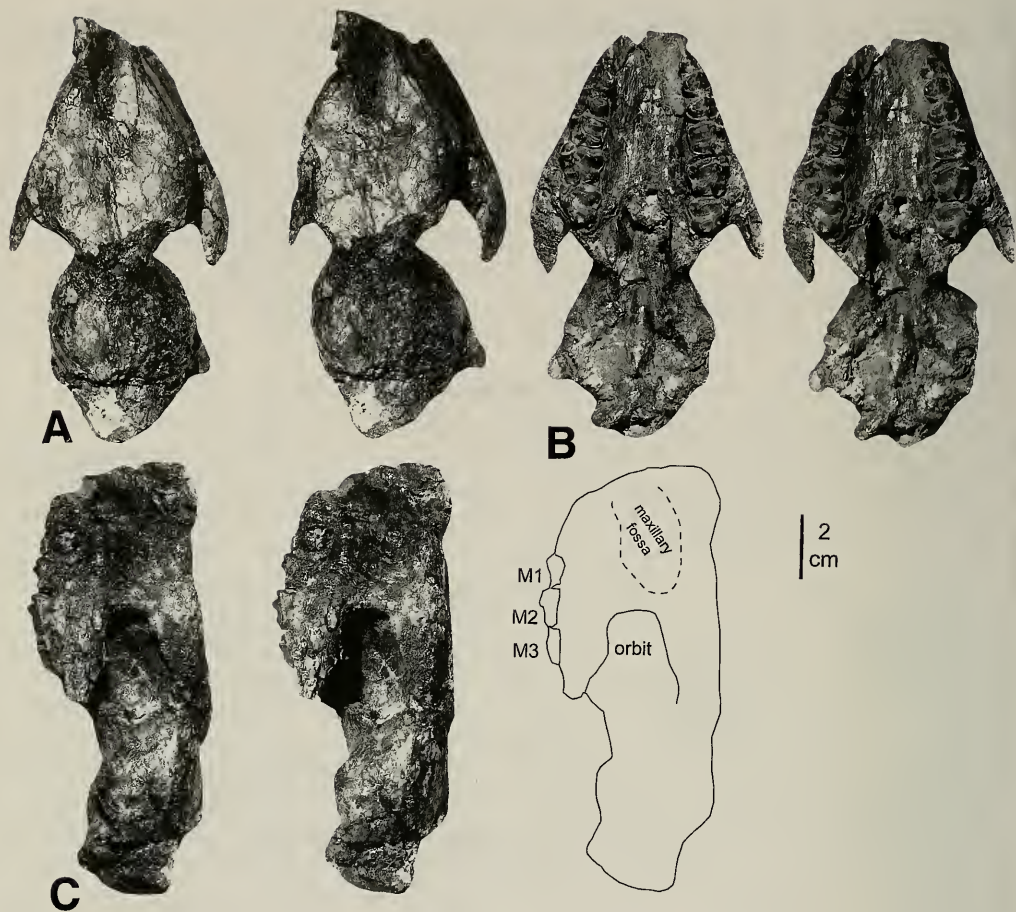


Fig. 2. IPGAN Z402, skull of *Eoletes tschakpaktasensis* in dorsal (A; stereophotos), ventral (B; stereophotos), and left lateral (C; stereophotos) views.

The facial portion of the maxilla bears a moderately deep preorbital fossa:

The nasals extend far anteriorly and apparently contact the premaxilla:

The supraorbital processes are damaged, so that their complete extent cannot be determined:

The P3 and P4 each bear a protoloph and metaloph that are joined lingually, forming a U-shaped loop. This is the “complete lophoid loop” character of Hooker (1989, p. 88, table 6.1, character 21):

The upper cheek teeth are relatively lophodont, with prominent, sharp ectolophs, prominent molar parastyles, lingually deflected molar metacones, and sharp, well-developed molar protolophs and metalophs

connecting the lingual cusps to the ectoloph:

Measurements of the cheek teeth of IPGAN Z402 (in mm) are: P2 L = 8.8, W = 8.6; P3 L = 9.4, W = 10.4; P4 L = 9.5, W = 11.4; M1 L = 12.3, W = 14.1; M2 L = 14.6, W = 15.5; M3 L = 13.9, W = 14.7:

*Discussion*—The U-shaped lophs of the premolars are a synapomorphy of the Lophialetidae (Hooker 1989, Lucas et al. 1997) and indicate that IPGAN Z402 is a lophialetid. In hyrachyids, the premolar metalophs are short and do not contact the protoloph. Lophialetids include the genera *Lophialetes*, *Schlosseria*, *Breviodon*, and *Eoletes*. *Lophi-*





Fig. 3. Occlusal views of upper cheek teeth of *Eoletes*. A, IPGAN Z402, *Eoletes tshakpaktasensis*, right P2-M3. B) KAN 5088/69, *Eoletes gracilis*, left P1-M3 (photo reversed).

*alates* differs from the others in possessing a narial incision that is retracted far posteriorly, similar to what is seen in living *Tapirus*. IPGAN Z402 is similar to many primitive perissodactyls, including *Hyrachyus* and lophialetids other than *Lophialetes* and *Schlosseria*, in possessing an unretracted narial incision. Among lophialetids without a retracted narial incision, only *Eoletes* possesses a well-developed maxillary fossa (Lucas et al. 1997). *Eoletes* also possesses a long supraorbital process.

The morphology of the premolars indicates that IPGAN Z402 is a lophialetid, not a hyrachyid. The absence of a retracted narial incision indicates that this specimen does not belong to *Lophialetes* or *Schlosseria*. IPGAN Z402 is very similar in its cranial morphology to specimens of *Eoletes gracilis* from the Shinzaly locality in eastern Kazakhstan, particularly in terms of the morphology of the preorbital fossa and dentition (Biryukov 1974, Reshetov 1979, Lucas et al. 1997, figs. 3–4). Unfortunately, the poor preservation of the supraorbital processes prevents any assessment of

whether IPGAN Z402 is similar to the Shinzaly specimens of *Eoletes* in this feature. Nevertheless, we feel that the similarities between these specimens justify assigning IPGAN Z402 to *Eoletes*.

IPGAN Z402 does differ from described species of *Eoletes* (*E. gracilis* and *E. xianensis* Zhang & Qi, 1981) in some minor features. Thus, IPGAN Z402 has relatively wider cheek teeth, more prominent ectoloph ribs on the upper premolars, and relatively larger upper molar parastyles than other specimens of *Eoletes*. Because little is known of dental variation in *Eoletes*, it is difficult to evaluate the taxonomic significance of these differences. Although we suspect that these differences may be found in the future to fall within the range of intraspecific variation for this taxon, we take the conservative course and tentatively retain Gabuniya's species, and we refer IPGAN Z402 to *Eoletes tshakpaktasensis*.

#### Biostratigraphy

The holotype of *E. tshakpaktasensis* is the first record of *Eoletes* from the Zaysan

Basin and is the oldest record of the genus. It is derived from the Chakpaktas svita, which is of Arshantan age (Lucas 2001). The type locality and only record of *E. gracilis*, at Shinzaly, is younger, of Irdinmanhan age (Lucas et al. 1997, Lucas 2001). The only occurrence of *E. xianensis* in the Bailuyuan Formation of Shaanxi is Irdinmanhan or possibly slightly younger (Lucas et al. 1997). *Eoletes* thus remains a rare tapiroid from the Eocene (Arshantan-Irdinmanhan) of Asia.

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**PROCEEDINGS  
OF THE  
BIOLOGICAL SOCIETY  
OF  
WASHINGTON**



**GUIDELINES FOR MANUSCRIPTS**  
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Guidelines for manuscripts for publications of the  
Biological Society of Washington

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Abstract.—The abstract should be  $\leq 3\%$  of the length of the text of the article. It should be a concise statement of findings, rather than a listing of subjects covered, and should be written as a single paragraph and double spaced. Except under unusual circumstances, references should not be cited in the abstract. All newly described taxa must be given by name in the abstract.

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This paper provides authors with guidelines and examples to aid in preparing manuscripts for the Biological Society of Washington. The required format for manuscripts for the Proceedings and Bulletin is presented and followed herein as a model of format and style. However, except for the title, author(s), author(s) address(es), abstract, and figure and table captions, the final printed papers appear in double-column format rather than occupying a complete page as does this manuscript. It is neither possible nor desirable to provide detailed examples of every format or style item, but we have attempted to address most of the potential questions facing an author preparing a manuscript.

As a general guide, we recommend the sixth edition of Scientific style and format: The CBE manual for authors, editors, and publishers (Style Manual Committee 1994), available from the Council of Biological Editors, Inc., New York. The latest edition is a more comprehensive guide for scientific writers than were previous editions. A shorter but useful guide is Day (1994) How to write & publish a scientific paper, fourth edition.

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Manuscript preparation.---Type all manuscripts on letter size (215- by 280-mm, 8½- by 11-in.) paper. All parts of the manuscript should be double spaced, including text, literature cited, tables, table headings, and figure legends, so that reviewers, editors, printers, and proofreaders can make essential notations. Use the same font size throughout the manuscript. Do not justify the right margin. Allow  $\geq 3$ -cm (1½ in.) margins on all sides.

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Titles should be brief and include key words that will be useful for indexing and information retrieval. Include phylum, class, order, and family names (separated by a colon and a space [e.g., Crustacea: Copepoda: Caligidae]) for species likely to be unfamiliar to many readers. In subsequent use of scientific names, abbreviate generic names where possible (e.g., “Studies on Botrychium meridionale and B. virginianum”); do not abbreviate scientific names in titles or subheadings if they have not been previously spelled out in the same title or subheading. Center the title and type it in uppercase letters, including underlined scientific names.

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In general, use no more than three levels of organization: primary headings (centered); secondary headings (indented from left-hand margin, underlined, followed by a period and three dashes); and tertiary headings (indented from left-hand margin, ending with a colon). New taxon names and associated citation of their taxonomic placement (phylum, class, order, family, etc.), and figure and table references are primary headings. (Note:

unless the higher taxonomic categories are the primary topic, author and date citations are not necessary.)

Systematic Paleontology  
 Class Mammalia Linnaeus, 1758  
 Order Chiroptera Blumenbach, 1779  
 Family Desmodontidae Gill, 1884  
 Genus Desmodus Maximilian, 1824  
Desmodus archaeodaptes, new species

Fig. 1

Long lists or complex material that is related only indirectly to the primary subject should be placed in an appendix at the end of the manuscript. Items that are appropriate for appendices include: lists of specimens examined; lists of morphometric characters, other morphological features, or ecologic characters; derivations of complex mathematical or statistical formulas; and algorithms for computer programs. Appendices may be arranged as paragraphs, in tables, or in other formats as appropriate. Short lists, single formulas, and material related more directly to the subject should be placed in the text. Material not essential to the article should be omitted.

Never break words at the right-hand margin anywhere in the manuscript for any reason. This includes hyphenated words and words divided into syllables.

Spell out the entire scientific name the first time a plant or animal is mentioned in the text; thereafter, abbreviate generic names (first letter and period), except at the beginning of a paragraph or sentence. Include author(s) and date where such is essential to identification of a taxon (such as in a synonymy). If subgeneric names are used, they should be placed between the generic and specific names, and be enclosed in parentheses; abbreviate them after their initial use, using the first letter of their name. Use subspecies or infraspecific names only when they are essential to the understanding of the article. Descriptions of new taxa in zoology should be spelled out, as: new genus, new species, new subspecies, and new combination, or for botanical papers use: gen. nov., sp. nov., subsp. nov., or comb. nov. Each of these should be preceded by a comma. Descriptions must be in English, except for Latin descriptions or diagnoses in botanical papers (fossils excepted).

Provide the scientific name (generic and specific names) of all organisms at first mention of the vernacular name both in abstract and text (even if the name appears in the title); use the scientific name of the appropriate taxon if a vernacular name is inclusive (e.g., crickets [Gryllidae]).

Tables and figures.---Because of the cost of publication, tables should be used only when large quantities of data must be summarized or trends in data illustrated to support inferences. Pertinent data in most small tables (two-row or two-column tables) usually can be presented in the text in less space and without loss of intelligibility. Consider carefully the presentation of non-tabular data in the two-column format of the Proceedings. In many instances, a table would be easier to read and type-set.

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Place any necessary identifications (e.g., symbols, cover types, scale bars, regression formulas) directly on the figure rather than in the figure legend. Scale bars should always be included in the figure, not in the figure legend. Do not submit figures larger than 215 by 280 mm (8½ by 11 in.). If original figures are larger than this please send a photographically reduced figure. Figures exceeding this size are difficult to mail, handle, and store. Prepare line drawings with lines of sufficient width and letters of sufficient size to remain legible when the figures are reduced to final page or column width (Style Manual Committee 1994). Line art should not be prepared for reduction greater than 50%. Graphics produced by coarse dot-matrix printers are not satisfactory for reproduction. Legibly mark all photographs and figures on the back with the author(s) name(s), figure number, and indicate "TOP." Use soft pencils (blue preferred) on the backs of photographs and drawings, because markings, pencil, and pen indentations may show through. Leave a margin at the top of each figure (including photographs) of at least 3.85 cm (1½ inches). Provide photocopies of figures to be sent with the manuscript to reviewers. Rub-on or transfer letters are preferred. Submission of photographs (either those produced by standard processes or by diffusion-transfer imaging [PMT]) of graphics is recommended. Submitted photographs must not be produced by making a photograph through a halftone screen (pre-screened). Mount original graphics or photographs on cardstock or other heavy material; use the same material when several small graphics are submitted for a composite figure. In the case of composite graphics, they must be mounted as the author desires. If more than one image is mounted on a figure, it is best to cut square edges and mount the images with edges touching but not overlapping (note: our printer will add narrow white rules between the

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## Results and Discussion

### Style and Usage

**Punctuation.**---Use quotation marks sparingly for emphasis or special use of a word or term, thus preserving them mainly for actual quotations. Use the slant line or solidus (*/*) only to indicate “divided by” or in dental, vertebral, or chaetotaxy formulas.

Underline generic and specific names in the text (underlined words will



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Spelling and use of words should be in accordance with Webster’s Third New International Dictionary, Unabridged. Use of words not included therein should be avoided, but newly coined words and foreign words may be used sparingly if precisely defined at first use. Scientific terms should follow recent specialized dictionaries and glossaries. Refrain from using words in other than their standard meanings.

Use only “male” and “female” to distinguish the two sexes. Avoid terms such as rams, ewes, bucks, or other similar names.

Numbers and mathematics.---Use decimals rather than fractions except in equations. Decimals not preceded by a whole number should always be preceded by a zero (0.75) in text, tables, and figures.

In the text (introduction, discussion, conclusions, etc.) and in titles, use numerals for numbers greater than nine except when starting a sentence (associated units should then not be abbreviated: “Eleven minutes,” but “About 11 min”; “Fifteen percent,” but “More than 15%”). For numbers one through nine, use words except when used with units of measure (6 mm), time (3 days, 3 summers, 4 years), but not enumeration (five dugongs, two crabs, seven observations). Also, use numerals for all items in a series that includes at least one number greater than nine (1 dik-dik, 7 numbats, and 19 slow lorises). Treat ordinal numbers in the same manner as cardinal numbers (first panda, 14th deer mouse, 1st month, 6th min, fourth trial).

In the specimens examined and description or diagnosis sections, use numerals throughout.

Avoid the use of numbered sentences or phrases in text. Reference to specific items by number in text is acceptable but names of items should be lowercase (e.g., day 1, experiment 4, setiger 5, grid 6, site 1, coxa 3, segment 7). Do not refer to individual animals either by name or field-catalog number; reference to individual animals tends to indicate that the material being presented is anecdotal.

Use commas in numbers of five digits or more (e.g., 10,000 and 100,000). The exceptions are field and catalog numbers of museum specimens, and pagination in references.

Use a colon (not a solidus [/]) to express ratios (e.g., 1:3.2, males: females). Do not present the numbers of males and females in a total sample (e.g., 15:48) as sex ratios but calculate the true ratio and give the sample size. For example, “. . . 1:3.2 ( $n = 63$ ) in favor of females.” Use  $<$  and  $>$  for “less than” and “greater than” with numerals (“ $<5$  g,” not “less than 5 g”; “ $>20$  captures,” not “more than 20 captures”). Use  $\leq$  for “equal to or less than” or “not more than” and  $\geq$  for “equal to or greater than” or “at least” with numerals.

When giving ranges, use “from 10.1 to 31.0 mm” or “ranges from 10.1–31.4,” but “the range is 21.3 mm.” In other words, do not use “to” unless it is preceded by “from.”

When presenting equations and formulas, use the solidus (/) for simple fractions and give the meanings of all symbols and variables in the text. When presenting values with respect to another factor such as time or space, use the solidus (/) if only two measurements are involved (g/ha); if three or more measurements are involved use the exponent  $-1$  as in “. . .

43 mg g<sup>-1</sup> h<sup>-1</sup>.” Do not present equations published elsewhere unless they have been modified; a simple reference will do.

In reporting measures of central tendency (means, modes, etc.) or dispersion (standard deviations, standard errors), units of measure should not be more precise than the original measurements. For example, if mammals are weighed to the nearest 0.1 g, then means such as 54.56 should be reduced to 54.6 and  $\bar{X} \pm \text{SE}$  should be  $54.6 \pm 0.1$ , not  $54.6 \pm 0.09$ , both in tables and in text.

Dental formulas should be presented as I 1/1, c 0/0, p 1/0, m 3/3, total 18. Vertebral formulas should be presented as 7 C, 13 T, 6 L, 2–3 S, and 26–31 Ca, total 55–60. Upper teeth should be referred to by capital letters and lower teeth by lowercase letters (e.g., P4 is the fourth upper premolar and ml is the first lower molar); do not use superscript and subscript numerals to designate upper and lower teeth.

Time and dates.---Write dates as 24 April 1989, with no internal punctuation; an exception is in the specimen examined section where the three-letter month code should be used. Indicate time of day on the 24-h system with four digits. Midnight is written as 0000 h, 8:30 a.m. as 0830 h, and 11:15 p.m. as 2315 h. Also, indicate time similarly as “4-h intervals,” and “3 h/day.” To express the age of a stratigraphic unit or the time of a particular geologic event, and where a specific dating technique has been used, employ “Ma” for mega-annum (time greater than one million years), or “B.P.” (years before present) for radiocarbon dated material, which goes up to 40,000 yrs. To express other time relations, use “m.y.” (million years) or m.y.a. (million years ago). For example, from 50 to 25 Ma, 25 m.y. elapsed and it is possible that these organisms lived at least 40 m.y.a. The ratio of light (L) hours to dark (D) hours under laboratory conditions is to be shown in this form: 14L:10D.

Units of measure.---Use of the metric system and the international system of units (Système International d’Unités) is advocated. Exceptions to the use of the metric system and the international system of units are English units in localities from specimen labels and in quotations from other publications. Also, the following variables may be reported in other units:

Temperature in degrees Celsius (°C) instead of Kelvin (°K).

Time in minutes (min) and hours (h) instead of seconds (sec).

Sound intensity (relative terms) in decibels (dB) instead of watts/meter square (W/m<sup>2</sup>).

Volume in liters (l) instead of cubic decimeters (dm<sup>3</sup>).

Area in hectares (ha) instead of 10<sup>4</sup> m<sup>2</sup>.

Accepted abbreviations that can be used in text, tables, and figures of manuscripts, without explanation or punctuation, and some words that should be spelled out follow:

Units of measure (use abbreviations only with numerical values, otherwise spell out; e.g., "... FN = 72–76, but populations with low fundamental numbers ..."):

°C	degrees Celsius
2N (not <u>2n</u> )	diploid number (N = chromosome number)
FN	fundamental number
n	nautical
g	gravity
sec	second
min	minute
h or hr	hour
d	day
wk	week
mo	month
yr	year
m.y.	million years
g	gram (not gm)
mg	milligram
kg	kilogram
Hz	hertz
kHz	kilohertz
MHz	megahertz
km	kilometer(s)
m	meter(s)
mm	millimeter(s)
cm	centimeter(s)
fm	fathom(s)
nm	nautical mile
mi	mile(s)
ft	foot (feet)
in.	inch (note period)
diam	diameter
ha	hectare
M	molar
ppm	parts per million
W	watt (or west)
X	magnification

μg	microgram
μm	micrometer (micron)
gal	gallon
ml	milliliter and cubic centimeter
liter*	should be spelled out when confusion can exist; mainly when it is used alone. When in print, "10 l" looks like a poorly spaced 101. Confusion does not exist in a list of ingredients [(i.e., 14 kg sawdust, 500 g potassium nitrate, 1.5 l water)] or when in combination (ml).

Miscellaneous: Standard abbreviations used in text, their proper punctuation, and some terms that should be spelled out.

AC DC	alternating current and direct current
B.A. B.S. M.A.	
M.S. M.Sc. Ph.D.	college degrees
Co.	county
counties	spell out (no abbreviation)
elev.	elevation (note period)
Fig. or fig.	figure
maximum	no abbreviation
minimum	no abbreviation
pers. comm.	personal (oral) communication
P.O.	post office
R/V <u>Searcher</u>	name of research vessel is underlined
SEM	scanning electron microscope
States	spell out to avoid confusion
Table	write out completely
TEM	transmission electron microscope
UK	United Kingdom (no spaces)
U.S.A.	United States of America
USNM	National Museum of Natural History
weight	no abbreviation

Directions and coordinates:

N E S W ENE	
SE SSW	(no periods)
T14N, R10W, SW¼	
Sec. 2	legal description for localities
10°06'N, 25°07'W	latitude and longitude

Latin and other foreign language terms (the following are accepted as written, without underlining; definitions follow terms).

aff.	affinis, having affinity with but not identical with
a posteriori	known from experience
a priori	intuitively, independent of experience
ad lib.	ad libitum, freely available
auct.	auctoris, of the author
auctt.	auctorum, or authors
ca.	circa, about
cf.	conferre, compare
e.g.,	(note comma) <i>exempli gratia</i> , for example
emend.	emended, emendation
en masse	in a body, as a whole
et al.	et alia, and others
etc.	et cetera, and so on
i.e.,	(note comma) such as
in litt.	in a letter (Note: data or information in recent unpublished manuscripts should not be cited in any form; however, quotations or use of data extracted from old manuscripts, as exist in archives, libraries, and occasionally herbaria, may be used)
in situ	in place
in utero	in the uterus
in vitro	outside the living organism
in vivo	in the living organism
leg.	collector or collected by
nec	not
nom. dub.	nomen dubium, name of doubtful application
nom. nud.	nomen nudum (plural, nomina nuda), name without validation
part.	partim, part
per se	by itself, as such
p.p.	pro parte, in part
sensu	as defined by
sic	thus (to signal exact transcription)
s.l.	sensu lato, in the broad sense
s.s.	sensu stricto, in the strict sense
via	by way of, by means of
vis-à-vis	in relation to, as compared with
viz.	videlicet, namely
vs. or versus	against, in contrast to

## Statistical terms:

<u>ANOVA</u>	analysis of variance
<u>CV</u>	coefficient of variation
<u>df</u>	degrees of freedom
<u>n</u>	sample size or number in sample
<u>P</u>	probability
<u>r</u> or <u>R</u>	correlation coefficient
<u>SD</u>	standard deviation
<u>SE</u>	standard error
<u>SEM</u>	standard error of the mean
<u>t f U Z X<sup>2</sup></u>	statistical tests
<u>X</u>	mean

Symbols.---Male ( $\delta$ ) and female ( $\varphi$ ) symbols should not be used in the text, but may be used in figures and lists of specimens examined (8  $\delta$  or 14  $\varphi$   $\varphi$ —note space between number and symbol). Write percent as one word in the text, but use the percent sign after numerals (1%, 99%) and in bodies of tables.

Because of possible confusion with similar symbols, do not use X as a symbol for the word “by.” Write, for example, “Traps used were 7.6 by 7.6 by 22.8 cm. . . .” If a multiplication sign is used in mathematical formulae or for indications of magnification, identify it as such in the margin of the manuscript.

### Documentation and Literature Citation

The function of literature citation is to assist readers in locating material referenced by the author, a process that permits an orderly growth of knowledge through continued testing and reassessment. Documents written primarily to fill administrative requirements are not catalogued in most libraries and do not enter the body of knowledge that supports research. Therefore, such documents are not to be included in the Literature Cited section; the quarterly reports of U.S. Fish and Wildlife Service Cooperative Wildlife Research Units and job completion reports for Pittman-Robertson Federal Aid in Wildlife Restoration projects are examples of this kind of material. Certain other state, provincial, and federal reports also are excluded from lists of citations. Abstracts of oral presentations delivered at professional meetings and printed separately are excluded, but references to abstracts in Dissertation Abstracts and Masters Abstracts and abstracts published in journals (e.g., American Zoologist, American Journal of Botany) are permitted.

Style of documentation.---When citing informational references in text, use the form “Jones (1983)” if the author’s name is part of the sentence and “(Jones 1983)” if it is not. Two articles by one author cited at one time should be written “(Jones 1975, 1982)”; two articles published by the same author in the same year, “(Jones 1981a, 1981b).” Other examples follow:

(Cameron 1977:507) or Smith (1957:23, table 3) [Note: only cite pagination in text references for direct quotations, in a synonymy, or in reference to a specific table or figure in another publication.] In text, citations of figures or tables other than those in the present manuscript should be in lowercase letters. Citations of figures or tables in the text should begin with a capitol letter, as: Fig. 1 or Table 2.

“In press” citations in text should not be used. Use the year of expected publication (current or subsequent year) and end the citation listing in the Literature Cited section with “(in press)”—see Appendix II. This allows for less costly corrections when the citation is updated at the page proof stage.

Citations with more than two authors are cited in the text as: Lidicker et al. (1976). Do not underline the “et al.” Multiple citations in the text should be ordered chronologically and then alphabetically if in the same year, for example (Jones 1961, 1963; Hennings & Hoffmann 1977, Phillips 1978, Jones & Smith 1981, Jones & Baker 1983, Mares et al. 1983) (Note: a semicolon should be used after citing two or more articles by the same author in a multiple citation, however, a comma should be used after different authors). Use an ampersand (&) between surnames of authors rather than “and.” In the text, multiple citations of three or more authors, in the same year with the same first author, should cite all authors, for example (Jones, Smith, & Williams 1988; Jones, Williams, & Smith 1988; Jones, Williams, Smith, & Baker 1988).

In the text, unpublished material can be referenced as follows: (pers. comm.) denotes information obtained orally; (in litt.) denotes information obtained in a letter. Names of persons providing unpublished information should include initials when referenced in text (e.g., R. H. Tamarin, pers. comm.; D. P. Christian, in litt.). In the Literature Cited section, do not cite or use information from unpublished recent manuscripts (except theses and dissertations) or papers in preparation. Unpublished data may not be referenced in any context.

Citations in the text that indicate the author(s) of zoological scientific names should be as follows: Family Caryophyllidae Dana, 1846; Didelphys microtarsus Wagner, 1842:359; and, Themiste dyscrita (Fisher, 1952). Note the use of a comma after the author(s) name(s). In botanical scientific



names, dates may be used in the case of homonyms. The proper form for new zoological descriptions, plus their associated synonymy, is as follows:

Chaceon bicolor, new species

Figs. 1--3

Geryon affinis.---Griffin & Brown, 1976:256, figs. 7--9.---  
Sakai, 1978:9, figs. 18--19, pl. 2, fig. D (color). [Not  
Geryon affinis A. Milne Edwards & Bouvier, 1894]

A more complete synonymy, with style examples, is as follows:

Chrysogorgia spiculosa (Verrill, 1883)

Figs. 5--6

Dasygorgia spiculosa Verrill, 1883 (in part: 1 of 2 specimens  
from BL-190, 1 of 2 specimens from BL-195, not BL-  
205,? BL-222,? BL227), 23--24, pl. 2, fig. 5.---not  
Wright & Studer, 1889:9--10 (= C. affinis/elegans).

Chrysogorgia sp. Agassiz, 1888:144, fig. 456.---Bayer, 1973:  
fig. 18.

Chrysogorgia spiculosa: Versluys, 1902:53, 60, 61.---not  
Nutting, 1908:591.---Kükenthal, 1919: 537, fig. 235;  
1924:406--407.---Bayer & Macintyre, 2001:342 (mi-  
nerology).

Chrysogorgia elegans: Deichmann, 1936:231--232 (in part:  
pl. 22, fig. 7, pl. 33, fig. 1: BL-44 (in part), BL-190, BL-  
195 (in part), BL-200, and MCZ 4861).

Note the names of subsequent users are separated from the name of the taxon by a distinctive and explicit manner (Article 51.2.1, International Commission on Zoological Nomenclature 1999), in this case by using a colon (: ) or a period and a 1-em dash (.-).

The proper form for new botanical descriptions, plus their associated synonymy, is as follows:

Pityrogramma mortonii Jackson, nom. nov.

Pityrogramma mutabilis Gleas., Proc. Biol. Soc. Wash. 46:  
278. 1933,

non L., 1753. Type: U.S.A.: Arizona: Cochise Co.: 7 mi NW  
of Wigwam, 4800 ft elev, Brooks 482 (US; isotype UC).

All citations of author and date, whether informational, taxon describers, or essential references in the synonymy, except for botanical synonymies, must be listed in Literature Cited. Literature in botanical synonymies should be abbreviated according to the Botanico-Periodicum-Huntianum or Taxonomic Literature, ed. 2.

The list of references at the end of the manuscript should have the primary heading "Literature Cited." Sample literature citations are listed in Appendix II. Like all other parts of the manuscript, this section must be double-spaced. Only papers referred to in the text may be listed. The list must be alphabetical by authors' last names. Therefore, within this structure, papers with one author would be listed first, then those with two authors (alphabetical by second author), then three authors, and so on. Use first author et al. (e.g., Patton, J. L., et al.) for papers having seven or more authors. Where the author line is identical, the listing should be chronological by publication date. If two or more papers by the same author or sequence of authors are listed, the name(s) are not repeated but are replaced by a 3 em dash (six dashes in typescript) and a period. Use a 3 em dash in subsequent entries for all repeated authors. For example:

Cockrum, E. L. 1974.  
 -----, 1975.  
 -----, & J. K. Jones, Jr. 1978.  
 -----, -----, & J. D. Smith. 1980.

(Note: Throughout the text and in the Literature Cited, insert a space between the initials of a persons name, as above.)

The volume number of a journal or other serial publication should be cited. However, do not include the issue number for journals having continuous pagination throughout the year or volume. When citing publications that have only a number and no volume, treat the number as a volume (Occasional Papers of the Museum of Natural History, University of Kansas 25:1–39). Underline scientific names or other words only if italicized in the original title. In citing books, omit Roman pagination (e.g., "J. Wiley and Sons, New York, 432 pp." not "xxii + 432 pp.") except in instances that those pages contain the first reference to a taxon under consideration. Also, provide only the first city listed for publishers (e.g., John Wiley and Sons, New York" not John Wiley and Sons, New York, Chichester, Brisbane, and Toronto"). Plates (or figures), if not included in paginated materials, should be referenced after pagination (e.g., 286 pp. + pls. 1–24 [or figs. 1–24]). If plates, figures, or tables are paginated, do not cite them again in the reference. Journal names and book titles are set in Roman type, so do not underline.

Abbreviations used in Literature Cited.---Abbreviations must not be used in the Literature Cited, except for those used in the title of the cited paper. Include and spell out all words that comprise the reference, including articles, conjunctions, and prepositions. Manuscripts will be returned to the author(s) if journal names are not completely spelled out.

### Conclusions

Before submitting your manuscript, carefully check all citations in the text, including figure and table captions, against listings under Literature Cited, and check each entry in the Literature Cited section against its original source to verify title, year of publication, names, quotations, and page numbers. Include all citations, when appropriate, in synonymy listings. The editors scan the Literature Cited and make spot checks for accuracy, but cannot assume responsibility for verifying all citations.

A summary in French, German, Russian, or Spanish is acceptable. This summary, which may be a translation of the abstract, should be placed immediately after the English abstract. Do not include an additional summary or summary paragraphs in English at the end.

The sequence of material in each copy should be: Title, Author(s), Author(s) Address(es), Abstract, Text, Acknowledgments, Literature Cited, Appendix, Figure Legends, Figure copies (each numbered and identified), Tables (each table numbered with an Arabic numeral and with heading provided). Number every page sent with the manuscript, including Literature Cited, figure legends, and tables. Any appendices should appear after Literature Cited. Figure legends and then copies of the figures follow. Next, the tables, each on a separate sheet. Glossy prints of each figure (or original artwork if high-contrast photographs of graphics cannot be obtained), should complete the parcel of manuscript materials. Three copies of all materials, including figures (legible photocopies acceptable), should be submitted with a cover letter stating the title, full name(s) of author(s), and availability of publication funds. Do not submit manuscripts under consideration for publication elsewhere. Author(s) address(es) must not have any abbreviations, including state or province names. Also, indicate country, including U.S.A., when appropriate.

### Acknowledgments

The acknowledgments section should contain a few brief statements in a single paragraph to recognize the contribution of others and support from patrons or agencies. Use only initials for names of persons acknowledged, but spell out names of agencies (e.g., National Science Foundation not NSF). Parts of this manuscript were extracted intact and other parts

paraphrased from a similar manuscript prepared by D. E. Wilson, A. L. Gardner, and B. J. Verts for The Journal of Mammalogy, from "Standard style for technical publications" prepared for customers of Allen Press, Inc., by G. Dresser, and "The Allen Press Guide to Illustration Preparation." Helpful suggestions for this publication were provided by C. C. Baldwin, S. D. Cairns, F. D. Ferrari, S. L. Gardiner, G. R. Graves, G. D. Johnson, R. Lemaitre, R. B. Manning, W. N. Mathis, and D. E. Wilson.

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- Couch, L. K. 1932. Breeding notes on a few Washington mammals.---The Murrelet 13:25.
- Day, R. A. 1994. How to write & publish a scientific paper. Fourth edition. Oryx Press, Phoenix, Arizona, 223 pp.
- 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.
- Junge, R., & D. F. Hoffmeister. 1980. Age determination in raccoons from cranial suture obliteration.---The Journal of Wildlife Management 44:725-729.
- Linsdale, J. M. 1946. The California ground squirrel: a record of observations made on the Hastings Natural History Reservation. The University of California Press, Berkeley, 475 pp.
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- Style Manual Committee. 1994. Scientific style and format: the CBE manual for authors, editors, and publishers. Sixth edition, Council of Biological Editors, Inc., Cambridge University Press, N.Y., 825 pp.
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## Appendix I

## Examples of Typescript for Page Having Figure Legends

Fig. 1. Localities at which Sorex trowbridgii (open circles) and S. bendirii (closed circles) were collected in Benton Co., Oregon, 1975–1986.

Fig. 2. Relationship between body mass and body length for (a) 12 Sorex trowbridgii, and (b) five S. bendirii collected in Benton Co., Oregon, 1975–1986.

Fig. 3. Syringonomus dactylatus. A. Photomicrograph of the cervical region of the holotype, USNM 77172; unlabeled arrows point to amphidial gland; scale equals 100  $\mu\text{m}$ . B. Photomicrograph of the posterior body region and tail of the paratype USNM 77175; scale equals 100  $\mu\text{m}$ . Abbreviations. ---AV, anal vent; CG, caudal gland; NR, nerve ring.

## Appendix II

## Examples of Literature Citations, with Parenthetical Comments on Style Following Some Entries

Journals. ---

- Bader, R. S. 1965. A partition of variance in dental traits of the house mouse. --- *Journal of Mammalogy* 46:384–388.
- Blair-West, J. R., et al. 1968. Physiological, morphological and behavioural adaptation to a deficient environment by wild native Australian and introduced species of animals. --- *Nature* 217:922–928. [use of “et al.” for papers with seven or more authors]
- Blake, J. A. 1985. Polychaeta from the vicinity of deep-sea geothermal vents in the eastern Pacific I: Euphrosinidae, Phyllodocidae, Hesionidae, Nereididae, Glyceridae, Dorvilleidae, Orbiniidae, and Maldanidae. Pp. 67–101 in M. L. Jones, ed., *Hydrothermal vents of the eastern Pacific: an overview*. --- *Bulletin of the Biological Society of Washington* 6:1–566.
- Carleton, M. D., & C. B. Robbins. 1985. On the status and affinities of Hybomys planifrons (Miller, 1900) (Rodentia: Muridae). --- *Proceedings of the Biological Society of Washington* 98:956–1003. [Underlined scientific names will be set in italics; note use of an ampersand (&) instead of “and” between authors’ names]
- Fauvel, P. 1936. Sur quelques annélides polychètes de l’Île de Pâques. --- *Bulletin du Muséum National d’Histoire Naturelle, Série 2*, 8:257–259. [Include all diacritical marks]

- Ortiz, D. L., P. Costa, & B. J. LeBoeuf. 1990. Water and energy flux in elephant seal pups fasting under natural conditions.---Physiological Zoology (in press). [Note use of probable year of publication after authors names and the use of "in press," in parentheses, after the journal name]
- Whitaker, J. O., Jr., & R. E. Wrigly. 1972. *Napaeozapus insignis*.---Mammalian Species 14:1-6. [underline scientific names only if italicized in original title]
- Wicksten, M. K. 1984. *Alpheopsis harperi* (Decapoda: Alpheidae): A new species of snapping shrimp from Texas.---Northeast Gulf Science 7(1):97-100.

Proceedings and transactions.---

- Chitty, D. 1952. Mortality among voles (*Microtus agrestis*) at Lake Vyrnwy, Montgomeryshire in 1936-9.---Philosophical Transactions of the Royal Society of London, Series B, 236:505-552.
- Kirsch, L. M., & A. D. Druse. 1973. Prairie fires and wildlife.---Proceedings of the Annual Tall Timbers Fire Ecology Conference 12: 289-304.
- Peek, J. M., M. C. Scott, L. J. Nelson, D. J. Pierce, & L. L. Irwin. 1982. Role of cover in habitat management for big game in northwestern United States.---Transactions of the North American Wildlife and Natural Resources Conference 47:363-373.

Books.---

- Baird, S. F. 1857 [1858]. Mammals. in Reports of explorations and surveys for a railroad route from the Mississippi River to the Pacific Ocean. Beverly Tucker, Printer, Washington, D. C., 8(part 1):1-757 + pls. 17-28, 30-60. [give correct publication date in brackets]
- Barbour, R. W., & W. H. Davis. 1969. Bats of America. The University of Kentucky, Lexington, 286 pp. [City is not followed by state when name of state is part of the name of the press]
- Eisenberg, J. F. 1981. The mammalian radiations: an analysis of trends in evolution, adaptation, and behavior. The University of Chicago Press, Chicago, 610 pp. [Names of large, universally recognized cities are not followed by state]
- Honacki, J. H., K. E. Kinman, & J. W. Koepl (eds.). 1982. Mammal species of the world: a taxonomic and geographic reference. Allen Press, Inc. and The Association of Systematics Collections, Lawrence, Kansas, 694 pp.
- Hsu, T. C., & K. Benirschke. 1969. *Microtus oregoni* (creeping vole) 2n =

- 17, 18. An atlas of mammalian chromosomes. Vol. 3, Folio 121, Springer-Verlag, New York, unpagged. [Pages are not numbered]
- Linnaeus, C. 1758. *Systema nature per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentii, synonymis, locis*. Tenth edition. Laurentius Salvius, Stockholm 1:1–824. [give complete title, do not use ellipsis]
- Nowak, R. M., & J. L. Paradiso. 1983. *Walker's mammals of the world*. Fourth edition. Johns Hopkins University Press, Baltimore, 1 and 2: 1–1362.

Part of book.---

- Bourliere, F. 1955. *Ordre des Fissipedes. Systématique*. Pp. 215–291 in P. P. Grasse, ed., *Traité de Zoologie*. Masson et Cie., Paris 17(1):1–1170. [period after title of volume]
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Table 1.---Some reproductive patterns in four species of Spermophilus in western United States.

Species and state	Litter size <sup>a</sup>		Range	Reproductive season <sup>b</sup>	Authority
	<u>n</u>	<u>X</u>			
<u>S. washingtoni</u>					
Washington	26	8.0	5-11	February--March	Scheffer 1941
<u>S. beldingi</u>					
Oregon	110	5.2	5-8	April--June	Costain 1978
California	37	7.1	3-10	April--July	McKeever 1966
<u>S. columbianus</u>					
Washington	21	5.8	2-7	March--May	Couch 1932
<u>S. beecheyi</u>					
California	40	7.5	5-12	February--April	Linsdale 1946
California	34	6.1	1-9	March--June	Tomich 1962

<sup>a</sup> Based on counts of embryos.

<sup>b</sup> From first evidence of reproduction behavior to first appearance of young.

Table 2.---Means ( $\pm$ SE) and ranges for mass and length of 514 bacula from raccoons (Procyon lotor) among five age classes, northwestern Oregon, 1982-1983 and 1983-1984 furbearer seasons.

Age class <sup>a</sup>	n	Baculum mass (g)		Baculum length (mm)	
		<u>X</u> $\pm$ SE	Range	<u>X</u> $\pm$ SE	Range
1	205	0.63 $\pm$ 0.01	0.30-1.22	71.8 $\pm$ 0.5	54.5-88.9
2	145	2.99 $\pm$ 0.04	2.03-4.16	105.9 $\pm$ 0.4	92.7-117.5
3	48	3.69 $\pm$ 0.08	2.63-4.76	107.9 $\pm$ 0.5	102.6-117.7
4	43	4.01 $\pm$ 0.07	2.76-4.86	109.3 $\pm$ 0.6	102.1-119.5
5 <sup>b</sup>	73	4.40 $\pm$ 0.07	3.05-5.67	109.2 $\pm$ 0.5	99.0-118.8

<sup>a</sup> Age classification based on cranial-suture technique (Junge & Hoffmeister 1980).

<sup>b</sup> Includes all individuals  $\geq$ 4.5 years old.







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