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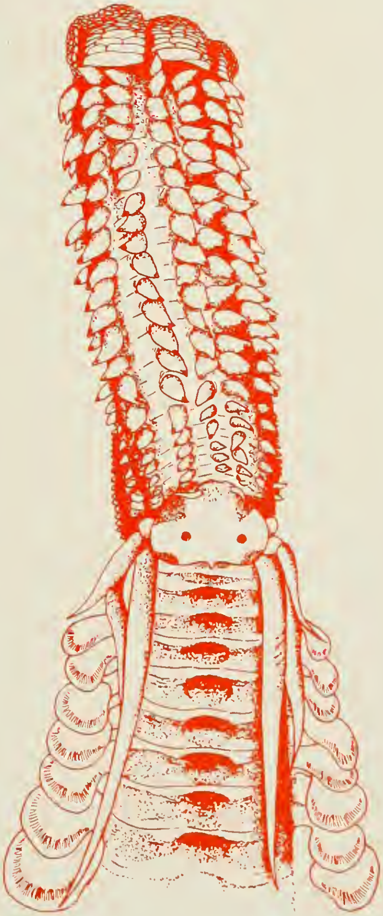

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Systematics and Ecology of Benthic Phyllodocidae (Annelida: Polychaeta) off the Columbia River, U.S.A.

Michael J. Kravitz and Howard R. Jones

Abstract.—The benthic phyllodocid polychaete fauna of the continental shelf off the Columbia River, northern Oregon, and southern Washington, at depths of 11 to 97 m, is reported. Three species of *Eteone* and one species of *Anaitides* are newly described. *Eteone* (*Mysta*) *barbata* is newly reported in the Northeast Pacific Ocean. Ranges are extended for *Eteone longa, Anaitides hartmanae* and *Anaitides longipes,* the latter two species new to Oregon and Washington; *E. longa* is new to Oregon. New records are given for *Eteone californica* and *Eulalia levicornuta*. The local distribution, including depths and sediment type(s), of each species is summarized. The distributions of all species in the genus *Anaitides* overlapped, while those of some species in *Eteone* were relatively segregated. The occurrence of *E. longa* following the dumping of dredged sediments from the Columbia River mouth is discussed.

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Phyllodocids are active, mainly benthic, polychaetes which are often brilliantly colored in life. The systematics and phylogenetic relationships within the family Phyllodocidae, as well as the geographical distributions of species in the polar basin and the Northwest Pacific Ocean, were treated by Ushakov (1972). Phyllodocid polychaetes have been reported from the Northeast Pacific Ocean off California by a number of workers, most notably Hartman (1936, 1968), and off Oregon and Washington by Carey (1972), Hartman and Reish (1950), Fauchald and Hancock (in press), Banse and Hobson (1974), and Richardson et al. (1977—a Final Report to the U.S. Army Corps of Engineers). Of these, only Richardson et al. (1977) dealt with the area off the mouth of the Columbia River. Richardson et al. (1977), making use of species identifications in all the major phyla, defined the benthic invertebrate assemblages in a 435 square km area extending from northern Oregon to southern Washington (Fig. 1). Of the 38 polychaete families represented in this area, the family Phyllodocidae was the most speciose, containing 14 species. The present paper discusses the systematics and ecology of those species. Other polychaetes off the Columbia River will be treated in a forthcoming paper.

Methods

1,665 quantitative samples were taken at 119 stations off the Columbia River from December 1974 through June 1976 using a 0.1 m^2 Smith-McIntyre grab on board the R/V *Cayuse*. Locations of stations are shown in Fig. 1 and the cruises during which they were sampled are listed in Table 1. Six replicate grab samples

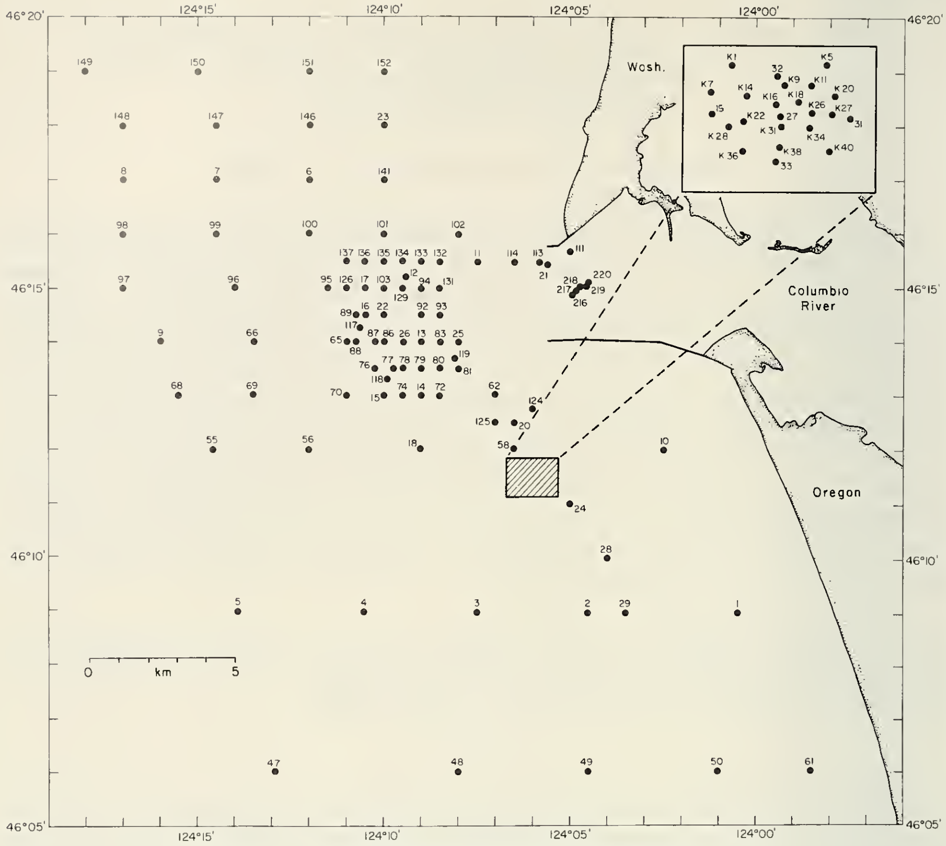

Fig. 1. Station locations off the Columbia River.

were obtained at each station during each cruise that the station was sampled. Two sets of six replicate grab samples were obtained at stations 14, 25 and 26 during cruise A. Of each set of six replicate grab samples, five were sieved through a 1 mm mesh screen, the polychaetes retained on the screen preserved in 10% Formalin and identified, and one was used for sediment analysis. In replicate sets 16E, 17E, 24D, 29D, 47A, 217D, K20E and K38E, polychaetes were identified from four rather than five samples. In 7B, 7C, 7D, 7E, 7G, 8B, 8C, 8D, 8E, 8G, 96A, 97A, 98A, 99A, 148B, 149B and 150B, polychaetes were identified from only three samples. Twenty-one grabs were taken at station 19 during cruise A, polychaetes identified from 20 of them. From cruise C onward, one grab of every replicate set was screened through a 0.5 mm screen and later divided into 1 mm and 0.5 mm fractions. Though a number of phyllodocid polychaetes in the 0.5 mm fractions were too small to be identified to the species level, none appeared to differ at the species level from those encountered in the 1 mm samples. Specimens in the 0.5 mm fractions are not reported herein.

Study Area

The major feature in the study area (Fig. 1) is the Columbia River, the largest river on the Pacific coast of North America. The Columbia River plume is delim-

Table 1. Sampling dates (cruises) of stations off the Columbia River.

	Cruises[1]								
	A	B	C	D	E	F	G	H	I
Stations	4–8 Dec. 1974	19–25 Jan. 1975	19–21 April 1975	23–27 June 1975	12–15 Sept. 1975	21–22 Oct. 1975	5–9 Jan. 1976	19–20 April 1976	7–8 June 1976
13, 25, 26	x		x	x	x				
11, 21		x	x	x	x				
1–5, 10, 14–16, 22	x		x	x	x		x		
6–8, 12, 17, 23		x	x	x	x		x		
18, 19	x	x	x	x	x		x		
20		x	x	x	x	x	x		
K7, K11, K18, K22, K26, K31					x	x	x	x	x
28, 31, 33				x	x	x	x	x	x
24		x	x	x	x	x	x	x	x
27				x	x	x		x	x
29				x	x	x	x		
K16					x	x		x	x
32				x	x				
216–220				x					
K1, K5, K9, K14, K20, K27, K28, K34, K36, K38, K40					x				
9, 47–93, 95–102	x								
111–152		x							
94, 103	x	x							

[1] Cruises A, B, C, D, E, F, G, H, I are designated, respectively, as the following in Richardson et al., 1977: C7412B, C7501D, C7504B, C7506C, C7509E, C7510E, C7601A, C7604B, C7606A.

ited by a 32.5‰ salinity isopleth which may extend to a depth of about 40 m (Barnes et al., 1972). Salinities at 20 m or more below the surface vary little throughout the year, about 32‰ to 34‰ (Duxbury, 1972). Bottom temperatures at these depths off the Columbia River probably do not differ appreciably from those reported off central Oregon (Adriana Huyer, pers. comm.), i.e. between 6°C and 7°C to nearly 11°C (Huyer, 1977). Bottom currents off the Columbia River are discussed in Barnes et al. (1972).

Stations directly off the Columbia River and south to 46°13′N, between 124°08′W and 124°11.5′W, exhibited large seasonal variation in sediment composition (Table 2A) in concordance with seasonal variation in river flow and wave conditions. Bottom sediments within this area contained the least mud (silt + clay) during the winter, when much of it is suspended in the water column by long-period surface waves, and the most mud during the summer or fall, when high river flow and moderate wave conditions favors deposition of silts and clays (Kulm et al., 1975). Sediment types of seasonally sampled stations within the above area changed from sand to muddy sand (silty or clayey sand) or sandy silt—or in one case, clayey silt. Stations outside this area (Table 2B) did not show large temporal variations in silt + clay content. Of these, the majority were sand.

Table 2A. Sediments and Depths off the Columbia River: Stations within area characterized by large seasonal variation in silt + clay content.[1]

		Percentage Silt + Clay				
		Winter	Spring	Summer	Fall	
Station	Range of Depths[2] in meters	Cruise A and/or B + sometimes G	Cruise C	Cruise D	Cruise E	Sediment Type(s)[3]
13	18–20	3.46	14.91	45.75	39.28	Sa, SSa
14	31–33	0.99–1.39	6.27	5.16	29.87	Sa, SSa
15	42–46	1.59–5.04	21.00	63.31	23.26	Sa, SSi
16	31–37	8.59–37.06	34.20	82.94	89.18	Sa, SSa, CSi
17	31–33	14.45–24.02	26.68	32.98	78.15	Sa, SSa, CSa, SSi
22	22–33	10.82–14.01	11.69	20.77	27.40	Sa, SSa
25	15–18	1.66–1.77	3.54	28.22	38.22	Sa, SSa
26	20–29	1.34–1.65	16.10	48.09	52.37	Sa, SSa
65	49	13.18	—	—	—	Sa, —
70	51	2.48	—	—	—	Sa, —
72	26	1.25	—	—	—	Sa, —
74	35	1.42	—	—	—	Sa, —
76	37	1.42	—	—	—	Sa, —
77	27	1.16	—	—	—	Sa, —
78	22	0.95	—	—	—	Sa, —
79	20	1.21	—	—	—	Sa, —
80	20	1.02	—	—	—	Sa, —
81	18	5.35	—	—	—	Sa, —
83	18	2.75	—	—	—	Sa, —
86	26	1.16	—	—	—	Sa, —
87	40	2.57	—	—	—	Sa, —
88	44	?	—	—	—	?
89	40	16.14	—	—	—	Sa, —
92	20	5.70	—	—	—	Sa, —
93	15	2.86	—	—	—	Sa, —
94	16–17	1.62–2.54	—	—	—	Sa, —
95	47	42.76	—	—	—	SSa, —
103	24–31	5.05–10.93	—	—	—	Sa, —
117	31	1.37	—	—	—	Sa, —
118	37	1.63	—	—	—	Sa, —
119	18	3.99	—	—	—	Sa, —
126	40	17.34	—	—	—	Sa, —
129	18	2.18	—	—	—	Sa, —
131	15	2.14	—	—	—	Sa, —
132	15	2.08	—	—	—	Sa, —
133	15	1.70	—	—	—	Sa, —
134	17	1.97	—	—	—	Sa, —
135	22	4.54	—	—	—	Sa, —
136	31	16.20	—	—	—	Sa, —
137	37	28.82	—	—	—	SSa, —

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[1] The area characterized by large seasonal variation in sediment composition is delineated in paragraph 2 under "Study Area."

[2] Depths are not corrected for tides or waves.

[3] Sa = sand, SSa = silty sand, CSa = clayey sand, SSi = sandy silt, CSi = clayey silt. Sediment types referred to in this paper are those of Shepard (1954).

Table 2B. Sediments and Depths off the Columbia River: Stations outside of area characterized by large seasonal variation in silt + clay content.[1]

Station	Range of Depths[2] in meters	Percentage Silt + Clay	Sediment Type(s)
1	17–20	1.24–2.84	Sand
2	29–35	1.21–1.73	Sand
3	45–53	1.68–3.16	Sand
4	66–70	3.13–6.23	Sand
5	82–88	14.49–28.33	Sand to Silty Sand
6	37–45	19.53–26.90	Sand to Silty Sand
7	55–66	22.52–42.40	Sand to Silty Sand
8	80–85	26.54–31.13	Silty Sand
9	81	23.06	Sand
10	15–17	1.12–1.23	Sand
11	11–13	1.21–5.27	Sand
12	15–16	1.73–8.13	Sand
18	40–46	1.47–12.06	Sand
19	29–31	1.25–2.03	Sand
20	22–24	0.97–5.16	Sand
21	17–20	1.32–16.91	Sand
23	27–31	10.13–29.23	Sand to Silty Sand
24	24–27	1.42–1.76	Sand
27	26–29	0.76–1.58	Sand
28	26–29	1.35–1.97	Sand
29	27–30	0.92–1.78	Sand
31	24–27	1.47–1.85	Sand
32	24	1.22–1.76	Sand
33	26–30	1.27–1.90	Sand
47	88–91	17.01	Sand
48	70	5.02	Sand
49	46	2.21	Sand
50	29	2.47	Sand
55	77	17.27	Sand
56	62	7.14	Sand
58	27	1.29	Sand
61	18	1.90	Sand
62	24	1.34	Sand
66	66	21.11	Sand
68	82	27.32	Silty Sand
69	68	15.51	Sand
96	67	21.25	Sand
97	97	31.19	Silty Sand
98	86	27.26	Silty Sand
99	68	24.25	Sand
100	48	27.07	Silty Sand
101	29	14.81	Sand
102	13	2.61	Sand
111	20	1.63	Sand
113	20	1.15	Sand
114	13	1.46	Sand
124	20	1.37	Sand
125	26	1.11	Sand
141	33	18.38	Sand
146	40	60.48	Sandy Silt
147	60	33.34	Silty Sand

Table 2B. Continued.

Station	Range of Depths[2] in meters	Percentage Silt + Clay	Sediment Type(s)
148	75	33.42	Silty Sand
149	84	39.14	Silty Sand
150	64	?	?
151	40	12.64	Sand
152	29	11.83	Sand
216	14	1.21	Sand
217	14	1.06	Sand
218	13	1.26	Sand
219	14	1.09	Sand
220	15	0.95	Sand
K1	29	1.28	Sand
K5	22	1.27	Sand
K7	22–29	1.19–1.69	Sand
K9	22	1.30	Sand
K11	22–27	1.21–1.52	Sand
K14	26	1.08	Sand
K16	25–27	0.89–1.48	Sand
K18	25–26	0.88–1.27	Sand
K20	24	1.18	Sand
K22	26–29	0.91–1.37	Sand
K26	24–27	0.97–1.59	Sand
K27	24	1.45	Sand
K28	29	1.45	Sand
K31	26–28	0.89–2.20	Sand
K34	27	1.11	Sand
K36	27	1.00	Sand
K38	27	1.42	Sand
K40	27	1.56	Sand

[1] The area characterized by large seasonal variation in sediment composition is delineated in paragraph 2 under "Study Area."

[2] Depths are not corrected for tides or waves.

In general, the silt + clay content of sediments north of the river exceeded that of sediments south of the river. Stations south of the river in less than 40–50 m (excluding those within the area of large seasonal variation in sediment composition) generally contained less than 5% silt + clay throughout the study period, the silt + clay fractions increasing further offshore. A detailed account of textural and mineralogical properties of sediments off the Columbia River is presented in Sternberg et al. (1977—a Final Report to the U.S. Army Corps of Engineers). Depths sampled in this study ranged from 11 to 97 m (see Tables 2A and 2B).

Species Accounts

Records of collected specimens are listed under the appropriate species by station and cruise. For example, three specimens collected at station 10 during cruise A would appear as 10A (3). Holotypes have been deposited in the United States National Museum. Paratypes have been deposited in the United States National Museum, the Allan Hancock Foundation, Oregon State University, and the Virginia Institute of Marine Science. Representative specimen(s) of every species reported herein (except *Paranaitis polynoides* and *Eulalia levicornuta*) have been deposited in the Allan Hancock Foundation.

Genus *Eteone* Savigny, 1818
Eteone fauchaldi, new species
(Fig. 2A–G)

Records.—2E (1); 3G (1); 6B (1), C (2), G (1); 12D (1); 13A (1); 14G (1); 16C (1), G (2); 17C (1); 18E (1); 19E (1, TYPE); 22C (1); 23E (1); 28F (1), H (1); 31H (1); 33E (1); 101A (1); 117B (1); 146B (1); K14E (1); K18E (1); K34E (2); K36E (1); K40E (1).

Description.—Length to 62 mm; width 0.5 to 1.9 mm; number of segments to 238. Prostomium long, trapezoidal with rounded anterior part having 2 pairs of slender, subulate antennae, the anterior pair slightly shorter (Fig. 2A). 2 widely set black eyes located slightly anterior to the small nuchal papilla at the posterior margin of prostomium.

First segment about 1½–2¼ times as long as segment 2, provided laterally with 2 pairs of tentacular cirri, similar in shape to the prostomial antennae. Ventral pair 1¼–1½ times as long as dorsal pair. Segment 2 with small setigerous lobe. Setae on segment 2 absent in the largest specimens (39 mm and longer), well developed in a juvenile (2.5 mm), and poorly developed in other specimens.

Dorsal cirri conspicuous, slightly asymmetrical, their posterior surfaces somewhat concave. Ventral cirri broad. Both dorsal and ventral cirri surpass acicular lobes throughout the body; the ventral cirri are shorter than dorsal cirri. Presetal lip of neuropodia exceeds postsetal one. Large acicula reaches or surpasses presetal lip. Length-width ratio of dorsal cirri in anterior and median segments varies with size of animal (Figs. 2B, 2E and 2G) and increases posteriorly in all specimens. In a large specimen the dorsal cirri are rounded and broader than long anteriorly at segment 24 (Fig. 2B), as long as wide at about segment 60 (Fig. 2C), broadly conical by segment 90 (Fig. 2D), and somewhat longer posteriorly. Anterior dorsal cirri of holotype (22 mm) nearly as long as wide (Fig. 2E), gradually becoming longer than wide posteriorly (Fig. 2F). Anterior dorsal cirri of younger specimens may be longer than wide (Fig. 2G). Setae with shafts ending in 2 very unequal prongs, these with associated spines. Appendage finely denticulated on concave edge.

Proboscis, when dissected, is tuberculate. Anal cirri long, tapering.

Color is whitish in alcohol.

It is our pleasure to name this species after Dr. Kristian Fauchald, who gave us so much of his time during our visits to the Allan Hancock Foundation.

Remarks.—As noted in the above description, setae on segment 2 are absent in the largest specimens, well developed in a juvenile, and poorly developed in other specimens. Thus, the setae on this segment may be lost with growth. Eliason (1962, *fide* Ushakov, 1972) observed a similar phenomenon in specimens of *Eteone lactea* Claparede from the Oresund.

Systematic discussion.—Eteone fauchaldi is not likely to be confused with any other Pacific species but it bears considerable resemblance to *E. heteropoda* Hartman, found in the Northwest Atlantic Ocean and the Gulf of Mexico. A comparison of the two species reveals the anterior ends (including the tentacular cirri) and posterior ends to be similar but the structure of the dorsal cirri to differ.

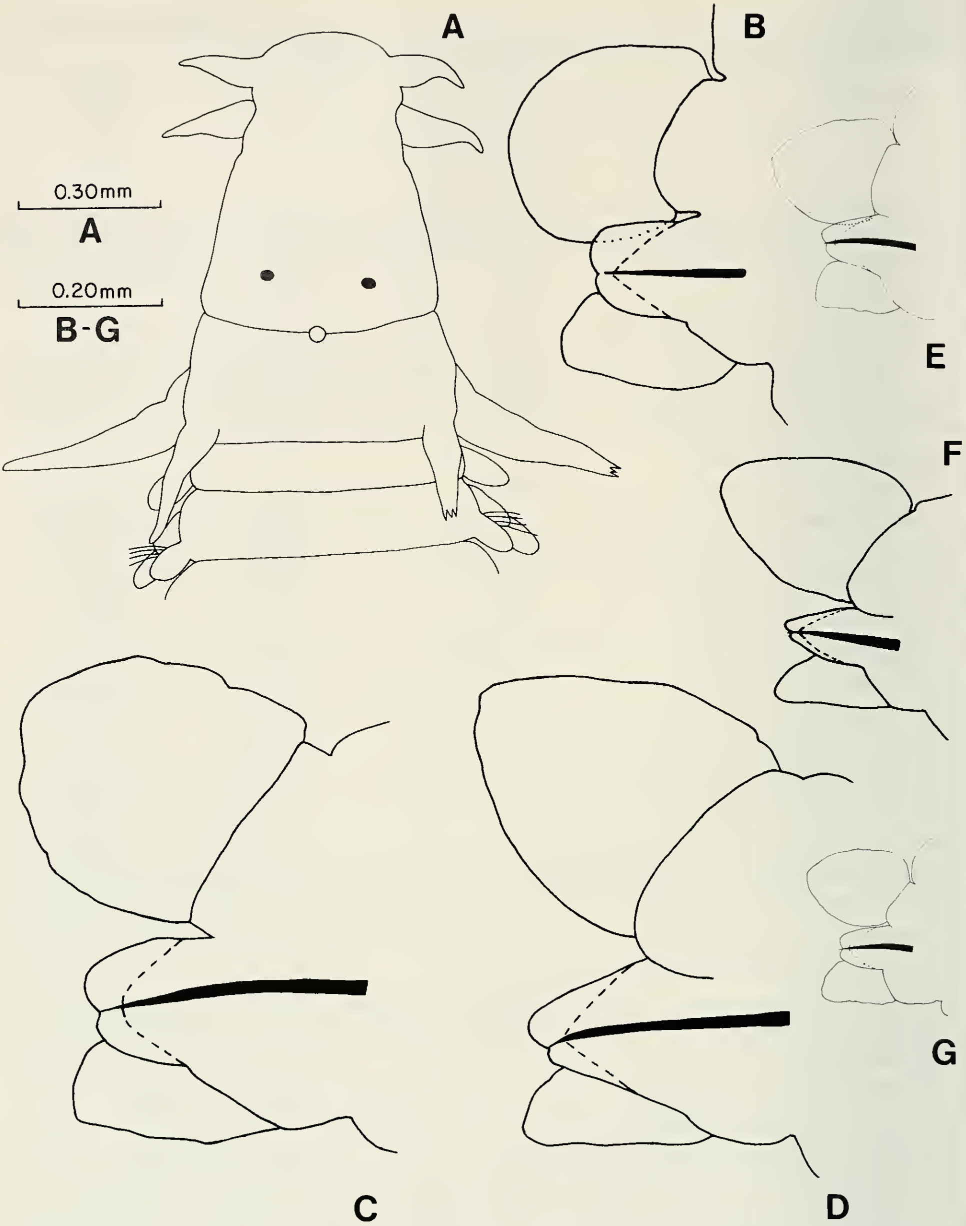

Fig. 2. A–G, *Eteone fauchaldi* new species. A, anterior end of a large specimen, dorsal view, ×100. B–D, from 39 mm specimen: B, parapodium from segment 24, anterior view, ×125; C, parapodium from segment 59, anterior view, ×125; D, parapodium from segment 90, anterior view, ×125. E–F, from holotype, approximately 22 mm: E, parapodium from segment 20, anterior view, ×500; F, parapodium from segment 92, anterior view, ×125. G (10 mm specimen), parapodium from segment 18, anterior view, ×500.

In *E. heteropoda* the middle and posterior dorsal cirri are distinctly asymmetrical, but in *E. fauchaldi* the dorsal cirri are only slightly asymmetrical.

Distribution.—Oregon to Washington in 15–50 m on sand, silty sand, and sandy silt (1).

Eteone longa (Fabricius, 1780)

Nereis longa Fabricius, 1780.

Eteone longa Pettibone, 1954; Berkeley and Berkeley, 1948; Banse and Hobson, 1974.

Records.—1D (1), E (5), G (1); 2E (3), G (6); 3E (2); 4E (1); 10E (1), G (1); 19E (1), G (1); 20G (1); 24F (2), G (1), H (6), I (2); 28E (2), F (3), G (1), H (8), I (2); 29E (3), F (1), G (1); 31E (3), F (5), G (2), H (3); 32E (1); 33E (2), F (2), H (1), I (2); K1E (2); K5E (1); K7E (2), F (2); K11E (2), F (1), G (1); K14E (2); K16E (1), H (1); K18E (1); K26E (2), F (2); K27E (2); K28E (2); K31E (1); K34E (1); K40E (1).

Pettibone (1954) synonymized *Eteone californica* Hartman, described from California, with *E. longa*. We consider the two as distinct species and have found both in the present study (see *E. californica* below). *E. longa* has dorsal cirri which are longer than wide, bluntly conical, but *E. californica* has broadly rounded dorsal cirri that are as wide as long. Specimens from Arctic Alaska and Washington identified as *E. longa* by Pettibone, 1954, were not examined by us, but the parapodium illustrated in that publication agrees with those of the present specimens.

In the Northeast Pacific Ocean, *E. longa* is previously known from British Columbia and Washington. The present records extend the distribution southward to northern Oregon.

Local distribution.—Off Oregon in 16–51 m on sand with less than 5% silt + clay. (One in 66 m on sand with 5.58% silt + clay.)

Eteone californica Hartman, 1936

Eteone californica Hartman, 1936, 1968.

Records.—2E (1); 3D (1), E (10); 4A (1), D (1), E (12), G (3); 5D (1), E (5), G (2); 6B (2), D (3), E (2), G (1); 7B (5), C (5), D (1), E (8), G (4); 8B (1), C (1), D (1), G (3); 9A (4); 13E (1); 16C (3); 18E (3); 19E (1); 20E (1); 28F (1); 48A (1); 55A (2); 56A (1); 65A (14); 66A (1); 69A (3); 70A (4); 96A (4); 98A (1); 99A (4); 100A (2); 147B (2); 148B (2); 149B (1); 150B (2).

Eteone californica differs from *E. longa* in having dorsal cirri as wide as long, broadly rounded, instead of longer than wide, bluntly conical.

These records are the first obtained off the coast of Washington and Oregon, but the species has been recorded both to the north and south.

Local distribution.—Oregon to Washington in 18–88 m on sand and silty sand.

Eteone spilotus, new species

(Fig. 3A–C)

Records.—5E (2), G (1); 7B (1), C (6), D (2), E (11), G (3); 8C (1), E (3), G (4); 15A (1); 16A (7); 22A (2); 65A (24); 88A (32, TYPE); 89A (2); 95A (1); 96A (1); 99A (1); 100A (8); 148B (2); 150B (1).

Description.—Length to over 26 mm; width 0.3 to 1.1 mm; number of segments to over 100. Prostomium slightly longer than wide, rounded anterior portion with 4 subequal antennae (Fig. 3A). 2 black eyes near posterior margin; a small nuchal papilla at postmedian margin.

Segment 1 about 1½ times as long as segment 2, with 2 pairs of subequal tentacular cirri longer than prostomial antennae. Segment 2 with setigerous lobes and setae well developed.

Parapodia with small dorsal and ventral cirri (Figs. 3B and 3C). Symmetrical dorsal cirri inflated and subquadrangular, about as long as broad, somewhat longer posteriorly. They reach or slightly surpass the acicular lobes throughout the body. In median and posterior segments neuropodial lips are subequal and elongated, ventral cirri reach to about middle of the acicular lobes (Figs. 3B and 3C). Setae with shafts ending in 2 equal prongs and numerous small spines. Appendage finely denticulated on concave edge.

Proboscis smooth when everted. Anal cirri 2, thick, twice as long as broad.

Color in alcohol pale, with distinct patches of black or brown pigment spots on dorsum of each segment—one patch at each side at base of parapodia, vaguely connected by a narrow transverse band; a smaller, medial patch anterior to transverse one on some segments. Pattern duplicated on ventrum. Dorsal cirri and some ventral cirri darkly pigmented.

Etymology.—The specific name is derived from the Greek *spilotos,* meaning spotted, in reference to the distinct patches of pigment spots on the body.

Systematic discussion.—*Eteone spilotus* differs from *E. californica* Hartman in body coloration and in having ventral cirri distinctly shorter than the acicular lobes.

Distribution.—Oregon to Washington in 33–88 m on silty sand and sand with greater than 10% silt + clay. (One on sand with 1.59% silt + clay.)

Eteone columbiensis, new species
(Fig. 3D–G)

Records.—11E (2); 21C (4), D (31, TYPE); 25D (1); 111B (8); 216D (2); 217D (2).

Description.—Length about 34 mm; width 0.4 to 1 mm; number of segments to over 150. Anterior region of body dilated through 15 to 20 segments. Prostomium elongate and abruptly tapered such that its broad posterior portion comprises about half the total length, sometimes less (Fig. 3D). Anterior margin of prostomium one third as wide as posterior margin, with 2 pairs of slender, subulate, subequal antennae. 2 black eyes in posterior part of prostomium, a small nuchal papilla at the posterior margin.

Segment 1 slightly longer than segment 2, with 2 pairs of tentacular cirri, dorsal pair shorter; both pairs slightly shorter than prostomial antennae. Segment 2 with setigerous lobes and setae well developed.

Dorsal cirri are symmetrical, subrectangular and inflated, very small in anterior setigers (Fig. 3E). They are larger and surpass the acicular lobes from setiger 10–20 through the mid-region (Fig. 3F), becoming smaller posteriorly (Fig. 3G). Pre- and postsetal lips of neuropodia subequal. Ventral cirri small, same length as acicular lobes in anterior region of body. Proceeding posteriorly acicular lobes become narrow, surpassing ventral cirri (Figs. 3F and 3G). Setae in median and

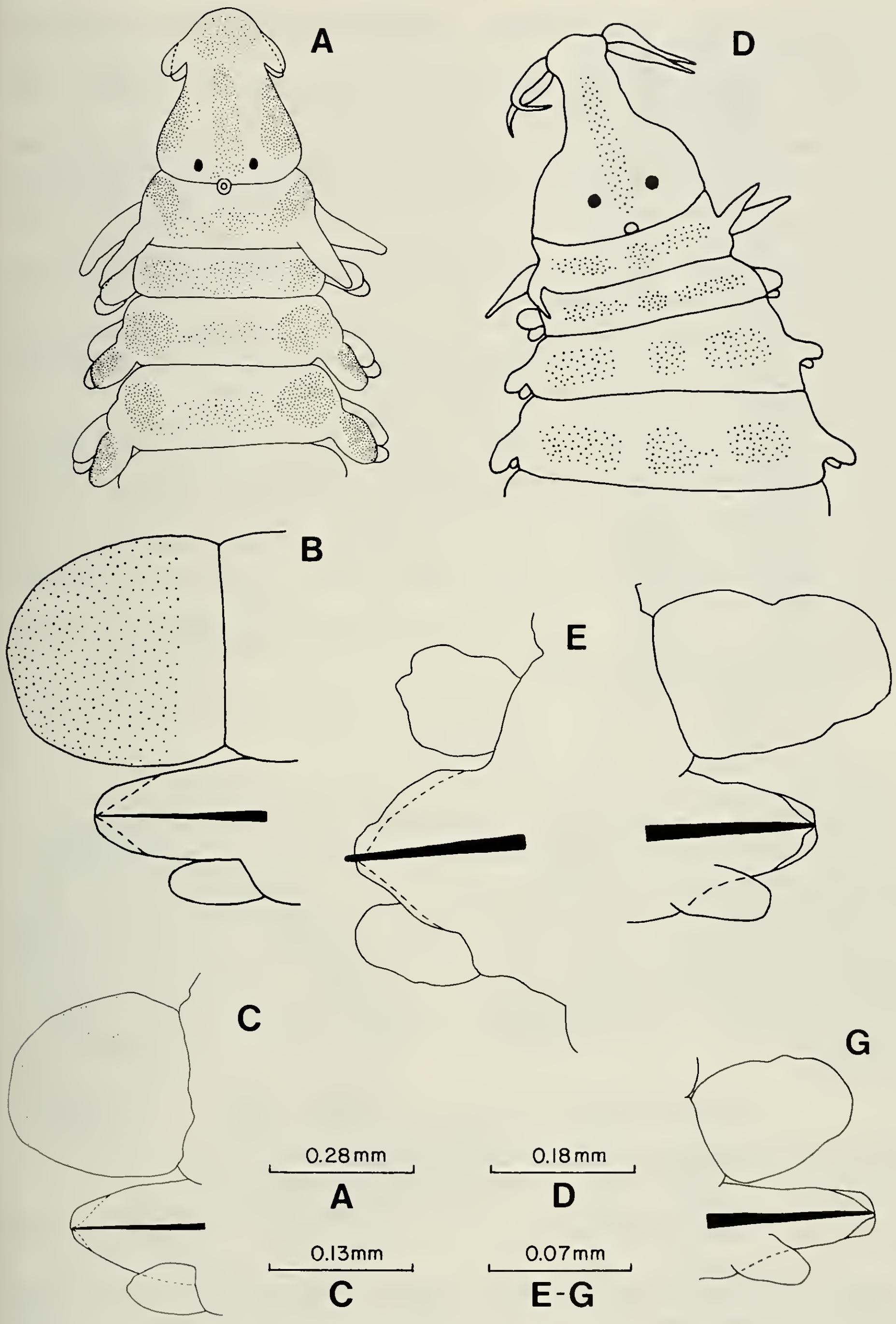

Fig. 3. A–C, *Eteone spilotus* new species. A, anterior end, dorsal view, ×125. B–C, from a 20 mm specimen: B, parapodium from segment 33, anterior view (diagram); C, parapodium from segment 71, anterior view, ×500. D–G, *Eteone columbiensis* new species. D, anterior end, dorsal view, ×100. E, parapodium from segment 7, anterior view, ×500. F, a median parapodium, posterior view, ×500. G, a posterior parapodium, posterior view, ×500.

posterior segments with shaft endings of equal length. Appendage finely denticulated on concave edge.

Proboscis smooth proximally; distal half with many small soft papillae. Anal cirri 2, thick, slightly clavate, twice as long as broad.

Color in alcohol pale green, with 3 distinct patches of dark green or brown pigment spots on dorsum of each segment—one patch at each side at base of parapodia and one medial. Pattern duplicated on ventrum. Dorsal cirri occasionally pigmented.

Etymology.—The specific name alludes to the Columbia River, in which region the present species was collected.

Remarks.—Four gravid individuals were collected at station 21, two in April 1975 (21C) and two in June 1975 (21D). The eggs are observed in the parapodial bases and give the egg-containing segments a light orange color.

Systematic discussion.—*Eteone columbiensis* appears to be closely related to *E. dilatae* Hartman, but differs from it in the shape of the prostomium and the body coloration. The prostomium of *E. dilatae* tapers gradually from the posterior to anterior margin, while that of *E. columbiensis* is abruptly tapered. *Eteone dilatae* is pale greenish yellow, while *E. columbiensis* is pale green with three distinct patches of dark green or brown pigment spots on dorsum and ventrum of each segment.

Distribution.—Within the mouth of the Columbia River to directly offshore in 11–20 m on sand, and silty sand (1).

Eteone sp.
(Fig. 4A–B)

Records.—4D (1), E (1); 5G (1); 6E (1); 18E (1); 31E (1); K40E (1).

These specimens, which belong to a single species, resemble *Eteone spetsbergensis* Malmgren in the form of the dorsal cirri. Dorsal cirri are asymmetrical and their length-width ratio in median segments can vary between individuals (compare Figs. 4A and 4B from two different specimens). Prostomium is about as long as wide. Setae on segment 2 are well developed. Ushakov (1972) and Pettibone (1954, p. 233) reported *E. spetsbergensis* as having setae poorly developed or absent on segment 2. Identification is uncertain at the present time.

Local distribution.—Off Washington in 44 m on sand (1); off Oregon in 26–82 m on sand.

Eteone (*Mysta*) *barbata* (Malmgren, 1865)

Mysta barbata Malmgren, 1865; Bergstrom, 1914.
Eteone (*Mysta*) *barbata* Ushakov, 1972; Pettibone, 1954.

Records.—4E (1); 6C (1), D (1); 14D (1); 15D (1); 16G (1); 17B (1), D (2); 22D (1).

Small individuals (about 9 mm) differ from large specimens in having a brown longitudinal stripe down each side of the dorsum. Also, the dorsal cirri of the small specimens have a greater length-width ratio, about 1 in posterior segments.

The present records are the first in the Northeast Pacific Ocean. Previously known in the Pacific only on the Asiatic coast, to the sea of Japan.

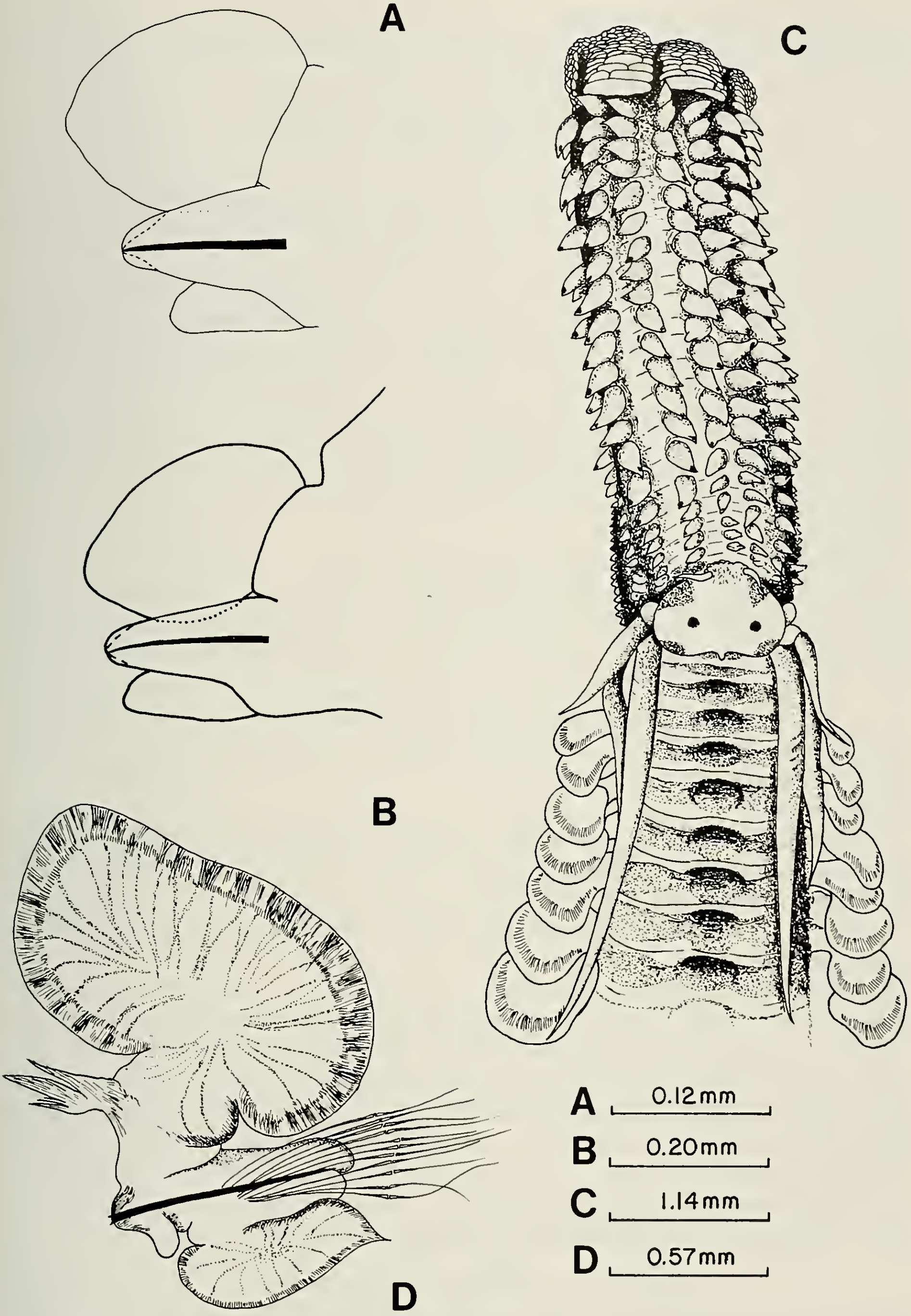

Fig. 4. A–B, *Eteone* sp. A–B, median parapodia from two different specimens. C–D, *Anaitides multipapillata* new species. C (holotype), anterior end and proboscis, dorsal view. D, 40th parapodium.

Local distribution.—Northern Oregon to Washington in 26–66 m on sand (with greater than 5% silt + clay), clayey sand (1), and sandy silt (1).

Genus *Anaitides* Czerniavsky, 1882

Anaitides multipapillata, new species

(Fig. 4C–D)

Records.—3D (1), G (1); 12E (2); 14C (1); 15D (1), G (1); 16D (1), G (1); 17B (1), D (1), E (1), G (1); 19D (1); 20D (1); 24I (1); 25E (1); 27H (1); 33G (1); 66A (1); 103B (1); 126B (1, TYPE); K31E (1); K40E (1).

Description.—Length to 95 mm; width excluding parapodia to 5 mm; number of segments to 200. Cephalic lobe subcordate with 2 dark circular eyes, a postmedian incision with a small occipital papilla, and a pair of small retractile nuchal processes at posterior margin of the cephalic lobe near base of first pair of tentacular cirri (Fig. 4C). Longest of four pairs of tentacular cirri drawn posteriorly reaches to segment 10–16. In preserved specimens, dorsum with dark iridescent transverse bars of olive green pigment, ventrum lighter, often whitish. Dorsal cirri usually olive green with a pale to white margin (Fig. 4D). Some preserved specimens are gray.

Prostomium with 4 antennae and pigmented in two triangular, olive green patches (Fig. 4C). Distal part of proboscis tuberculate with tubercles arranged in six rows. Proximal portion of proboscis with 12 evenly spaced rows of 20–24 papillae per row (Fig. 4C). Papillae large and turgid, often with red pigmented tips. Setae from third segment. Formula of anterior segments: $\left(1 + 0\frac{1}{1} + S\frac{1}{N}\right)$, with dorsal tentacular cirri on second segment the longest. Setae are homogomph compound spinigers, appendage finely denticulated along one edge, shaft distally spinous.

Dorsal cirri large, subquadrangular, covering about ¼ of the dorsum. Ventral cirri distally pointed, extending beyond setal lobes (Fig. 4D). Pygidium blunt. Anal cirri 2, cylindrical, tapering, about twice as long as width of pygidium.

Etymology.—The specific name derives from the numerous papillae per row on the proboscis.

Systematic discussion.—*Anaitides multipapillata* is distinguishable from *A. groenlandica* (Oersted) and *A. mucosa* (Oersted) by the absence of a distinct dorsal and ventral separation in the rows of proboscideal papillae and by the large size of these papillae. The papillae are more numerous than in *A. mucosa*. However, large specimens of *A. groenlandica* may have about the same number of papillae per row as *A. multipapillata*. Identification of *A. multipapillata* requires examination of proboscis.

Distribution.—South of Columbia River to directly off mouth in 15–66 m on sand, silty sand (1), clayey sand (1), sandy silt (2), and clayey silt (1).

Anaitides groenlandica (Oersted, 1843)

Phyllodoce (*Anaitides*) *groenlandica* Ushakov, 1972; Pettibone, 1954, 1963; Berkeley and Berkeley, 1948.

Records.—2D (1); 3E (2), G (1); 4D (3), E (3), G (3); 5D (2), E (1); 7B (1), D (4), E (1); 8B (2), C (1), D (5), E (6), G (2); 9A (4); 25E (2); 29D (1); 31E (1), G

(1); 47A (2); 56A (1); 65A (6); 68A (1); 69A (2); 70A (7); 89A (1); 95A (5); 98A (1); 137B (1); 147B (3); 149B (1); 150B (1); K7E (1).

The shape of the ventral cirri in our specimens varied from small to large animals. Small specimens had pointed ventral cirri as described for *Anaitides mucosa* (Oersted); large specimens had ventral cirri as described for *A. groenlandica,* i.e. oval with asymmetrical acuminate tip; intermediate sized specimens had ventral cirri intermediate in shape between *A. groenlandica* and *A. mucosa. Anaitides groenlandica* reportedly has a greater number of papillae per row on the proboscis than *A. mucosa,* 12–15 vs. 8–10 (Ushakov, 1972); 10–20 vs. 8–12 (Pettibone, 1963); greater than 12 vs. not more than 10 (Banse and Hobson, 1974), and their color patterns differ (see respective descriptions in Ushakov, 1972). In our material, the larger specimens among those with *groenlandica* type ventral cirri had greater than 12 papillae per row on the proboscis and a color pattern as described for *A. groenlandica,* brown, with dark brown transverse stripes on dorsum; dorsal cirri brown with pale margins, thus fitting the definition of this species completely. All remaining specimens, those with *groenlandica* type ventral cirri, those with *mucosa* type ventral cirri, and those with intermediate shaped ventral cirri, had 12 papillae per row on the proboscis and the same color pattern described above. We therefore conclude that all our specimens belong to *A. groenlandica*; those with *mucosa* type ventral cirri are merely juvenile *A. groenlandica.* The largest specimen (6 mm wide) had about 25 papillae per row on the proboscis. As far as we know, no workers to date have reported greater than 20 papillae per row in specimens of *A. groenlandica.*

Local distribution.—Oregon to Washington in 15–88 m on sand and silty sand.

Anaitides hartmanae (Blake and Walton, 1977)

Phyllodoce hartmanae Blake and Walton, 1977.

Records.—2G (1); 3G (1); 6E (1); 7C (2), D (4), E (1), G (2); 8C (1), G (1); 14A (1); 18B (1); 19E (1); 24H (3); 28E (1), G (1); 29G (1); 31G (1); 33D (1), E (1); 97A (1); 147B (1); K1E (1); K28E (1); K34E (1); K36E (1).

The present species is herein referred to the genus *Anaitides* Czerniavsky, rather than *Phyllodoce* Savigny, because the papillae on the basal half of the proboscis are arranged in rows; see Fauchald (1977), p. 48. The rows of papillae are oblique (spirally arranged, according to Blake and Walton, 1977).

Anaitides hartmanae is previously known only from California where it was described. The present records extend the distribution northward to Oregon and Washington.

Local distribution.—Oregon to Washington in 26–97 m on sand and silty sand.

Anaitides longipes (Kinberg, 1866)

Phyllodoce (*Anaitides*) *longipes* Kinberg, 1866.
Anaitides longipes Hartman, 1968.

Records.—3D (1); 8B (1); 15D (1); 18D (1).

In the Pacific Ocean, *Anaitides longipes* is previously known from Chile and California. The present records extend the distribution northward to Oregon and Washington.

Local distribution.—Off Washington in 80 m on silty sand (1); off Oregon in 44–53 m on sand and sandy silt.

Genus *Paranaitis* Southern, 1914
Paranaitis polynoides (Moore, 1909)

Anaitis polynoides Moore, 1909.
Paranaitis polynoides Hartman and Reish, 1950; Hartman, 1968; Ushakov, 1972.
Phyllodoce (*Paranaitis*) *polynoides* Berkeley and Berkeley, 1948.

Records.—4E (1); 147B (1).

Local distribution.—Off Washington in 60 m on silty sand (1); off Oregon in 66 m on sand (1).

Genus *Eulalia* Savigny, 1818
Eulalia levicornuta Moore, 1909

Eulalia levicornuta Moore, 1909; Hartman, 1968.
Eulalia (*Eulalia*) *levicornuta* Banse and Hobson, 1968.

Records.—5C (1), D (1).

These records are the first off Oregon, but the species has been recorded both to the north and south.

Local distribution.—Off Oregon in 86–88 m on sand with greater than 15% silt + clay. (Note that both specimens were collected at the same station but during different cruises.)

Genus *Eumida* Malmgren, 1865
Eumida sanguinea (Oersted, 1843)

Eulalia sanguinea Oersted, 1843.
Eumida sanguinea Hartman and Reish, 1950; Hartman, 1968; Ushakov, 1972.
Eulalia (*Eumida*) *sanguinea* Berkeley and Berkeley, 1948.

Records.—4E (1); 5C (1); 7D (1), E (1); 8B (2), D (1); 47A (1); 48A (2); 55A (2); 68A (2); 69A (2); 97A (1); 148B (1).

Local distribution.—Oregon to Washington in 55–97 m on sand (with greater than 5% silt + clay) and silty sand.

Distributional Patterns Within the Genera *Eteone* and *Anaitides*

The local distribution, including depths and sediment type(s), for each phyllodocid species is given in the previous section. Seven species of *Eteone* occurred in the study area. *Eteone columbiensis* occurred only in shallow water (11–20 m) within and directly off the mouth of the Columbia River, in sand and silty sand. *Eteone longa* was restricted to sediments with less than 5% silt + clay and occurred only in 16–51 m off Oregon (except one specimen referred to under "local distribution" in the previous section), south of the area characterized by large seasonal variation in sediment composition.[1] *Eteone spilotus* occurred in sand with greater than 10% silt + clay and silty sand from Oregon to Washington (except one specimen referred to under "distribution" in the previous section).

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[1] The area characterized by large seasonal variation in sediment composition is delineated (and discussed) in paragraph 2 under "Study Area."

The distributions of the above three species did not overlap one another; that of *E. columbiensis* did not overlap any other species of *Eteone*. *Eteone californica, E. fauchaldi, E. barbata,* and *E.* sp. each had a distribution which overlapped that of every species of *Eteone* except *E. columbiensis*. The first three occurred in sand and muddier (greater than 25% silt + clay) sediments from Oregon to Washington. *Eteone* sp. occurred off Washington and Oregon in sand.

Each of the four species of *Anaitides* in the study area occurred in sand as well as muddier (greater than 25% silt + clay) sediments and their distributions overlapped one another. *Anaitides groenlandica* occurred off Oregon, Washington, and directly off the Columbia River. *Anaitides multipapillata* occurred south of the Columbia River and directly off it. *Anaitides hartmanae* occurred off Washington (21 specimens) and Oregon (18 specimens), but only one specimen (station 97A) was collected directly off the Columbia River, in deep water (97 m). In contrast to *A. groenlandica* and *A. multipapillata,* only one specimen of *A. hartmanae* (station 14A off Oregon) was found within the area characterized by large seasonal variation in sediment composition resulting from seasonal differences in river flow and wave intensity.[1] Though the latter species occurred in sediments ranging from 1% silt + clay to 42% silt + clay, perhaps it is less tolerant than the other two species to the temporal fluctuations in habitat within the above area. Only four specimens of *A. longipes* were collected, three off Oregon and one off Washington.

Members of the family Phyllodocidae occurred commonly but in low numbers. Species were represented by only one or two individuals in the majority of replicate sets in which they occurred. For this reason, it is impossible to detect seasonality in the abundance of the phyllodocid species, even within the area characterized by large seasonal variation in sediment composition.

One species which exhibited a temporal change in occurrence is *Eteone longa*. This species occurred commonly within and adjacent to the rectangular area delineated in Fig. 1 from cruise E (September 1975) to cruise I (June 1976), but only one specimen was collected prior to cruise E. (Considering *E. longa*-containing stations sampled both before cruise E and from cruise E onward, the species occurred in 1 of 33 replicate sets taken before cruise E, and in 32 of 39 replicate sets taken between cruise E and I.) In July and August 1975, between cruises D and E, the U.S. Army Corps of Engineers dumped approximately 460,000 m^3 of dredge material in the area delineated by the rectangle in Fig. 1 (Richardson et al., 1977; this area is referred to as experimental site G in that publication). Prior to disposal, the median diameter of sediment in this area ranged from 2.70 to 2.89 ϕ. As the dredge material, derived from the mouth of the Columbia River, had a high percentage of 2.0–2.5 ϕ size particles, the sediment within the rectangular area following disposal was a coarser sand, the median diameter of most stations between 2.1 and 2.4 ϕ. *Eteone longa* appeared at this time (i.e. following disposal) outside the rectangular area, in sediments not affected by dumping, most of these finer grained (median diameter greater than 2.7 ϕ), as well as within the rectangular area, in finer sediments, and coarser ones (median diameter = 2.1–2.4 ϕ) resulting from dumping. As *E. longa* did not show any preference for the coarser sediments, its sudden appearance in this general area is probably not due to the increase in sediment grain-size. Though it is tempting to postulate that *E. longa* was transported to the disposal vicinity from the mouth of the Columbia River during dredging and dumping operations, the species was never collected at the stations within or just outside the mouth. We are unable to explain the temporal disparity in the occurrence of *E. longa*.

Acknowledgments

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Recognition of Quaternary Wave Formed Marine Terraces on Santa Catalina Island

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Abstract.—Four previously unconsidered and undescribed terrace locations have been identified as Quaternary wave cut, emergent, marine terraces. The presumption has persisted that there apparently are no identifiable, marine terraces on Santa Catalina Island. This is, in large part, due to the absence of corroborative Pleistocene marine fossil assemblages and the extensive erosion of suspected terrace locations. However, there does exist an abundance of water rounded pebbles and cobbles. These are in relatively distinct concentrations in at least four locations, especially along the western margins of the island. Utilizing the methodology developed by Dodkins and Folk in 1970, the authors determined that the Maximum Projection Sphericities ($\psi\rho$) of the pebbles and cobbles were generated by wave not fluvial action, thereby establishing them as artifacts from wave cut benches.

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The paucity of identifiable marine terraces on Santa Catalina Island has remained an enigma, albeit on a relatively local level, since Smith (1847) first observed that the most striking difference between Santa Catalina and the slopes of San Pedro Hill (Palos Verdes Peninsula, Los Angeles County) and of San Clemente Island is the marked absence of marine terraces. Lawson (1893) concluded that there is no trace of an elevated wave cut terrace, sea cliff, or strand line of any kind observable on the island. Smith (1897) later observed that the island yielded extremely poor Pleistocene subtidal and intertidal marine invertebrate faunal assemblages on its ill defined emergent terraces.

The insular neighbors of Santa Catalina are San Clemente, San Nicolas, Santa Barbara, Anacapa, Santa Cruz, Santa Rosa and San Miguel Islands (Fig. 1). All have more or less well defined, wave formed, marine terraces. This indicates a period of extensive subsidence and subsequent emergence from the Late Pliocene through the Pleistocene. Therefore, Santa Catalina Island should not be an exception to this pan-insular pattern of subsidence, emergence and subsequent terracing so characteristic of the islands as well as the coastal margin of Southern California.

Structural Considerations

Santa Catalina Island is a melange composed of rocks of the Catalina Schist (it is understood, although not absolutely proven, that this complex belongs to the Franciscan Formation) of Jurassic-Cretaceous age, capped by Tertiary volcanics.

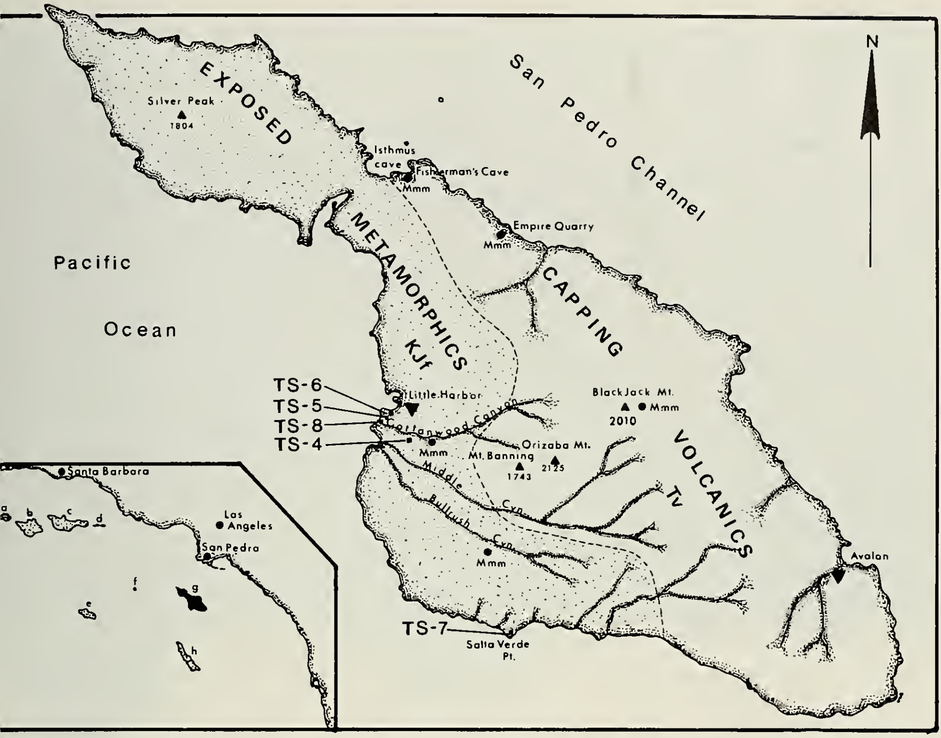

Fig. 1. Locations of wave cut marine terraces on Santa Catalina Island identified from Pleistocene ave abraded pebbles and cobbles. The inset map indicates the geographic relationship of Santa atalina Island (g) to the mainland and to the other channel islands: a. San Miguel; b. Santa Rosa; . Santa Cruz; d. Anacapa; e. San Nicolas; f. Santa Barbara; and, h. San Clemente. The map symbols ndicate: TS is Terrace Site; Mmm is Middle Miocene marine; Tv is Tertiary volcanics; KJf is Catalina chist; ● is Pre-Quaternary sedimentary deposits; ■ is a survey and sampling site; ▼ is previously efined terrace site; ----- is the generalized separation between (Tv) capping volcanics and (KJf) xposed metamorphic rocks.

The rocks of the metamorphic basement range from glaucophane and chlorite-ctinolite rich schist to hornblende-garnet schists. The capping volcanics consist f rhyolite, dacite, andesite and some basalt. Consequently, the highly dissected, ronounced vertical relief of the island, with its lack of definable marine terraces, nay be due to differential patterns of weathering controlled by the diverse character of its lithology.

Former Indian inhabitants extensively used the relatively flat areas as habitation ites and middens so that invertebrate fossil material has either been obscured or nidentifiably incorporated, with midden deposits. A few areas of Santa Catalina sland geomorphically have the appearance of probable marine terraces. These ocations are strewn with pebbles and cobbles that have been abraded by some orm of water action, either marine or fluvial.

Pre-Quaternary Insular Submergence

Evidence of Pre-Quaternary (Tertiary) periods of submergence exist. An exosure of poorly consolidated, unfossiliferous limestone is exposed in Cotton-

Fig. 2. The slide depressed, basin like marine terrace (site TS-7) behind Salta Verde Point on the west side of Santa Catalina Island. The Palisades (light colored cliffs) and the east end of the Island are in the background.

wood Canyon (Fig. 1). This limestone unit unconformably overlies Catalina Schist and is overlain by Upper Miocene andesite. Two small deposits of fossiliferous limestone are located on the flanks of Mt. Banning (439 m a.s.l.) and Bald Peak (427 m a.s.l.) on the south side of Bullrush Canyon (Fig. 1). These limestones overlie earlier Miocene volcanics. They are intercalated by andesitic tuffs and lapilli and overlain by andesitic lavas of Upper Miocene age. A tuffaceous diatomite deposit, extending from sea level at Big Fisherman Cove to about 150 m a.s.l. at Empire Quarry (Fig. 1), is intercalated by beds of lapilli and capped by Upper Miocene andesitic volcanics.

Defined Terraces

Apparent terraces were observed and described by Smith (1847) from the upper sections of Avalon Canyon (Fig. 1). Rounded pebbles that he found on the surface of apparently terraced areas in the vicinity of Little Harbor were interpreted as

Table 1. Computed Percents of Certainty for wave formed vs. river formed pebbles and cobbles.

Wave Formed Pebbles/Cobbles (Beach)		River Formed Pebbles/Cobbles (Fluvial)	
$\psi\rho$	% Certainty	$\psi\rho$	% Certainty
0.60	95%	over 0.65	76%
up to 0.65	76%	0.70	95%

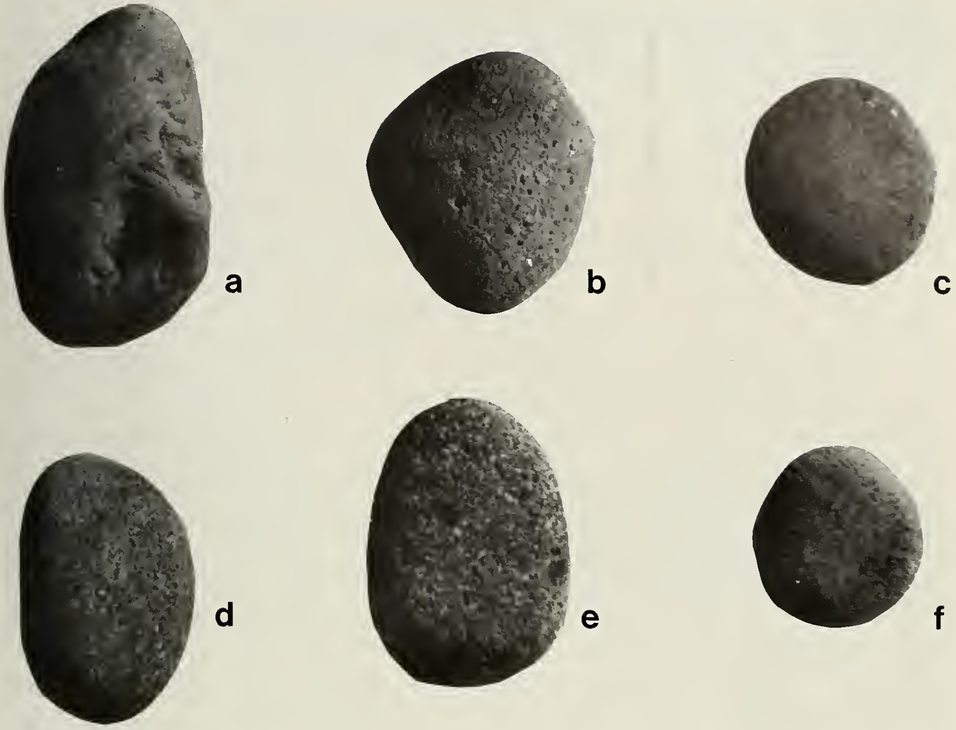

Fig. 3. General terrace deposited pebble shapes and measurements relative to Maximum Projection Sphercities ($\psi\rho$). a) andesite cobble approaching prolateness from site TS-5, L = 138.4 mm, I = 81.8 mm, S = 53 mm, with a $\psi\rho$ of 0.62; b) oblate andesite cobble from site TS-6, L = 105.3 mm, I = 88.3 mm, S = 52 mm with a $\psi\rho$ of 0.66; c) oblate dacite pebble from site TS-4, L = 86 mm, I = 77 mm, S = 30 mm with a $\psi\rho$ of 0.51; d) oblate andesite cobble from site TS-5, L = 104.7 mm, I = 68 mm, S = 64.4 mm with a $\psi\rho$ of 0.83; e) oblate andesite cobble from site TS-6, L = 111.6 mm, I = 78.4 mm, S = 39.2 mm, with a $\psi\rho$ of 0.56; f) oblate dacite pebble from site TS-4, L = 71.4 mm, I = 64.4 mm, S = 25.7 mm, with a $\psi\rho$ of 0.52.

having been abraded and subsequently deposited by ancient fluvial action as were pebbles later found in association with angular lithoclasts from terraces in Avalon Canyon. Smith (1933) identified a few surfaces he believed to be terraces, but conjectured their origins on the basis of notched and beveled salients and apparent strand lines. Bailey (1941) and Slosson (1973) identified these previously described areas as Quaternary terraces.

Methodology

Exploratory surveys over most of the island identified water rounded pebbles and cobbles from the flanks of Mt. Banning, along promontories such as Salta Verde Point and Indian Head Rock and on canyon slopes. The only location where Quaternary fossils (primarily molluscan) were found in association with water rounded pebbles was on the north slope above the mouth of Cottonwood Canyon (site TS-5). They were exposed along the margin of a landslide displaced block of blue schist.

Tables 2–6. Computed Maximum Projection Sphericities for pebble suites analyzed. In all the Tables (2–6) of computed Maximum Projection Sphericities, the pebble size classification is based on the L or Long Axis (Figure 6). In the column expressing Percent of Certainty (%), the letter F indicates Fluvial (river) origin while the letter W indicates Wave (beach) origin. Control Site (TS-8): Cottonwood Canyon Beach.

Pebble Size (mm)	8–16	16–32	32–64	64–128	128–256
Number of Pebbles	2	29	46	30	3
Mean ψp	0.76	0.62	0.55	0.54	0.56
% Certainty	95% F	76% W	95% W	95% W	95% W

Mean ψp for suite 0.572
σ 0.116
% Certainty for suite .... 95% Wave-Formed

Pebble Lithology: 110 andesite pebbles and cobbles

The pebbles and cobbles observed and collected were primarily andesite. Although andesite is not always the predominant rock exposed, it is much more resistant to weathering than the metamorphics. The landslide modified, terraced area behind Salta Verde Point (Figs. 1 and 2) provided the exception to the predominance of andesite pebbles and cobbles. The pebbles and cobbles at this site are a green dacite porphyry (hornblende-quartz-diorite of Bailey, 1941). This is the most abundant rock type comprising the pebbles and cobbles on the contemporary beaches in the immediate area of Salta Verde Point.

The overall shape of the water abraded rocks tends to be more oblate rather than prolate (Fig. 3). Random pebble suites were collected from four possible terrace locations: 1) the top of the ridged terrace on the south side of Cottonwood Canyon (Site TS-4); 2) the remnant terrace on the slide block behind Indian Head Rock (Site TS-5); 3) Rancho Escondido terrace on the south side of Little Harbor (Site TS-6); and 4) Salta Verde Point terrace (Site TS-7) as in Fig. 1. A total of 370 pebbles and cobbles were collected in random samplings from these locations. The number of rocks taken from each site was determined by abundance and availability, not by size or shape preference.

Standardization (Table 2) was accomplished by collecting 110 structurally iso-

Table 3. Site TS-4, South side of Cottonwood Canyon.

Pebble Size (mm)	8–16	16–32	32–64	64–128	128–256
Number of Pebbles	8	31	46	22	—
Mean ψp	0.778	0.629	0.593	0.603	—
% Certainty	95% F	76% W	95% W	95% W	

Mean ψp for suite 0.619
σ 0.115
% Certainty for suite .... greater than 76% Wave Formed

Pebble Lithology:

71 andesite	18 quartz	8 scoria
3 tuff	5 schist	2 metasandstone

Table 4. Site (TS-5), Behind Indian Head Rock.

Pebble Size (mm)	8–16	16–32	32–64	64–128	128–256
Number of Pebbles	26	32	43	29	6
Mean $\psi\rho$	0.691	0.687	0.526	0.573	0.583
% Certainty	76% F	76% F	95% W	95% W	95% W

Mean $\psi\rho$ for suite 0.612
σ 0.141
% Certainty for suite .... 90–95% Wave Formed

Pebble Lithology:
118 andesite 12 quartz
4 schist 2 metasandstone

tropic andesite pebbles and cobbles from a Holocene beach at the mouth of Cottonwood Canyon, Site TS-8 (Fig. 1). Shaping on this beach is controlled by moderate to heavy wave energy. The beach is approximately fifty meters wide with a foreshore slope averaging 10°. The beach faces west on the seaward side of the island. It grades from sand subtidally, coarse sand and gravel intertidal, to pebbles and cobbles in the supratidal. The backbeach grades into fluviatile sands deposited by Cottonwood Creek (Fig. 5).

The shape development study conducted by Dodkins and Folk (1970) showed that beach pebbles have a much lower sphericity than river pebbles. They stated that, "the maximum projection sphericity averages 0.68 for rivers, 0.64 for low-wave-energy beaches, and 0.58 for high-wave-energy beaches." The authors utilized the method developed by Dodkins and Folk (1970) to identify the origin of the water rounded pebbles and cobbles found on the island. Because of the lack of fossils, reliance was placed on the determination of the mean sphericities of available gravels and scattered concentrations of water rounded pebbles. The long, intermediate and short axis of each pebble from each pebble suite was calculated (Fig. 6) and their individual Maximum Projection Sphericities ($\psi\rho$) computed using the formula developed by Folk (1955):

$$\sqrt[3]{\frac{S^2}{LI}} = \psi\rho;$$

Table 5. Site (TS-6), Rancho Escondido Terrace.

Pebble Size (mm)	8–16	16–32	32–64	64–128	128–256
Number of Pebbles	2	17	16	9	—
Mean $\psi\rho$	0.64	0.66	0.58	0.44	—
% Certainty	76% W	76% F	95% W	95% W	

Mean $\psi\rho$ for suite 0.587
σ 0.148
% Certainty for suite .... 95% Wave Formed

Pebble Lithology:
14 andesite 14 schist
12 quartz 4 metasandstone

Fig. 4. In situ, wave formed conglomerates exposed in a low road cut at marine terrace site TS-4 on the south side of Cottonwood Canyon.

where S is the short axis; L the long axis; and I is the intermediate axis. The Maximum Projection Sphericity is a comparative relationship between the maximum projection area of a pebble ($L \cdot I$) and the maximum projection area of a sphere of equal volume. The Mean Maximum Projection Sphericity for each pebble suite is computed by adding the individual $\psi\rho$ together then dividing the sum by the total number of pebbles measured. The Percent of Certainty for each pebble size classification and each pebble suite is computed in Table 1.

The Percent of Certainty is a function of probability percentages. If the $\psi\rho$ mean is under 0.65, there is a 76% probability that the pebble suite was wave formed (beach); if the mean $\psi\rho$ is less than 0.60, there is a 95% certainty that the

Table 6. Site TS-7, Salta Verde Terrace.

Pebble Size (mm)	8–16	16–32	32–64	64–128	128–256
Number of Pebbles	—	15	51	14	3
Mean $\psi\rho$	—	0.709	0.667	0.582	0.580
% Certainty	—	95% F	95% F	95% W	95% W

Mean $\psi\rho$ for suite 0.657

σ 0.100

% Certainty for suite .... 76% Fuvial

Pebble Lithology:

73 dacite porphyry 10 andesite

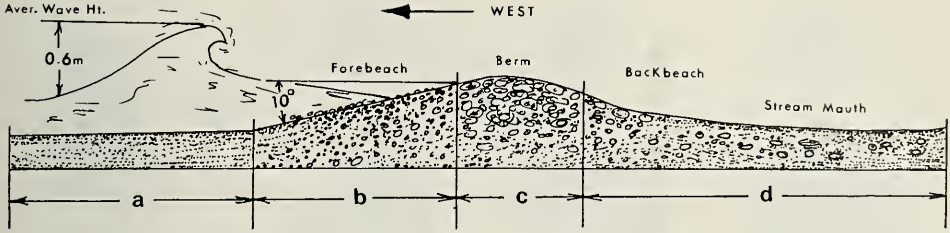

Fig. 5. Profile of the control beach (Site TS-8 and Table 2) at the mouth of Cottonwood Canyon. a. subtidal zone, medium sized sand grain bottom; b. intertidal zone, grading from coarse sand to gravel; c. splash and supratidal zone, pebbles and cobbles; and, d. fluviatile sand in creek bed behind berm.

pebble suite originated on a beach. Conversely, if the mean $\psi\rho$ is greater than 0.65 there is a 76% probability that the pebble suite is from a river. The break point between fluvial and wave formed is from $\psi\rho$ 0.65 to 0.66. This is due to the difference between the mechanics of fluvial and beach abrasion and independent of lithology as long as the rocks are structurally isotropic (Dodkins and Folk, 1970).

Pebble size classification was adapted from Dodkins and Folk (1970). The analysis on Santa Catalina Island necessitated the addition of a smaller pebble category, 8–16 millimeters. The addition was made to accommodate the abundance of small pebbles available in the areas surveyed and to provide the analysis with as random a selection, free from size bias, as possible. Of the 370 pebbles and cobbles collected, 336 were structurally isotropic (213 andesite, 42 quartz, 73 dacite prophyry and 8 scoria). The remaining 34 rocks (23 schist, 8 metasandstone and 3 tuff) generally lacked flow structure or planar features.

Terrace Site Description

Terrace site TS-4 (Table 3) is on the south side of Cottonwood Canyon (Fig. 1), at latitude 33°10′18″ north, longitude 118°27′42″ west, on the west side of Santa Catalina Island. One hundred and seven pebbles and cobbles were collected from exposed gravels near a low road cut (Fig. 4).

Site TS-5 (Table 4) is the remnant of a terrace situated on a slide block within a landslide complex located along the seaward flank of Cottonwood Canyon, behind Indian Head Rock. Although the terrace surface is physically lower in elevation (45 meters a.s.l.) than the adjacent TS-6 site (74 meters a.s.l.) it was obviously continuous prior to the sliding. It is located at latitude 33°10′36″ north, and longitude 118°28′42″ west, on the south side of Little Harbor. One hundred and thirty six pebbles and cobbles were collected from a small gravel exposure near the seaward margin of the slide block.

Site TS-6 (Table 5) is the most distinctly terraced location surveyed and sampled. Its relatively broad, flat surface stretches inland past Escondido Ranch. There are no *in situ* gravels exposed on this terrace location. Rather, the pebbles are strewn about, generally becoming more numerous downslope near the seaward margin. Terrace TS-6 is located between Cottonwood Canyon to the southeast and Little Harbor on the northwest, at latitude 33°22′18″ north, longitude

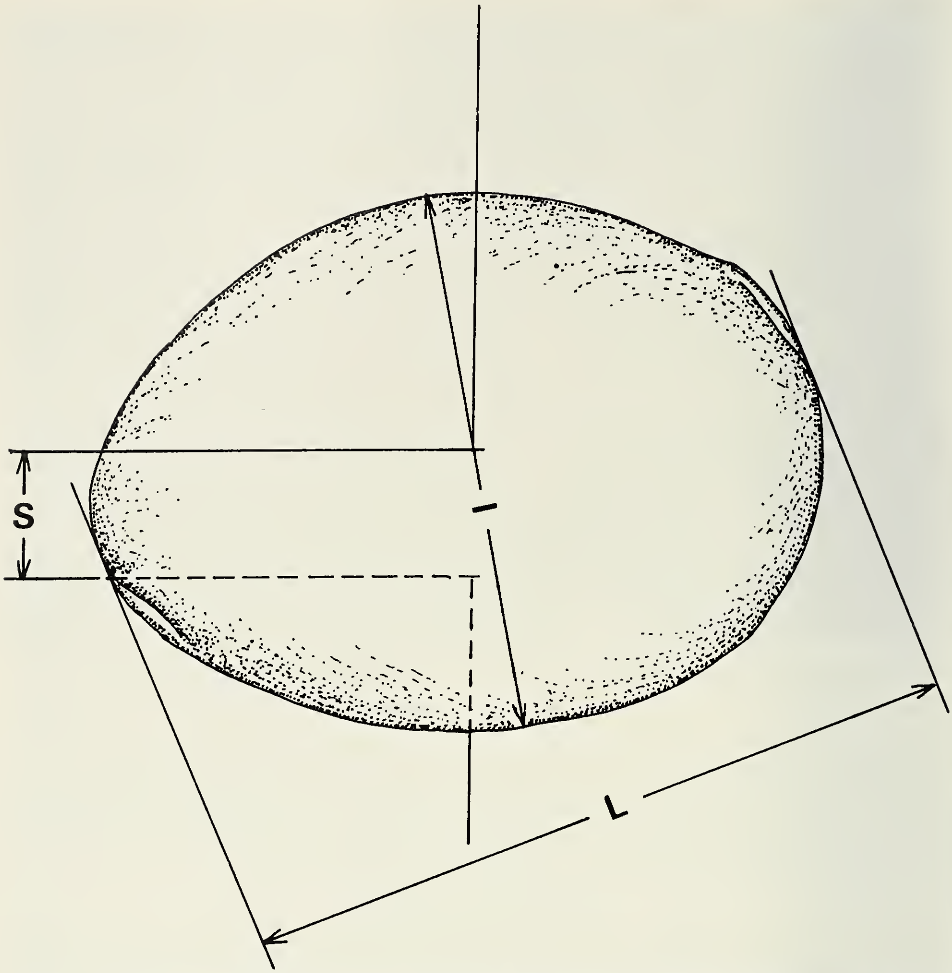

Fig. 6. Projection of the coordinates for computing the Maximum Projection Sphericity of a water rounded rock. L represents the maximum projected length, I the intermediate length (width) and S the short axis or thickness of the rock.

118°28′42″ west. This location is referred to as Rancho Escondido Terrace. Forty four pebbles were collected from this site.

Site TS-7 (Table 6) is a slide modified, basin shaped terrace behind Salta Verde Point (Figs. 1 and 2). It is at latitude 33°19′12″ north and longitude 118°25′12″ west on the west side of Santa Catalina Island. Eighty three pebbles were collected from the surface of the terrace. The present terrace lies at an average elevation of 45 meters a.s.l.

Discussion

In three of the five sites sampled, including the control site (TS-8), the smallest pebble classification, 8–16 mm, produced a high mean $\psi\rho$ indicative of fluvially formed rocks. On the other hand, in all of the sites sampled the large pebble size

Fig. 7. Anomalous cobble modifications. Fragments d, e, g, i, l, and m are spalled off pieces of cobbles found in Indian middens on Santa Catalina Island. These were used as choppers, scrapers, gravers, etc. (Santa Catalina Island Museum Anthropological Collection). Spalls c and h are from Salta Verde Point terrace (TS-7) and j is a quartzite spall from Ripper's Cove. a' is a spall chipped by the authors from a prolate cobble from the Salta Verde Site (TS-7). The spalls illustrated are composed of dacite porphyry and quartzite.

classifications, especially 128–256 mm, produced characteristically low $\psi\rho$. These low mean sphericity values are indicative of wave formed rocks. This apparent bimodal condition had been found on high wave energy, gravel beaches by Dodkins and Folk (1970). Under these conditions there is a tendency for smaller pebbles to be tossed about randomly, to be abraded more uniformly and to fall into the interstitial spaces between larger rocks where they are rolled back and forth by wave action rather than slide. In the case of sandy beaches, it was found that pebbles of all sizes have uniformly low sphericities.

This condition of wave force discrimination in pebble shaping, producing wide range of Maximum Projection Sphericities, is evident in all of the sites sampled. We conclude, therefore, that similar physical conditions existed during the Quaternary period for at least 3 of the 4 sites sampled (sites TS-4, TS-5, and TS-6), and, in all probability, for the TS-7 site. The Cottonwood Canyon Beach control site is typical of the aforementioned physical parameters to pebble type development, namely, high wave energy (waves averaging over 0.6 m in height) and a gravel beach. These parameters have produced a low mean Maximum Projection Sphericity for the site of 0.572, giving it at least a 95% certainty that the pebbles are wave formed.

Interpretation of Apparently Non-Supportive Data From Salta Verde

The mean $\psi\rho$ for the Salta Verde Point (TS-7) site (Figs. 1 and 2) in the two smaller pebble groupings (Table 6) indicate a fluvial origin. Conversely, the mean $\psi\rho$ for the two larger pebble categories indicate a wave/beach controlled origin. This enigma is compounded by the fact that the TS-7 site is the most obviously terraced location of the four sampled and analyzed. Extensive field observations at this location turned up a peculiar repetition of broken cobbles above 128 mm size, rendering them useless for accurate measurement. Only three found in the 128–256 mm range were not broken (Fig. 7). Contrarily, only a very few pebbles in the 64–128 mm range were found broken and none in the smaller ranges. The cobbles were also broken in an unusual fashion; rather than being broken in half through their short axis, the well rounded ends along their long axis were spalled off as by a deliberate, well directed blow (Fig. 7). In searching through the Santa Catalina Island Museum's Indian artifact collection, we found similar spalled off pieces identified as crude choppers and scrapers (Fig. 7). Also an abundance of midden sites in the Salta Verde area indicates that it was used extensively as a habitation area by the former Indian population.

Therefore, the relatively high mean $\psi\rho$ of 0.656 for this particular terrace may well be directly related to the toolmaking needs of the Island's original inhabitants. The paucity of large pebbles, along with the broken condition of those found, seems to indicate that the Pleistocene deposited gravels served as readily available raw material for paleolithic toolmakers well into Holocene times. Consequently, the larger pebbles and cobbles with significantly lower sphericities, well into the wave formed category as indicated in Table 6, were apparently either removed from the area long ago or were rendered useless for interpretive data by being broken. This is also indicated by the average of the mean $\psi\rho$ for each size range of 0.634 rather than by the mean $\psi\rho$ for the entire suite. Given the evidence on hand, albeit much of it circumstantial, it is the authors' opinion that the Salta Verde Point Terrace was also formed by wave action during a period of submergence and subsequent emergence.

Conclusion

The mean $\psi\rho$ for the four suspected terrace sites sampled is 0.618, with a standard deviation (σ) of 0.028. This figure coincides almost exactly with the mean $\psi\rho$ for ten known ancient beach sites on the Atlantic and Gulf coasts sampled by Dodkins and Folk (1970) with a mean $\psi\rho$ of 0.61. This coupled with the fact that the surrounding islands and coastal margin all show conclusive signs of Quaternary subsidence and emergence in the form of wave formed marine terraces, supplies strong evidence that Santa Catalina Island is no exception.

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Species Diversity and Distributional Relationships of Pseudoscorpions from Slash Pine (*Pinus elliottii* Eng.) in Florida (Arachnida: Pseudoscorpionida)

Vincent Brach

Abstract.—Nine species of pseudoscorpions associated with living and dead slash pine, *Pinus elliottii* Eng., in south central Florida were studied with respect to distribution and species diversity. Trees offering the greatest diversity of bark microhabitats have the greatest species diversity. Most of this diversity is in the fauna of the flake bark, which is the commonest and least patchily distributed bark microhabitat. However, some species may be unable to utilize this microhabitat unless other types of bark microhabitats are available simultaneously.

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Despite the fact that pseudoscorpions are widely distributed and often abundant in habitats containing crevices, the ecology of pseudoscorpions is described by Muchmore (1973) as being "sadly neglected." Hoff and Bolsterli (1956), Ressl and Beier (1958), Hoff (1959, 1961, 1963a) and Nelson (1975) have presented the results of systematic collections of pseudoscorpions from broad geographic areas together with some habitat information, the studies of Ressl and Beier (1958) and Hoff (1959) being the most detailed. A few species of pseudoscorpions have received detailed treatment with respect to particular ecological parameters such as desiccation resistance [Kensler, 1967—*Neobisium maritimum* Leach; Cloudsely-Thompson, 1956—*Withius subruber* (Simon) and *Dactylochelifer latreillei* (Leach)]. Faunal studies of restricted habitats in which pseudoscorpions occur as minor components have yielded some additional ecological information (e.g. Morton, 1954; Graves and Graves, 1969; Richards, 1971). Only the studies of Hoff and Clawson (1952), Chamberlin and Malcolm (1960) and the review of Weygoldt (1969) deal entirely with the distributional relationships of pseudoscorpions with respect to a particular habitat (rodents' nests, caves and the sand islands near Beaufort, North Carolina respectively). However, no studies have been made of the distributional relationships and species diversity of the pseudoscorpion fauna of a particular microhabitat.

Among the most important microhabitats in which pseudoscorpions may be found are the subcortical or underbark spaces of trees. Several families of pseudoscorpions (Cheliferidae, Cheiridiidae, Chernetidae and Atemnidae) are very commonly encountered in such situations and several genera (e.g. *Parachelifer, Dendrochernes*) are almost exclusively associated with the loose or started bark of a variety of tree species, usually conifers. The types of bark found on trees are quite variable and offer widely varying conditions of crevice size, humidity and permanence which not only change from one tree species to another but also with the age and state of health of a particular tree. Thus, a particular tree may show a microsuccession of arthropod communities during its existence (Blackman and Stage, 1924; Savely, 1939) and at different times may be expected to support different associations of pseudoscorpions as well.

The purpose of this study was to investigate the species diversity and distributional relationships of the pseudoscorpions found on living and lightning struck slash pines, *Pinus elliottii* Eng., in south central Florida.

Materials and Methods

This study was conducted at the Archbold Biological Station, Highlands County, Florida during October–April 1975–1976. The topography and vegetation types characteristic of the Station have been described elsewhere (Woolfenden, 1969). Pseudoscorpions were collected from 25 mature slash pines ranging from 30–80 cm diameter at breast height growing in slash pine-turkey oak and scrubby flatwoods habitats. The method of sampling was to conduct a ½ hr timed search of the entire trunk from a height of 1.5 m to the ground. Pseudoscorpions were collected with an aspirator or a brush as they were exposed. Since the bark of living trees was found to contain pseudoscorpions only beneath exfoliating flakes, live bark was not removed from these, but the started bark on dead trees was removed from the trunk after the remaining flake bark had been searched. Almost all of the trees selected could be thoroughly sampled in the allotted time; comparison with three untimed trial searches lasting over 1 hr suggested that at least 90% of the pseudoscorpions present are collected within the first ½ hr.

Lightning strikes on *P. elliottii* are a major cause of tree mortality at the Archbold Station. Thirteen of the 25 trees sampled had been killed by lightning (the passage of the bolt is visible as a spiral channel down the trunk) and exhibited a regular sequence of decay stages. The study of Baker (1973) on lightning caused mortality in the closely related loblolly pine, *P. taeda* L., at the Tall Timbers Research Station in Leon County, Florida, and my own observations of lightning killed slash pines at the Archbold Station suggested the following classification of decay stages:

Stage 1. Live, healthy trees. Flake and live bark present, foliage dark green. Few or no pitch tubes from wood boring beetles visible.

Stage 2. Freshly hit trees (approximately 1 mo). Foliage partly or all brown, beginning to fall off. No loss of bark, but pitch tubes from wood boring beetles evident. Lightning streaks clearly evident on trunk.

Stage 3. Early decortication. Pitch tubes no longer evident. Bark not loose but removable with a knife. Flake bark reduced. Upper branches often missing; no foliage.

Stage 4. Intermediate. Tree reduced to trunk and a few stubs of larger branches. Extensive decortication on parts of trunk, especially above 2 m. Basal bark loose and easily removed in large strips with fingers. The wood and undersurface of the bark often moist, especially on the north side, and may support large termite colonies. Wood may be punky and "red-rotten" in places.

Stage 5. Advanced. Decortication almost complete, with only a small region of easily removed bark fragments remaining at the trunk base. Wood be-

> neath the bark largely dry and "white-rotten." Sections of sapwood may be gone, producing a "necked" effect. The trunk often can be pushed over with slight effort.

Of the 25 trees examined, 14 were in stages 3–5 with six in stage 3, seven in stage 4, and one in stage 5. A single tree was found in stage 2 but could not be quantitatively sampled because of its location on the landscaped Station grounds. However, a brief examination showed that this tree had not decayed long enough for its bark to differ significantly from that of a live tree. The remaining 11 trees were all stage 1 (had not been struck by lightning).

Representative specimens of each species of pseudoscorpion collected were deposited in the Archbold Station collection. All species determinations were made by William B. Muchmore.

Results

Nine species of pseudoscorpions were collected at least once during the course of this study. These are:

Family Tridenchthoniidae
  Verrucaditha spinosa (Banks)
Family Cheiridiidae
  Cheiridium sp.
Family Sternophoridae
  Garyops depressa Banks
  Idiogaryops paludis (Chamberlin)
Family Chernetidae
  Parachernes latus (Banks)
  Americhernes longimanus Muchmore
  Dendrochernes morosus (Banks)
Family Atemnidae
  Paratemnus elongatus (Banks)
Family Cheliferidae
  Parachelifer superbus Hoff

The occurrence of each species with respect to the decay stage of the tree, number of specimens per collection, and type of bark from which collected is summarized in Table 1.

Discussion

Following a lethal lightning strike, a mature pine tree follows a roughly predictable sequence of decay stages which spans a period of several years, ending when the tree falls over and becomes a log (Baker, 1973). During this time, its subcortical microhabitats undergo profound changes with respect to humidity and the number and types of available crevices. The trunk of a mature slash pine is typically covered with close fitting patches of tightly appressed bark which provide little shelter where they join the trunk. However, the laminated, exfoliating exterior of the live bark provides a distinctive and unique microhabitat for those species which are extremely flat and are able to tolerate dryness. At the Archbold Station, the foremost of these species are the sternophorid pseudoscorpions *G.*

Table 1. Summary of pseudoscorpion collections from 25 slash pines, *Pinus elliottii*, at the Archbold Biological Station, Highlands County, Florida during October–April 1975–1976.

	Stage of Tree							# per Coll. Site		
Species	1	2	3	4	5	# of Colls.	Total # Coll.	Flake Bark	Started Bark	Sapwood
V. spinosa	—	—	1 (7)*	2 (14)	1 (6)	4	27	0	27	0
Cheirid. sp.	2 (7)	—	—	—	—	2	7	7	0	0
G. depressa	7 (19)	—	5 (38)	3 (30)	1 (7)	16	194	194	0	0
I. paludis	2 (8)	—	1 (3)	1 (3)	—	4	14	14	0	0
P. latus	3 (4)	—	3 (7)	—	—	6	11	11	0	0
A. longimanus	—	—	3 (8)	4 (25)	1 (8)	8	37	11	27	0
D. morosus	2 (3)	—	1 (3)	2 (6)	—	5	12	2	3	0
P. elongatus	6 (+)	—	—	4 (+)	1 (5)	15	>200	(+)	3	0
P. superbus	—	—	3 (7)	3 (8)	1 (4)	11	19	9	9	1

* The number of collections is followed by the number of specimens in each collection.
+ Visually estimated at >20 per collection (explanation in text).

depressa and *I. paludis*. *P. latus* and *Cheiridium* sp., while much less common, were also found exclusively in this microhabitat. *G. depressa* was usually abundant when it occurred at all, but typically each patch of flake bark (approximately 50 × 50 mm) sheltered a single specimen. Hoff (1963b) found that 13 out of 15 collections of *G. depressa* at the Archbold Station were from the exfoliating bark of standing slash pines, with some collections containing between 25 and 50 specimens. Since the two collections not made from standing slash pines were small but still slash pine associated (stump bark and a rotten fallen limb), Hoff (1963b) concluded that *G. depressa* is restricted to slash pines. However, while a living slash pine may support a very large population of *G. depressa*, as soon as the tree dies and stops replacing its bark the population begins to deteriorate, a few individuals perhaps remaining as long as there are patches of flake bark left.

I. paludis is a less common species which Hoff (1963b) found to be less restricted to slash pine than *G. depressa*, since he also collected it from beneath the bark of several species of hardwoods. Although Hoff (1963b) recorded *I. paludis* and *G. depressa* in one collection at the Archbold Station, I never found these two species together on the same tree.

The tridenchthoniid pseudoscorpion *V. spinosa* is said to migrate from the soil to the subcortical spaces of dead trees during the summer over some parts of its range in southeastern North America (Weygoldt, 1969). This species was always found beneath the started bark of dead slash pines in stages 3–5, usually on those trees which were quite moist and rotten beneath the bark. *V. spinosa* was collected only four times from slash pine during this study but was found to be relatively abundant under the bark of fallen logs and in the moist litter beneath.

The genus *Parachelifer* is interesting in that all of its species are predominately subcortical in occurrence and several species are restricted to particular species of trees. Hoff (1959) states that *P. persimilis* (Banks) and *P. scabriculus* (Simon) are associated with yellow pine (*Pinus ponderosa* Laws) and occasionally with other trees, while Hoff and Bolsterli (1956) report that *P. longipalpus* Hoff occurs "beneath the bark of broad-leafed deciduous trees" in the Mississippi Valley. *Parachelifer archboldi* Hoff, which is sympatric with *P. superbus* in Florida but was not collected in this study, is apparently restricted to the subcortical spaces of live oaks (*Quercus virginiana* Mill) (Hoff, 1964). *P. superbus* often occurred beneath well started bark on dead slash pines at the Archbold Station but was most often encountered under the bark of trees which had begun to dry out and were approaching stage 5 of the decay sequence.

The chernetid pseudoscorpions *D. morosus* and *A. longimanus* showed very different microhabitat preferences. *D. morosus* had the least restricted microhabitat of all of the pseudoscorpions studied, occurring beneath the started and flake bark of living and dead slash pines in approximately equal numbers. This species was also collected from the punky sapwood of a decaying sand pine, *Pinus clausa* Sarg., in sand pine scrub at the Archbold Station and may occur on other trees as well. Nelson (1975) records Michigan specimens "under the bark of dead trees" and Hoff (1959) found that the related *D. crassus* Hoff is apparently associated with yellow pine logs. The wide distribution of *D. morosus* and perhaps other congeners may be due to the fact that these pseudoscorpions are commonly phoretic on beetles and other insects (Muchmore, 1971) and have been taken at light traps at the Archbold Station, presumably having been carried there by insects (Frost, 1966). On the other hand, at the Archbold Station, *A. longimanus* is largely restricted to the moist subcortical spaces of stage 3–5 slash pines, only eight out of 37 specimens having been taken from beneath flake bark. Muchmore (1976) also records this species from light traps at the Archbold Station, suggesting phoretic dispersal.

The two collections totalling seven specimens of *Cheiridium* sp. taken from beneath the flake bark of living slash pines may represent accidental associations, since the bark from which these specimens were taken was almost level with the forest floor. However, this or a very similar species is relatively common under the breast height flake bark of slash pines in suburban Coral Gables, Dade County, Florida, where *G. depressa* is rare or absent (my unpublished observations). The extremely small size of *Cheiridium* pseudoscorpions may make them suitable as prey items for *G. depressa,* which did not occur on the trees from which the specimens of *Cheiridium* sp. were collected.

P. elongatus is in several ways a most atypical pseudoscorpion. It is always found in aggregations around semipermanent communal silken molting nests and exhibits a marked degree of social behavior involving cooperative prey capture and nest construction (Brach, 1978). The dense aggregations of this species made quantitative collecting difficult, since the members of a colony would scatter when uncovered and all could not be collected. I therefore visually estimated the sizes of the colonies. In most cases, the number of animals per colony was estimated at about 20. Over 200 specimens were collected during the course of this study, supporting Hoff's statement (Hoff, 1964) that *P. elongatus* is "one of the common Florida pseudoscorpions." *P. elongatus* occurs under started and flake bark but shows a distinct preference for flake bark and is usually found within 0.25 m of the ground, often below the level of the litter. Since flake bark on the lowermost portions of the trunk is always the last to disappear from a dead tree, *P. elongatus,* like *G. depressa,* can be expected to occur on slash pines in any stage of decay as long as at least some flake bark remains.

The presence of a pseudoscorpion fauna on slash pine can be expected whenever bark is still on the trunk. Only a single pseudoscorpion (*P. superbus*) was collected from the dry punky heartwood of a late stage 5 tree, and this animal may have been dislodged from its subcortical resting place during the course of collecting. Hence, it may be safely said that the pseudoscorpion fauna of slash pine in Florida is essentially a bark fauna. The pseudoscorpion fauna of slash pine bark can be divided into three categories based on microhabitat preference. *G. depressa, I. paludis, P. latus, Cheiridium* sp. and *P. elongatus* are more or less restricted to the dry flake bark, the last two species being further restricted to the lowermost portions of the trunk. *P. superbus* and *D. morosus* were found beneath flake and dry subcortical bark in approximately equal numbers; apparently humidity, rather than bark type per se, influences microhabitat selection by these species. *V. spinosa* and *A. longimanus* were largely or entirely restricted to the moist subcortical spaces of dead trees. Since the nine specimens of *A. longimanus* taken from beneath flake bark were all from dead trees, it is possible that *A. longimanus,* which is more heavily sclerotized than *V. spinosa,* may occasionally forage in low humidity microhabitats, returning periodically to the moist subcortical spaces to rehydrate. In the laboratory, I found that *A. longimanus* desiccates rapidly in dry culture jars and must be provided with a moisture source, such as a cotton plugged vial of wet sand, for long term maintenance.

The diversity of pseudoscorpions inhabiting slash pines at the Archbold Station probably is most strongly influenced by the relative permanence of their respective microhabitats, the distribution of these microhabitats in time and space, and the history of each tree with respect to colonization. Clearly, the least patchily distributed microhabitat in time and space is that of flake bark, and therefore one would expect this microhabitat to show the largest number of species. Lightning struck trees constitute a small fraction of the total number of slash pines in an area at any given time. Since a dead tree has a "life span" of only a few years at best (Baker, 1973), during which its subcortical environments are changing continuously, it would be expected that pseudoscorpions restricted to the transient, relatively rare microhabitat of the moist subcortical spaces of dead trees would be relatively few in species and patchy in occurrence, the latter phenomenon probably reflecting the chances of colonization and extinction. *V. spinosa* was collected only four times, although 14 of the 24 trees examined had apparently suitable moist subcortical spaces. By contrast, *G. depressa* and *P. elongatus* were found on 16 and 15 of the 25 trees examined, respectively. This proportion might have been increased for both species had the number of live trees examined been proportionate to their abundance. Pseudoscorpions such as *A. longimanus* and *P. superbus,* which made use of more than one microhabitat, showed an intermediate abundance.

The data of this study did not permit critical analysis of seasonal differences or of intraspecific competition or predation, any of which might be expected to have a significant effect on abundance and diversity. However, both Hoff (1963b) and I noted that *G. depressa* and *I. paludis* rarely occur together on the same tree. In the laboratory, *P. elongatus* readily used *G. depressa* as prey; in nature, this could be expected to produce some of the observed habitat partitioning of flake bark. However, it is likely that the most significant factor determining species diversity is the microhabitat diversity of the tree. The most diverse pseudoscorpion fauna observed on a single tree was six species, taken from the single stage 5 tree examined. This tree was somewhat unusual for a tree of its class in that it had patches of flake bark, moist and dry subcortical spaces, and a region of dry punky heartwood; it therefore possessed the greatest number of potential microhabitats of any of the trees examined. When the flake bark microhabitat alone is considered, the greatest number of species collected from one tree is four (five trees), although eight of the nine species studied occurred in this microhabitat. Only *P. elongatus* occurred on all five of these trees. Thus, it appears that most of the diversity of the slash pine pseudoscorpion fauna occurs in the commonest and most permanent of the available microhabitats, even though two of the species (*A. longimanus* and *P. superbus*) are apparently unable to utilize this microhabitat unless started bark is also present, *A. longimanus* preferring the moist, and *P. superbus* the dry, subcortical spaces.

Conclusions

Although my data are limited with respect to the number of trees sampled, it is apparent that the greatest overall species diversity occurs on slash pines offering the greatest microhabitat diversity. The specific microhabitat showing the greatest species diversity is that of flake bark, which was present in varying amounts on all of the trees examined. The two commonest species, *G. depressa* and *P. elongatus*, are found exclusively beneath flake bark but differ greatly in behavior and distribution on the trunk, the former being a solitary species which ranges over the entire tree and the latter being a subsocial species which largely restricts its activities to the lowermost portions of the trunk. Two species, *A. longimanus* and *P. superbus*, appear unable to utilize the flake bark microhabitat unless started bark is also present; thus, they are not found on live trees. A single species, *V. spinosa*, is entirely restricted to the relatively rare and transient moist subcortical spaces and is one of the least commonly encountered species. All of the remaining species occur sporadically on slash pine but may either not be restricted to this tree species (e.g. *I. paludis, D. morosus*) or may not be able to maintain populations in the presence of the diffuse competition or predation produced by the activities of the commoner, more closely slash pine adapted species such as *P. elongatus* and *G. depressa*. The maintenance of slash pine populations of these "fugitive species" at the Archbold Station and elsewhere may depend upon reservoir populations on other tree species and upon effective dispersal systems, such as phoresy.

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Summer Mean Diurnal Water and Air Temperature Distributions in the Cape Mendocino area, California

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Abstract.—This study is concerned with the spatial analysis of the mean air and water temperature distributions recorded at sampling sites located throughout the Cape Mendocino area of northern California. Employing a three hour sampling interval, it was found that the basic northerly air flow in summer was quite important to the resulting distributions of air temperatures computed for each individual site. Furthermore, elevation and distance from the coastline were also quite important to the resulting air temperature distributions. However, the mean water temperatures examined were slightly modified, if any, by the diurnal heating cycle.

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Atmospheric temperatures in coastal environments are modified through heat exchanges with the marine environment (Hasse, 1971; Roll, 1965). For example, modifications can be brought about by the movement of marine air associated with a basic sea breeze flow (Hannes, 1977). Thus, the diurnal temperature range could be reduced by such factors as the cooler air temperatures associated with marine air or by the presence of a cloud cover.

This study is concerned with the spatial analysis of the mean air and water temperature distributions throughout the Cape Mendocino area of northern California. It deals with a number of sampling sites and the data employed extend from July 8, 1970, through August 17, 1970.

This paper has several objectives: 1) to study the spatial distribution of the mean diurnal atmospheric temperature distributions obtained from a coastal north–south instrument transect; 2) to study the mean diurnal air temperature distributions gathered at weather stations in an east–west transect along a ridge; 3) to assess, if possible, the effects of elevation on the air temperature distributions; and, 4) to analyze the mean diurnal water temperature distribution and their possible relationships to the near coastal air temperature distributions.

Data Source and Study Area

The Cape Mendocino area of northern California was chosen because of the possible interactions of the cold upwelled waters with the atmosphere in the area (Reid et al., 1958), as well as the investigation of the possible effects of the general northerly air flow (Robinson et al., 1965) on air temperatures. With cold water offshore during the summer months, maximum land water temperature contrasts would occur. These thermal contrasts could then lead to a potentially strong sea breeze flow. But with a strong, persistent northerly summer air flow over the Cape Mendocino area, the basic land sea breeze circulation may be modified. This situation might lead to differences in air temperature distributions between

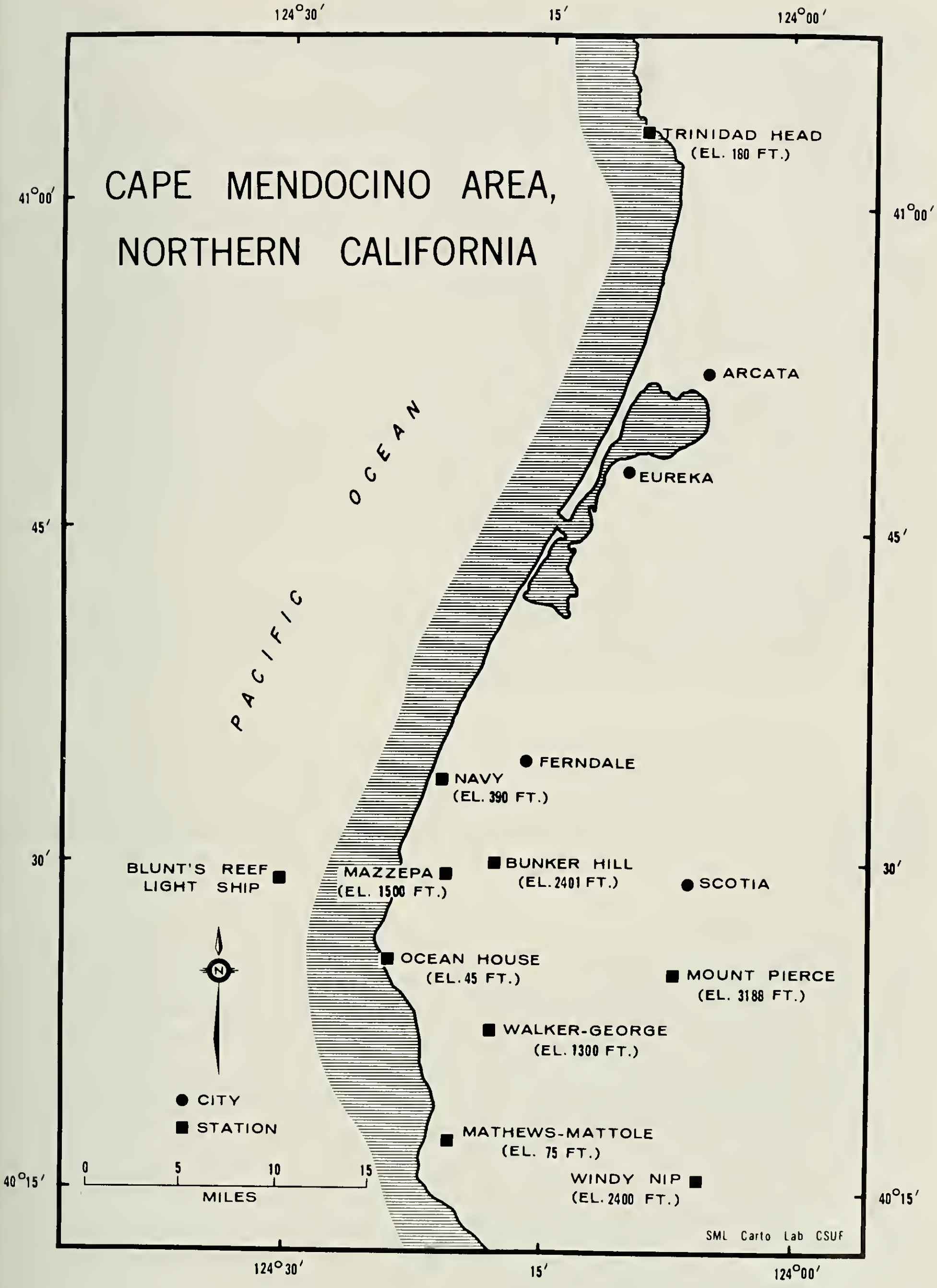

Fig. 1. Study Area

upstream and downstream stations. Thus, the resultant mean air temperature distributions should indicate the interaction of the two previously mentioned modifiers of air temperature (Hannes, 1974; Lahey, 1974).

A majority of the data used in this study was gathered by standard weather instruments on loan from the National Center for Atmospheric Research and the University of Illinois. The Blunt's Reef Light Ship data were obtained on microfilm from the National Climatic Data Center, Asheville, North Carolina.

Air temperatures were sampled at ten locations, while water temperatures were sampled at two locations (see Fig. 1). The variables studied were averaged by hours. In total, eight samples were obtained per day. Of the ten stations recording air temperatures, five stations are classified as low level coastal stations: Navy, Ocean House, Mathews-Mattole, Blunt's Reef, and Trinidad Head. One station, Walker-George, is intermediate in geographical location from the coast as well as in elevation. The other remaining four stations are classified as ridge top locations: Windy Nip, Mount Pierce, Bunker Hill, and Mazzepa. The coastal locations nearly make a north–south transect, while the ridge top sites are aligned in a basic east–west transect (see Fig. 1). Progressing inland from the coast, the ridge top sampling sites of Mazzepa, Bunker Hill, and Mount Pierce are found at increasing elevations respectively.

The atmospheric temperature data were gathered on hygrothermographs. Each hygrothermograph had a seven day recorder. Since the Blunt's Reef Light Ship data were taken only every three hours, the continuous weekly hygrothermograph data were reduced to match the sampling interval of the Blunt's Reef Light Ship data.

Water temperatures were gathered by the bucket method at Blunt's Reef and with a Barnes Infrared Radiation thermometer at Trinidad Head (see Fig. 1 for location). Once again, the Blunt's Reef data were sampled every three hours; therefore, the Trinidad Head water temperatures had to be extracted at three hour intervals to correspond to the Blunt's Reef sampling interval.

Results

The mean diurnal air temperatures and water temperatures are presented in Figure 2. These hourly values were obtained by averaging all values available for each individual hour sampled. As might be expected, geographical position with respect to the coast seems to have an important effect on the different air temperature distributions. For example, the minimum temperature at Navy, Mazzepa, Bunker Hill, and Mount Pierce indicate a general increase in magnitude from the coastal low level site to the higher, more interior ridge top site of Mount Pierce.

Air temperatures: coastal.—The coastal stations of Ocean House, Navy, and Trinidad Head have the lowest diurnal temperature ranges. However, the air temperatures of Blunt's Reef exhibit the smallest diurnal range. This small temperature range is probably due to the station's marine location. On the other hand, the Mathews-Mattole site has the greatest mean diurnal range.

The Mathews-Mattole site is the southernmost low level coastal site (see Fig. 1). With respect to the various intermediate ridge systems, this location is possibly very important to the resultant higher afternoon air temperature. If the northerly marine air flows over the various ridges and is forced to mix turbulently with air

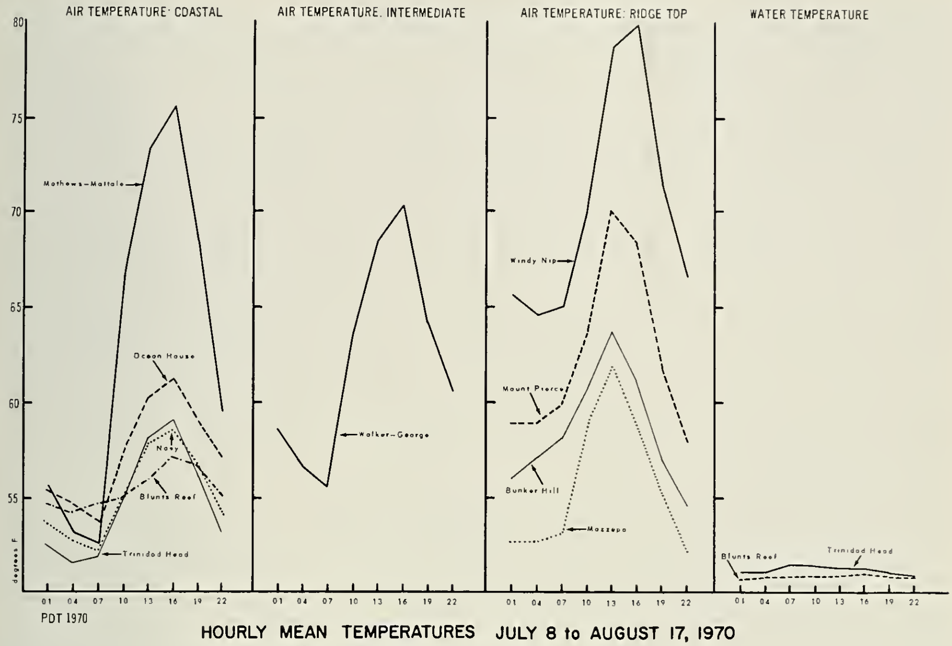

Fig. 2. Water and Air Temperatures

from the inversion layer aloft, then the marine air could be modified. This topographically induced mixing could cause the resultant high afternoon temperatures. Atmospheric wave activity is also suggested as a possible mechanism to mix the air turbulently over the various ridges. The possible existence of atmospheric waves in the Cape Mendocino area was shown by Hannes, 1972.

Air temperatures: intermediate.—The only intermediate sampling station, Walker-George, has a temperature distribution similar to that of the Mathews-Mattole and Windy Nip (Fig. 2). Walker-George records its highest average temperature at 1600. The occurrence of the high temperature at 1600 is in general agreement with the high temperatures at the two other southerly stations, i.e., Mathews-Mattole and Windy Nip. Comparing the high at 1600 to the temperatures recorded at the ridge top locations, Walker-George's high is equal to or greater than those at Bunker Hill, Mazzepa, and Mount Pierce (see Fig. 2). Furthermore, Walker-George's early morning temperature declines in magnitude from 0100 to 0700. This decrease is similar to the temperature changes attained at Ocean House, Mathews-Mattole, and Navy sites. However, the ridge stations do not exhibit major decreases during these morning hours. Thus, the greater diurnal range and the shape of the distributional curve is akin to the distributional curves at Mathews-Mattole and Windy Nip, and not to the ones located on the more northern ridge system (i.e., Mazzepa, Bunker Hill, and Mount Pierce). This is likely due to topographically induced mixing over the ridges (Hannes, 1972).

Air temperatures: ridge top.—The last category of the air temperature distributions examined is that of the ridge top sites (Fig. 2). The shapes of the four distributional curves examined are somewhat different. The station with the lowest elevation, Mazzepa, has the smallest average hourly temperatures of all the ridge top sites. Further inland from the coast, and at higher elevations, Bunker Hill and Mount Pierce's maximum and minimum temperatures are greater than the more coastal site of Mazzepa, suggesting the decreasing effects of the marine environment and possible diurnal variations in the height of the inversion base. The exact nature of the marine inversion in this study area is unknown due to the lack of continous upper air data; however, from limited data sampled at Arcata, Hannes (1972) found the morning inversion base approximately at 900 meters. The marine inversion on the west coast of the United States also exhibits diurnal height fluctuations (Meitin and Stuart, 1977; Schroeder et al., 1967). Thus, the diurnal changes in the height of the inversion base could logically affect the air temperatures recorded at the ridge top stations. With a low inversion base, the ridge top stations could be under the influence of warm, dry air rather than cool, moist marine air.

Windy Nip, the southernmost of all the stations (Fig. 1) has the highest average temperatures at all hours examined. These high values are probably due to the modification of the northerly air flow passing over the transverse ridges. In addition to the high temperature values, there is another distinction between Windy Nip and the other ridge top sites. This difference is apparent during the early morning hours (0100 and 0400). At those hours, Windy Nip experiences a decline in air temperature while the stations to the north are nearly constant and in the case of Bunker Hill, there is a temperature rise. Thus, each individual site along the northern ridge experiences some form of heat importation at those hours (0100 and 0400); otherwise, under normal conditions, air temperatures should decline. Possibly local fluctuations in inversion height could affect the night temperatures at Bunker Hill.

Furthermore, Windy Nip displays its highest average temperature at 1600 while the other ridge top sites experience their respective maximums at 1300. This fact suggests that there is a modification of the marine air downstream at Windy Nip, while this air is modified to a lesser extent along the more northerly ridge complex. Thus, the high temperature recorded at Windy Nip at 1600 is similar to the respective highs at Mathews-Mattole and Walker-George.

Water temperatures.—The average hourly water temperature distributions at both Trinidad Head and Blunt's Reef show very little variation throughout the diurnal cycle (Fig. 2). Trinidad Head's water temperature is diurnally slightly greater in magnitude than the water temperature at Blunt's Reef. The major difference between the two distributional curves occurs in the late morning and early afternoon hours (0700 to 1600). The water temperatures recorded at Trinidad Head are decreasing while Blunt's Reef water temperatures are increasing slightly. The reason for this difference is not fully understood at this time. Possibly the difference is due to various forms of ocean and air interactions occuring along the coast (Lahey, 1977). But in general, the water temperatures recorded at both locations are quite cool during the summer period examined. The cool water temperatures found off Cape Mendocino more than likely cause the small diurnal range in air temperatures at the low level sites.

Summary

In a coastal area such as Cape Mendocino, the direction of general air flow along with local topography are very important to the resultant air temperatures experienced at a specific location. Ocean House, of all the land stations, is closest to the ocean; yet air temperatures at Navy were lower during the average diurnal cycle. Ocean House which is located on the leeward side of Cape Ridge probably experiences more modified air than Navy, which occupies a windward location.

However, in regard to the east–west trending ridge top sites of Mazzepa, Bunker Hill, and Mount Pierce, location with respect to distance from the marine environment as well as elevation are suggested as the causes of their appropriate temperature distributions. Elevation is very important to the resultant diurnal air temperature distribution because of nearness to the base of the inversion layer. Since the nocturnal inversion layer is not stationary throughout the night, its fluctuations could directly influence the air temperatures at various ridge top sites and not the low level sites. It is possible for a ridge top site to be in an inversion layer during a portion of the night and not at any other hour. This might account for some of the early morning temperature rises (0400 at Bunker Hill). Also 'breaking' atmospheric waves and turbulent mixing of the inversion layer air downward could account for heating and the early morning temperature rise.

Concerning the water temperatures, it was found that they are slightly modified by the diurnal heating cycle. In fact, Trinidad Head experiences a slight temperature decline in the late morning and early afternoon hours (1000 to 1600). The cause of this decrease is not fully understood but could be due to different forms of upwelling operating near each of the sampling sites.

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Niche Separation Within a Population of Freshwater Fishes in an Irrigation Drain Near the Salton Sea, California

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Abstract.—The fish fauna of the King Street canal is a mixture of native and introduced species. Inflow from a thermal well at 42°C and irrigation runoff at 22°C were responsible for a thermal gradient that, in addition to differences in flow, held fishes in remarkably pure species populations. On 19 March 1977, *Cyprinodon macularius* was found most abundantly in water 10 cm deep at 39°C. *Gambusia affinis* occurred in flowing water 25 cm deep at 32°C. Only *Poecilia sphenops* inhabited a cool water outflow 18 cm deep at 22°C. Downflow, *Poecilia latipinna* was taken most commonly in slow moving water up to 50 cm deep at 26°C, and *Notropis lutrensis* occurred in riffles up to 25 cm deep at similar temperatures. Flooding during late summer 1977 and subsequent reconstruction of the canal obliterated most of the habitat diversity. All five species survived, albeit seriously reduced in number, and the species sorting that was previously observed also was no longer in evidence. Thermal differences remained, and a pond was constructed that impounded hot water. Later, on 17 July 1978, the pond included *Cyprinodon macularius, Gambusia affinis, Poecilia latipinna* and a new introduction, *Tilapia zilli.* Downstream, *Cyprinodon macularius, Poecilia sphenops,* and *Notropis lutrensis* were taken in flowing water.

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Introduction

An interesting assemblage of freshwater fishes inhabits waterways and canals draining into the Salton Sea in Riverside and Imperial Counties, California (Table 1). Most of these drains carry irrigation runoff, and represent permanent aquatic habitats. The fish fauna of these waterways is a mixture of aquarium species, escaped bait fishes, introduced game fishes, introduced "weed eaters," and one native form, a subspecies of *Cyprinodon macularius,* the desert pupfish.

On the northwest side of the Salton Sea, in the King Street canal, a thermal outflow was responsible for marked diversity in habitats not apparent in other drains (canals). In most of these canals fish species are found in mixed assemblages. Fish distributions in the King Street canal seemed to reveal preferences for distinct habitats, each occurring in virtually pure species populations. Flooding and subsequent reconstruction of the canal appeared to obliterate the distinct habitats and thus provided an opportunity to study the influence of habitat diversity on fish distribution.

This study documents nearly complete niche separation among introduced freshwater fishes in an "unnatural habitat," illustrating rapid selective forces in action, and it describes the effect of habitat alteration on niche stability. The study also describes habitat and potential threats to the desert pupfish, *Cyprinodon macularius,* the only native fish in the area.

Table 1. Fishes known to inhabit irrigation canals and waterways in the vicinity of the Salton Sea, Riverside and Imperial Counties, California.

Species	Reference
Dorosomidae	
Dorosoma petenense	Black, pers. comm.
Cyprinidae	
Carassius auratus	Personal observation
Cyprinus carpio	Mearns, 1975
Notropis lutrensis	Personal observation
Notemigonus chrysoleucus	Soltz, pers. comm.
Cyprinodontidae	
Cyprinodon macularius	Personal observation
Poeciliidae	
Gambusia affinis	Personal observation
Poecilia latipinna	Personal observation
Poecilia mexicana	Personal observation
Poecilia sphenops	Personal observation
Poeciliopsis gracilis	Mearns, 1975
Xiphophorus helleri	Mearns, 1975
Xiphophorus variatus	St. Amant and Sharp, 1971
Centrarchidae	
Micropterus salmoides	Soltz, pers. comm.
Lepomis cyanellus	Personal observation
Ictaluridae	
Ictalurus nebulosus	Personal observation
Ictalurus punctatus	Soltz, pers. comm.
Sciaenidae	
Bairdiella icistia	Soltz, pers. comm.
Cyonoscion nobilis	Personal observation
Cichlidae	
Tilapia mossambica	St. Amant, pers. comm.
Tilapia zilli	Personal observation
Gobiidae	
Gillichthyes mirabilis	Personal observation

Materials and Methods

The canal that parallels King Street lies 7 km north of the Riverside Imperial County line on the northwest side of the Salton Sea. Observations and collections of fishes were made on 3 March 1977, 21 May 1977, 18 March 1978, and 17 July 1978. The area provided a unique opportunity to study factors that influence fish distribution because depth varied only slightly (5 to 50 cm) and there was present a striking thermal gradient in addition to variations in turbulence and velocity. Flow was generally shallow and linear. Riffles alternated with laminar flow and undercut banks were present in association with meanders. A hot artesian well flowed into the canal. At its source the water was 46°C. Approximately 50 m downflow where the water cooled to 39°C fishes began to appear. From that point

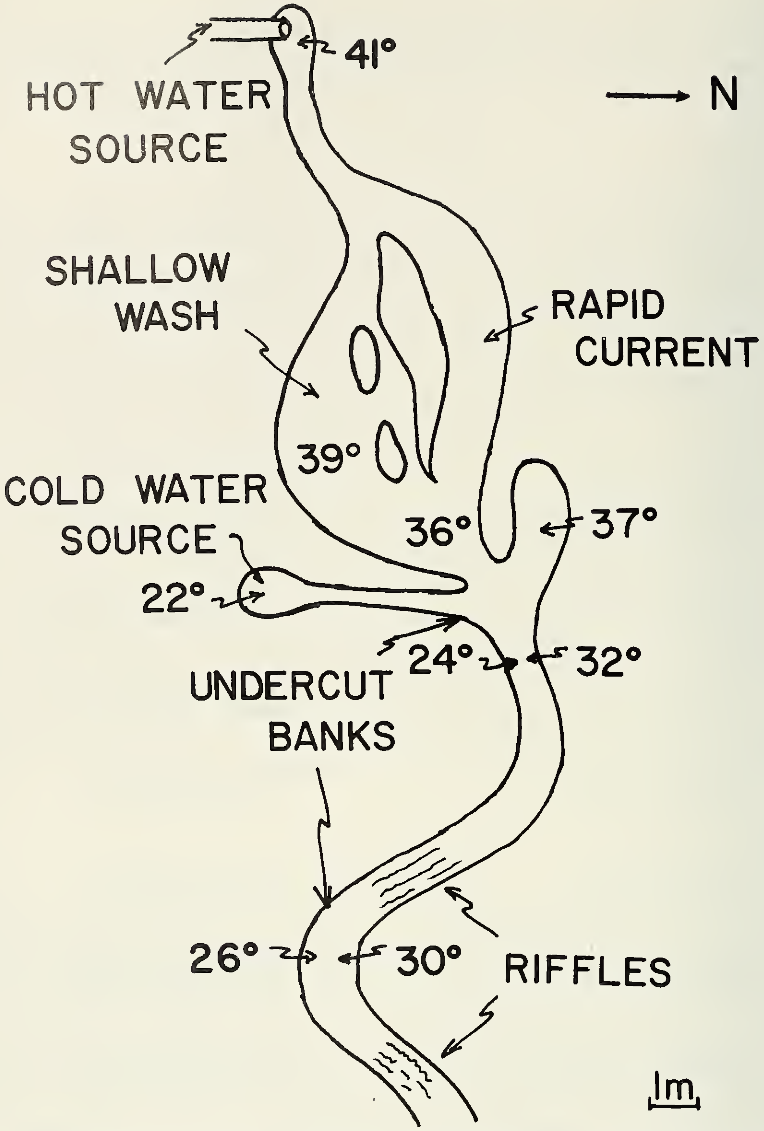

Fig. 1. Diagram of upper portion of King Street canal indicating differences in stream flow and temperature (3 March 1977). Fishes occur in nearly pure species groups as follows: *Cyprinodon macularius*, shallow wash; *Gambusia affinis*, flowing water at 32°C; *Poecilia sphenops*, cold water source; *Poecilia latipinna*, undercut banks; and *Notropis lutrensis*, riffles. Temperatures in °C.

to the mouth of the canal fishes were collected using a 1 m nylon seine with *ca.* 3 mm bar measure. Some specimens of each species were preserved in 10% formalin to insure correct identification. In order not to damage living fishes, counts of individuals were not made, and most fishes were released at their collection sites after identification. Temperatures at each collection site were recorded. Dissolved oxygen was determined using a Beckman Fieldlab Oxygen

Table 2. Habitat preferences for fishes inhabiting the King Street canal, Riverside County, California on 3 March 1977.

Species	Water Temp. (°C)	Diss. O_2 (mg/l)	Depth (cm)	Flow	Physical habitat
Cyprinodon macularius	39	6.8	5–10	slow	shallow wash
Gambusia affinis	32	7.0	25	moderate	stream margin
Poecilia sphenops	22	8.5	18	rapid	stream source
Poecilia latipinna	26	8.5	50	slow	undercut banks
Notropis lutrensis	26	8.7	8–15	rapid	riffles

Analyzer, and other chemical aspects of water quality were determined using a Bausch and Lomb Minispec 20 spectrophotometer.

Results

On 3 March 1977 collections of fishes revealed nearly complete species separation along various parts of the canal (Fig. 1, Table 2). Only desert pupfish, *Cyprinodon macularius,* were found in the shallowest, hottest water. They were abundant in water up to 10 cm deep at 39°C. An adjacent area of faster moving water at 32°C and 25 cm deep was inhabited only by schools of mosquitofish, *Gambusia affinis.* A few meters downflow, cold water at 22°C bubbled from a submerged pipe. At that point a small pool, 18 cm deep, contained in abundance only one species of fish. These were mollies of the "shortfin" group that have been identified by their dentition in accordance with Hubbs (1961) as *Poecilia sphenops,* although in coloration they resemble a variety of *Poecilia mexicana* known in the aquarium trade as "liberty mollies" (Miller, pers. comm.). Mature males and females of this variety have a distinctive orange band in the dorsal fin and carry no striking colors on the caudal fin. In the Johnson Street canal on the eastern side of the Salton Sea "typical" *Poecilia mexicana* have a metallic blue caudal fin with a distal orange band. These mollies are found in a similar habitat along with the porthole fish, *Poeciliopsis gracilis.* The assemblage in the Johnson Street canal has been described by Mearns (1975).

Water mixed slowly as it flowed in the King Street canal, the southern half of the stream remaining noticeably cooler for approximately 100 m. Water in this channel varied from 1 to 4 m in width and never was more than 50 cm deep. It meandered numerous times. Slow moving water up to 50 cm associated with undercut banks alternated with broad, fast moving riffles *ca.* 8 to 15 cm deep. Temperature varied from 24° to 27°C. Sailfin mollies, *Poecilia latipinna,* inhabited slow moving portions of the run, and red shiners, *Notropis lutrensis* were found in the riffles. Species overlapped very little in these habitats, although some *Poecilia sphenops* occurred in faster moving water with *Notropis* in upper portions of the run where the water temperature was 27°C. Approximately 2 km downflow the stream broadened to a floodplain no more than 10 cm deep and up to 5 m wide. *Cyprinodon* abounded in this area among roots of cattails (*Typha*), and rushes (*Juncus*).

On 21 May 1977 the area was revisited. Distribution of fish species had changed little. Water temperatures varied slightly from the determinations of 3 March.

Fig. 2. View east of upper portion of King Street canal (3 March 1977). Cold water source to extreme right center and undercut bank to left of center. Shallow wash to lower right.

The thermal water measured *ca.* 2° cooler. The cold source was the same. Dissolved oxygen measurements ranged from 7.2 mg/l at 37°C to 8.5 mg/l at 22°C. Other measures of water quality such as total dissolved solids at 1.1‰ showed little variability between the stations.

On 18 March 1978, one year later, the area was visited in order to assess the influence of flooding on the previously observed niche separations. Heavy rains occurred during late summer 1977 and winter 1978. The area barely was recognizable. Discussion with nearby residents revealed that flooding had obliterated the stream banks, allowing water to flow over 3 m deep and 15 m wide. Virtually all rooted vegetation was removed. The following February, the channel was rebuilt. Bulldozers reconstructed canal walls, the bottom was scraped, and portions were stabilized with rocks held in place by wire mesh and iron posts. Figures 2 and 3 depict the canal before and after reconstruction.

Reconstruction greatly reduced habitat diversity and sorting of fish species was poorly defined (Table 3). The hot water and cold water inflow pipes were in their former positions and a temperature gradient remained. Above the cold water inflow a small earthen dam had been constructed, apparently to impound the hot water. This impoundment was a full meter in depth at the center and apparently was being used by local residents for bathing, washing clothes, and swimming.

Fig. 3. View east of King Street canal following reconstruction (18 March 1978).

Water temperature in the upper 3 cm was 36°C and dissolved oxygen was 7.2 mg/l. At the upper, shallow end of the pond numerous young *Cyprinodon* were collected and released. A small number of *Poecilia latipinna* and *Gambusia affinis* also were collected in this shallow area although they were more common in deeper portions of the pond.

Downstream *ca.* 2 km the water course broadened as before, although distinct high banks had been constructed. No fishes were collected here, and there was no rooted vegetation. At the mouth of the channel, where it opened into the Salton Sea, *Poecilia latipinna* was abundant. It also abounded along the edge of the Salton Sea, in areas where the substrate was an odoriferous, black organic ooze.

On 17 July 1978 another visit to the canal revealed that a portion of the dam that impounded the water had broken down and the pond was only 60 cm deep. No collections were made, but visual observations were enhanced by very clear water. Apparently *Tilapia zilli* had been introduced since the last visit. Two adults were observed swimming in the pond. The surface temperature was 40°C. In a shaded shallow of approximately one square meter surface, in water 32°C and no deeper than 3 cm, were swarming a mixture of *Cyprinodon macularius*, *Poecilia latipinna*, *Gambusia affinis*, and juvenile *Tilapia zilli*. Backs of the fishes frequently protruded from the water giving the area the appearance of boiling.

Collections of fishes from other canals in the Salton Sea area seemed to confirm

Table 3. Habitat preferences for fishes inhabiting the King Street canal, Riverside County, California on 18 March 1978.

Species	Water Temp. (°C)	Diss. O_2 (mg/l)	Depth (cm)	Flow	Physical habitat
Cyprinodon macularius	36	7.2	2–100	slow	pond margin
	27	8.3	10	rapid	riffles
Gambusia affinis	36	7.2	2–100	slow	pond center
Poecilia latipinna	36	7.2	2–100	slow	pond center
	28	7.8	50	slow	stream margin
Poecilia sphenops	27	8.3	10	rapid	riffles
Notropis lutrensis	26	8.3	10	rapid	riffles

the preferences exhibited by the population in the King Street canal. Some differences, however, are worth noting.

In the Garfield Street canal *Cyprinodon macularius* were collected as recently as 7 December 1975 in water 50 cm deep among roots of cattails. That area is now inhabited by *Tilapia zilli* which were introduced to the Salton Sea area in 1971 for the purpose of weed eradication (St. Amant, pers. comm.). *Tilapia* are aggressive, feeding on detritus as well as aquatic vegetation. They probably also eat fish eggs. My collections seem to indicate that where pupfish formerly abounded, *Tilapia* are now common. *Tilapia* apparently were not present in the King Street drain until recently. Observations of relative abundance of the two species will be continued to determine if *Tilapia* appears to replace *Cyprinodon.*

Desert pupfish formerly were abundant in shoreline pools at the edge of the Salton Sea (Barlow, 1958a, b; Walker et al., 1961), and even were able to dive into the reducing, malodorous mud without apparent harm (Lowe et al., 1967). During rainy months certain pools along the north shore still are inhabited by pupfish (Black, pers. comm.), but such habitat adjacent to the mouth of the King Street canal seemed to be inhabited solely by swarms of sailfin mollies. It likewise seemed true near the mouth of the Avenue 81 canal where seine hauls yielded only *Poecilia latipinna.* Perhaps something about newly inundated land is hostile to desert pupfish. The Salton Sea is rising rapidly. Surface level has risen *ca.* 60 cm since September 1975 (Skjold, pers. comm.). Perhaps nesting is upset when the water level rises too rapidly. Perhaps there is too much organic material in the substrate or water. Perhaps peculiar combinations or lethal concentrations of mineral ions are responsible. Whatever the case, it appears that the natural range of *Cyprinodon macularius* in the area has shifted such that freshwater drains and water courses leading to the Salton Sea are now the primary habitat.

Discussion and Conclusions

The sorts of preferences indicated by this study are notable in view of the wide range of tolerances exhibited by these fish species. The hottest water inhabited by fishes in the King Street canal, 40°C, is either within, or not far above the known upper limit of these species as follows: *Notropis lutrensis,* 39.5°C (Brues, 1928); *Poecilia sphenops,* 35.6°C (Miller, 1949); *Gambusia affinis,* 39.5°C (Hubbs, 1959); and *Cyprinodon macularius,* 44.6°C (Barlow, 1958a, b; Lowe and Heath, 1969). *Poecilia latipinna* was recorded in the pond at 36°C and *Tilapia zilli* at 40°C. Of course, temperature stratification occurs and fishes may not necessarily occur at the temperature where the reading was taken. Nevertheless, when several species occur together, and the habitat is suitably diverse it is notable that they disperse themselves according to definable preferences.

Temperature tolerances notwithstanding, the oxygen supply of natural waters is probably the most frequent single factor influencing the life of desert fishes (Deacon and Minckley, 1975). In the King Street canal, however, all water is flowing and approaches saturation for dissolved oxygen. Prior to construction of the pond, depth varied only slightly, ranging from 5 to 50 cm, therefore, temperature and physical characteristics such as turbulence and velocity are most likely the significant parameters responsible for the observed sorting of species. Comparing the King Street canal to other canals in the area, it leads one to the conclusion that temperature is a very important factor. The pronounced thermal gradient, from 46°C to 22°C superimposed upon differences in flow and slight differences in depth was responsible for a nearly pure sorting of species based on habitat preferences. Considering that all but one of the species is introduced it further indicates that selective forces act rapidly.

The native pupfish, *Cyprinodon macularius,* formerly inhabited marshes, sloughs, and backwaters of the Colorado, Gila, and Sonoyta Rivers (Hubbs and Miller, 1941; Miller, 1961). That habitat in the Salton Sea area is most closely approximated by warm, shallow, slow moving waters, particularly in association with rooted aquatic vegetation or algal mats. Desert pupfishes also inhabit saline pools along the edge of the Salton Sea, at least during the rainy season, but these habitats now seem mainly to contain sailfin mollies, perhaps due to unstable conditions associated with the rapidly rising water, *ca.* 60 cm since September, 1975. In the King Street canal *Cyprinodon* was most abundant in a shallow wash at 39°C. It also was common *ca.* 2 km downflow in shallow water among roots of cattails and sedges.

"Liberty mollies," identified on the basis of dentition as *Poecilia sphenops,* appeared to inhabit only the King Street canal, and were found most abundantly near the outflow of water at 22°C. In some of the other canals this habitat is occupied by the closely related shortfin molly, *Poecilia mexicana,* and/or *Poeciliopsis gracilis,* neither of which was collected in the King Street canal. Red shiners, *Notropis lutrensis* were the only fishes collected in riffles of the King Street canal although they also were taken in small numbers with *Poecilia sphenops* in fast moving water other than riffles. By comparison, it is interesting to note that my collections of *Notropis* from the Gila and Verde Rivers in Arizona seemed to indicate that they preferred slow moving water deeper than 20 cm.

The most common fishes of the canal system were sailfin mollies, *Poecilia latipinna.* In the King Street canal they preferred slow moving water in association with undercut banks. They reached their greatest abundance in brackish water near the mouth of the canal, and in shallows at the edge of the Salton Sea where the substrate had become an odoriferous, black, anaerobic gel.

Mosquitofish, *Gambusia affinis,* occurred in slow moving waters at 32°C in the King Street canal. In other canals they were found in slow moving water with *Poecilia latipinna,* but advanced farther into vegetation, and not as far into the current as the mollies. Also, they seemed to avoid shallow or weedy areas inhabited by desert pupfishes.

The impact of flooding or other forms of habitat destruction on niche preferences is marked. In the Avenue 81 canal *Notropis lutrensis* used to be common along with *Poecilia latipinna*. Since the flooding of September 1976, however, it appears that *Notropis* may have been eliminated. After three pronounced floods, *Cyprinodon macularius*, the native species, and *Poecilia latipinna* occur there as before. Regarding *Poecilia latipinna*, it is interesting to note that it apparently was the only species extirpated from the Salt River near Mesa, Arizona by the flood of 1970 (Minckley, 1973). Apparently the ability of sailfin mollies and desert pupfish to tolerate saline waters of the Salton Sea enables them to reinhabit these canals after flooding. Perhaps the absence of such a refuge in the Salt River led to the demise of *Poecilia latipinna* in the Salt River.

In the King Street canal, flooding and subsequent reconstruction dramatically reduced the diversity of habitat and the striking examples of niche separation observed in 1977 were obliterated. All original species were still present as recently as 17 July 1978 and some examples of species sorting were still observable, but they were far less obvious. Essentially two habitats remained, cool flowing water and impounded hot water. The former was inhabited by *Notropis lutrensis, Poecilia sphenops*, and a few *Cyprinodon macularius*. The impounded hot water apparently is used for washing clothes and human bathing. Recently *Tilapia zilli* was introduced here. *Poecilia latipinna, Gambusia affinis*, and *Cyprinodon macularius* were found there with the *Tilapia*. The ability of this population of desert pupfishes to tolerate pollutants from human bathing and washing clothes as well as encroachment by *Tilapia zilli* remains to be seen.

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Research Notes

Two Asiatic Gobiid Fishes, *Tridentiger trigonocephalus* and *Acanthogobius flavimanus*, in Southern California

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While SCUBA diving in Los Angeles Harbor I collected mature adults and eggs of one Asiatic goby, *Tridentiger trigonocephalus* (Gill) and photographed another, *Acanthogobius flavimanus* (Temminck and Schlegel). Subsequent collections indicated that both are established in Los Angeles–Long Beach Harbors and vicinity, and that the latter species may be rapidly extending its range in southern California.

The chameleon goby, *T. trigonocephalus* (Fig. 1), reaching a length of approximately 90 mm TL, is larger than most native Californian gobies, while the yellowfin goby, *A. flavimanus,* which grows to approximately 240 mm TL, is larger than all Californian gobies (Miller and Lea, 1976). The latter species seems to be highly adaptable to marine and fresh waters and able to extend its range rapidly (Brittan et al., 1970; Kukowski, 1972).

Tridentiger trigonocephalus

Tridentiger trigonocephalus occurs in marine and brackish waters from Hong Kong to the Amur River Basin, USSR, and the Japanese Islands (Fowler, 1961; Tomiyama, 1936), on hard and soft substrata (Carl L. Hubbs, Scripps Institution of Oceanography, pers. comm.; Dôtu, 1957, 1958). This goby has been reported from Los Angeles Harbor (Hubbs and Miller, 1965; Miller and Lea, 1976), and is established in San Francisco Bay (Ruth, 1964; Brittan et al., 1970) and Sydney Harbor, Australia (Hoese, 1973; Friese, 1973).

On 1 June 1960, Jim Wright of Marineland of the Pacific observed two, but could only collect one goby at Fish Harbor in Los Angeles Harbor (John H. Prescott, New England Aquarium, pers. comm.). The single specimen (Fig. 1) was identified by Carl L. Hubbs as *T. bifasciatus* Steindachner, a synonym of *T. trigonocephalus* (Tomiyama, 1936; Koumans, 1940), and was the first capture of this goby in American waters. It is a 70.4 mm SL male captured on a rock jetty at a depth of 3 m. The specimen is deposited in the fish collection of Scripps Institution of Oceanography (SIO 77-337). This specimen is the basis of the report by Hubbs and Miller (1965) of this goby being in Los Angeles Harbor.

On 24 May 1977, I collected three females, 49.2 to 57.2 mm SL, and twelve males, 56.7 to 77.3 mm SL, chameleon gobies in Los Angeles Harbor on the rocky "rip-rap" under Pier 228, Slips D and E, in depths of 0.3 to 3 m. Most specimens were collected from discarded bottles littering the bottom. The surface water temperature was 18°C and salinity was 34.3‰ at the surface and at 3 m. Visibility was 1 to 2 m. These specimens are deposited in the fish collection of the Natural History Museum of Los Angeles County (LACM 36989-1).

Gonadal inspections of all specimens revealed well developed eggs and testes. Gut examinations of all specimens revealed, in order of decreasing frequency: crustaceans, including gammarid and caprellid amphipods, copepods, isopods,

Fig. 1. The first *Tridentiger trigonocephalus,* captured in Los Angeles Harbor. Standard length is 70.4 mm.

and ostracods; polychaete worms; gastropods; and fish eggs, as evidenced by one gut containing 478 eggs.

On 22 September 1977, I collected two males, 44 and 78 mm SL, and a 66 mm SL female *T. trigonocephalus* from the same location. The larger male and the female, together with a clutch of 300 eggs, were collected from an aluminum beer can.

Acanthogobius flavimanus

Acanthogobius flavimanus occurs naturally in Japan, Korea, and China (Fowler, 1961; Tomiyama, 1936) in marine, brackish, and river waters (Okada, 1955). It has been introduced into Sydney Harbor, Australia (Hoese, 1973; Friese, 1973). This goby was first found in California in 1963 in the San Joaquin River and the Stockton Deepwater Channel (Brittan et al., 1963). Since then it has been reported from the Sacramento Delta, the San Francisco Bay area, and Bolinas Lagoon (Brittan et al., 1970), Elkhorn Slough (Kukowski, 1972), and Tomales Bay and Estero Americano (Miller and Lea, 1976). It has not heretofore been reported from southern California.

An underwater photograph (Fig. 2) taken in Los Angeles Harbor under Pier 228 on 22 September 1977, revealed the presence of *A. flavimanus* in the rocky "rip-rap." No specimens were captured. On 29 March 1978, biologists from Marine Biological Consultants, Inc., Costa Mesa, California, took a 156 mm SL male (Fig. 3) in a gill net (1½ in. bar mesh) at a depth of 18 m in the back harbor, Channel 3, of Long Beach Harbor (John L. Wintersteen, pers. comm.). This specimen is deposited in the Natural History Museum of Los Angeles County (LACM 37346-1). The testes of this individual were not well developed. Stomach

Fig. 2. Underwater photograph of *Acanthogobius flavimanus,* taken in Los Angeles Harbor. Standard length is estimated at 100 mm.

contents included a crab, ostracods, amphipods, copepods, and a large amount of unidentifiable digested material.

On 15 April 1978, two specimens of *A. flavimanus,* 24 and 30 mm SL, were collected in a beach seine over the silty substratum of Upper Newport Bay, about 37 km southeast of Los Angeles Harbor, by Michael H. Horn, of California State University at Fullerton, and Larry G. Allen, of the University of Southern California (pers. comm.). They subsequently collected another specimen, 48 mm SL on 4 May 1978, and a fourth specimen, 57 mm SL, on 14 May 1978, from the same locality. These gobies are being retained in the fish collection of California State University at Fullerton (uncataloged). Stomach contents of these four gobies included ostracods, copepods, and amphipods.

On 26 June 1978, Eric H. Knaggs of the California Department of Fish and Game (pers. comm.) beach seined four yellowfin gobies, 66 to 90 mm SL, in the sandy mud bottom of the San Gabriel River, between the Westminster Avenue and Seventh Street bridges (Long Beach, Los Angeles County) about 13 km east of Los Angeles Harbor. These gobies are deposited in the Natural History Museum of Los Angeles County (LACM 37711-1). On 31 July 1978 he collected two more specimens, 71 and 84 mm SL, from the Long Beach Swimming Lagoon, near the mouth of the Los Angeles River. These latter specimens were sacrificed for other studies. The salinity and temperature of the localities of these two collections are unknown, but both areas are influenced by marine and fresh waters.

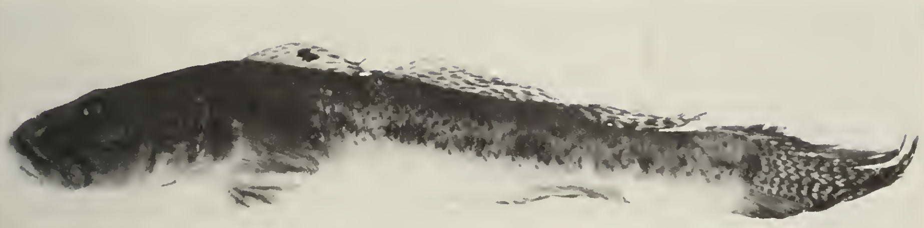

Fig. 3. *Acanthogobius flavimanus*, collected in Long Beach Harbor. Standard length is 156 mm.

Discussion

The occurrence of numerous mature and spawning adults is evidence that an established population of *T. trigonocephalus* exists in Los Angeles Harbor. The presence of small, probably locally spawned, *A. flavimanus* can be taken as evidence that it is established in Newport Bay. An observation in Los Angeles Harbor and a collection of yellowfin gobies in Long Beach Harbor waters and the San Gabriel River are strong evidence that this goby is established and may be expanding its range in southern California.

Because of the nature of international shipping, there is little doubt that the Los Angeles–Long Beach Harbors are the locations of introductions of both gobies into southern California. There is no regular international shipping into Newport Bay or the San Gabriel River. The fact that these gobies only occur extralimitally in widespread Pacific port cities and vicinities would also seem to implicate shipping.

The actual method of introduction is unknown, but suggested mechanisms generally involve the transport of eggs on fouling organisms growing on the hulls, or in the seawater systems of ships (Brittan et al., 1963; Hubbs and Prescott *in* Hubbs and Miller, 1965; Dawson, 1973; Hoese, 1973). Another mechanism, that of egg transport on oysters, would not be applicable to Los Angeles–Long Beach Harbors, as no oysters have been introduced there.

Dawson (1973) estimated that minimum ship transit time from Yokohama, Japan to San Francisco was eight days in 1972. The average incubation time of eggs of *T. trigonocephalus* is 8.5 days at 20°C (Dôtu, 1958), while that of *A. flavimanus* is about 28 days at 13°C (Dôtu and Mito, 1955). Therefore, it is possible that eggs of both gobies could be laid on fouling organisms of ships hulls in the Orient, and be transported to the west coast of the United States in time for hatching. Seawater temperatures along likely transpacific shipping routes are sufficient for egg development.

Dawson (1973) convincingly related the recent (since the mid-1950's) increase in exotic introductions of Indo-West Pacific organisms into the Americas to the increased speeds of modern ships. John E. Fitch (California Department of Fish and Game, pers. comm.), suggested another mechanism of introduction of exotic marine organisms might occur when occupants of aquaria, found on many large ships, were dumped into foreign harbors.

The problems associated with the introductions of exotic species into a habitat were discussed by Lachner et al. (1970). Such introductions, be they deliberate or accidental, are no longer unusual, and most ecologists would consider them unwise.

It appears that these two Asiatic gobies have become a permanent part of southern California's ichthyofauna. One, *T. trigonocephalus*, seems to be restricted (in southern California) to Los Angeles, and probably Long Beach Harbors, while *A. flavimanus* is extending its range down coast from Los Angeles Harbor, a situation reminiscent of the "explosive spread" reported by Brittan et al. (1970) in the San Francisco Bay-Delta region.

Virtually nothing is known about the effect of these gobies on native species. If *A. flavimanus* continues to expand into streams, lagoons, and bays down coast, there is a possibility that some populations of tidewater gobies, *Eucyclogobius newberryi* might be eliminated (Moyle, 1976), and staghorn sculpin, *Leptocottus armatus* might be displaced (Brittan et al., 1970). The longjaw mudsucker goby, *Gillichthys mirabilis* is collected in back bays and sloughs for use as bait in local lakes, the Salton Sea, Lake Mead, and the Colorado River (Turner and Sexsmith, 1964). If *A. flavimanus* is collected with bait species, it could be transported to other marine and freshwater habitats, where it could become established.

I wish to thank Carl L. Hubbs, John H. Prescott, John L. Wintersteen, Michael H. Horn, Larry G. Allen, and Eric H. Knaggs for making goby specimens and various data available to me.

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The Velvet Whalefish, *Barbourisia rufa,* added to California's Marine Fauna, with Notes on Otoliths of Whalefishes and Possible Related Genera

California's north coast trawl fishermen normally sort their catches at sea and deliver the most desirable species (rockfishes, *Sebastes* spp. and *Sebastolobus* spp.; sablefish, *Anoplopoma fimbria*; lingcod, *Ophiodon elongatus*; and several kinds of pleuronectid flatfish) in a fresh state to shoreside markets where most are filleted, packaged, and frozen. If, when sorting his catch, a fisherman finds what he believes is a rare or unusual fish, mollusk, crustacean, or other organism he often will leave it at the market with a request that it be placed in their freezer and saved for the California Department of Fish and Game (DFG). Similarly, if while processing a load, plant personnel encounter an "odd-ball" (some animal of unusual color, size, or condition; or an organism that is tagged or one that cannot be identified by those present at the time; etc.) that specimen too will be saved.

Unless forgotten or overlooked, this material is then turned over to the first DFG employee to stop at the plant during routine surveillance or sampling operations, and at that time he is informed (usually verbally) of the name of the boat and/or skipper who caught the oddity. It is then necessary for the DFG employee to contact the vessel skipper during his next trip to port, and obtain complete collecting data for the specimen or specimens in question.

Unfortunately, as in the present case, an occasional item is saved for which collecting data cannot be obtained, even after making dozens of inquiries over a lengthy period of time. In these instances, it is necessary to make assumptions based upon available evidence, which if actual facts were known, might not hold up. The whalefish in question, 330 mm standard length (SL) and weighing 456 g, was picked up by DFG biologist Lawrence Quirollo at Eureka Fisheries in Crescent City on 18 June 1974, and represented the first record of *Barbourisia rufa* from the eastern Pacific. It was thought to have been in Eureka Fisheries' freezer for about one month before it was picked up, but even though an enlarged photograph of the fish was circulated among all the then employed plant personnel, no one could remember having seen the fish previously, nor did they know who might have placed it in the freezer. The photograph also was shown to all fishermen who had made deliveries to Eureka Fisheries during the first six months of 1974, with similar negative results. It was assumed then, that the fish had been saved by some former employee of Eureka Fisheries, but several individuals who fitted this concept could not be located.

An examination of fish landing receipts for several months prior to June 1974 indicated that all catches delivered to Eureka Fisheries at Crescent City during that period had been made off California, most in the vicinity of Redding Rock. No records were found of deliveries by vessels that had been fishing off Oregon, so it must be assumed that this whalefish had been caught off California.

Previously, based upon fewer than 20 specimens, *Barbourisia rufa* had been reported from a number of localities throughout the world: Gulf of Mexico (type locality), Indian Ocean near Madagascar, South Africa, Kurile Islands, Florida, Japan, and the south Pacific near New Caledonia (Trunov, 1968; Penrith, 1969; Fourmanoir, 1970a, 1970b; Maruyama and Ono, 1973). John R. Paxton, the Australian Museum, has informed me (personal comm.), however, that he has been able to locate published and unpublished capture records for 43 specimens of *B. rufa,* with eight from the Hawaiian area representing the closest previous captures to our shores. His records extended into the first few months of 1976. Only two of the 43 individuals were larger than the Californian whalefish: one from off South Africa at 345 mm SL, and one from lat. 22°14′S long. 02°56′E at 333 mm SL. Meristic data on the Californian *Barbourisia,* as determined from X-rays are: dorsal rays 22, anal rays 17, caudal rays 5 + 19 + 4 (dorsal rudimentary, principal, and ventral rudimentary), and vertebrae 44. The otoliths (sagittae) of this fish were removed and examined for evidence of age, and although numerous alternating opaque and hyaline zones could be discerned, these could not be interpreted as being annuli. The finely spinulose scales, which are unique to *Barbourisia rufa,* give a velvety texture to the skin which eased the task of coining a vernacular.

Among recent publications, Rosen and Patterson (1969:457), after considerable discussion, state that they "feel confident that the correct position of the cetomimoids is within the Beryciformes." They mention that *Rondeletia bicolor* lacks a swimbladder, as does *Scopelogadus beani,* but go no further in drawing conclusions regarding affinities of these two genera (families). Earlier (p. 373), Rosen and Patterson, in discussing family Neoscopelidae, point out that in *Scopelengys,* one of the three genera assigned to the family, "the arrangement of the adductor mandibulae was found to be characteristic of all members of Berycoidei and of the single melamphaid [*Melamphaes bispinosus*] examined."

Gosline (1971:134–136) divides the order Cetomimiformes into three groups of families depending upon placement of pelvic and dorsal fins. He states that *Ce-*

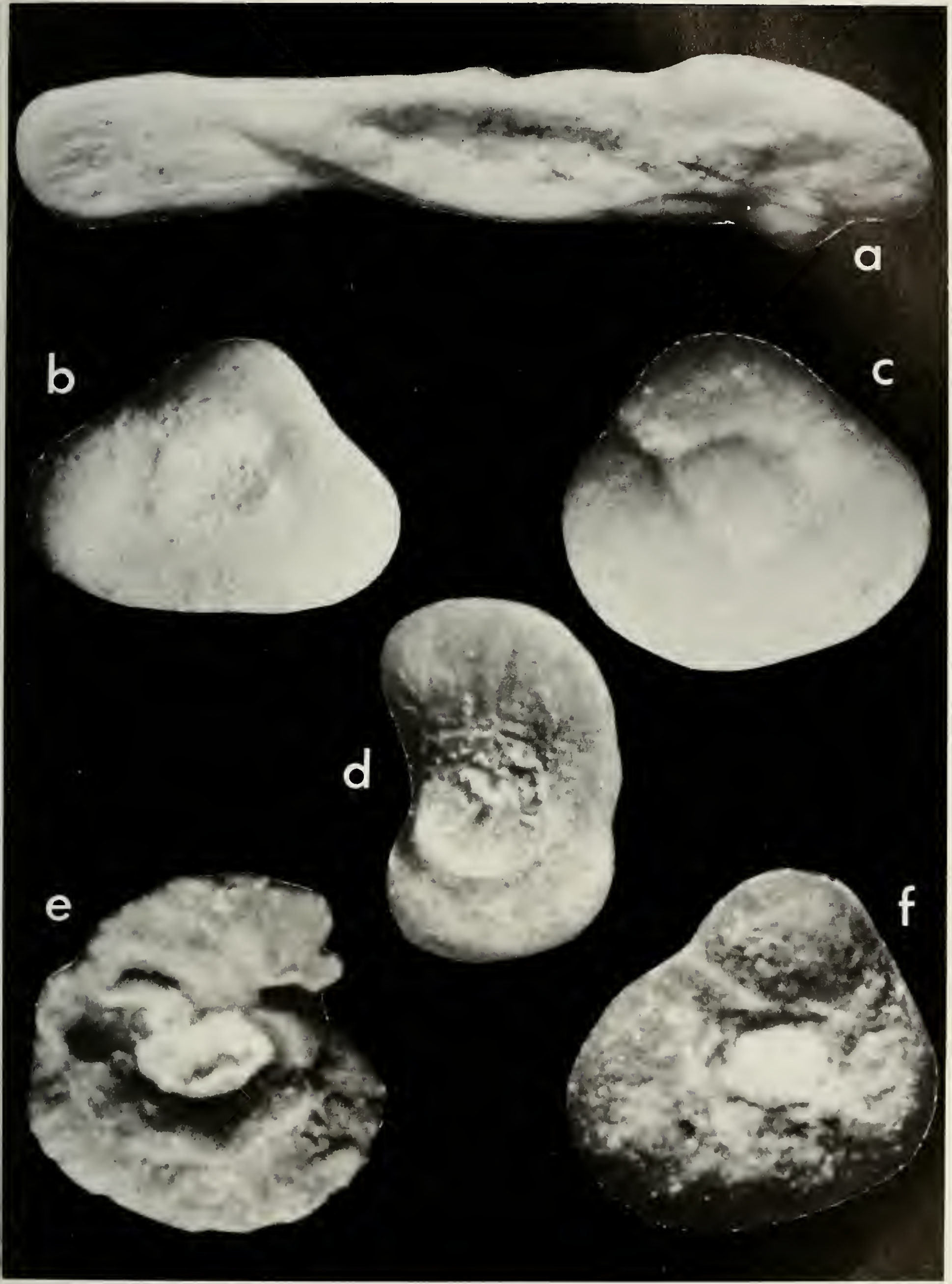

Fig. 1. Right sagittae from known whalefish genera (otolith length by height and fish standard length also noted): a) *Barbourisia rufa* 5.0 × 1.1 mm (330 mm SL); b) *Gyrinomimus* sp. 2.0 × 1.5 mm (310 mm SL); c) *Cetomimus* sp. 1.4 × 1.2 mm (159 mm SL); d) *Rondeletia loricata* 1.2 × 1.9 mm (83 mm SL); e) *Cetostomus regani* 1.3 × 1.3 mm (213 mm SL); f) *Ditropichthys storeri* 1.4 × 1.6 mm (SL unk.).

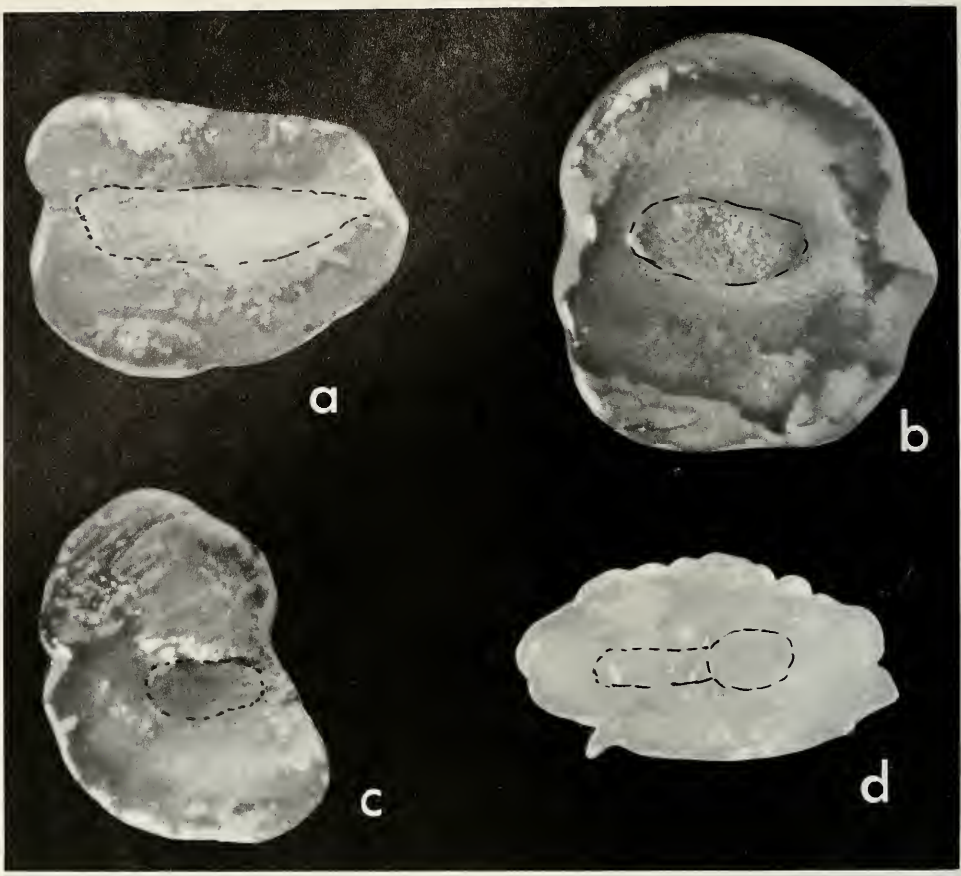

Fig. 2. Left sagittae of fishes belonging to suborder Stephanoberycoidei (otolith lengths and fish standard lengths in mm are noted): a) *Stephanoberyx monae* (2.4, 99.5); b) *Scopelogadus bispinosus* (2.3, 80); c) *Gibberichthys latifrons* (1.5, 95); d) *Melamphaes lugubris* (3.7, 41). Outline of sulcus has been indicated with broken, inked-in line.

tomimus (Cetomimidae) "has been shown (Parr 1929) to have strong osteological affinities with myctophiform fishes," and includes it in his second group of families (pelvic fins jugular or absent; dorsal fin posterior). In discussing his third group (pelvics subabdominal) he concludes that, "aside from *Barbourisia,* there seems no reason to think that all of the members of the present group are not beryciform derivatives, possible [*sic*] related to the Melamphaidae and Stephanoberycidae."

Finally, Nelson (1973:190) places the three whalefish families in the suborder Cetomimoidei (Order Beryciformes), following the lead of Rosen and Patterson (1969). He does not discuss their possible ancestry.

Since whalefish otoliths previously had not been discussed, illustrated nor compared, and since I had material from all extant genera in the three whalefish families (Cetomimidae, Rondeletiidae and Barbourisiidae), it seemed worthwhile to determine if they might be useful in whalefish taxonomy or in discerning familial relationships.

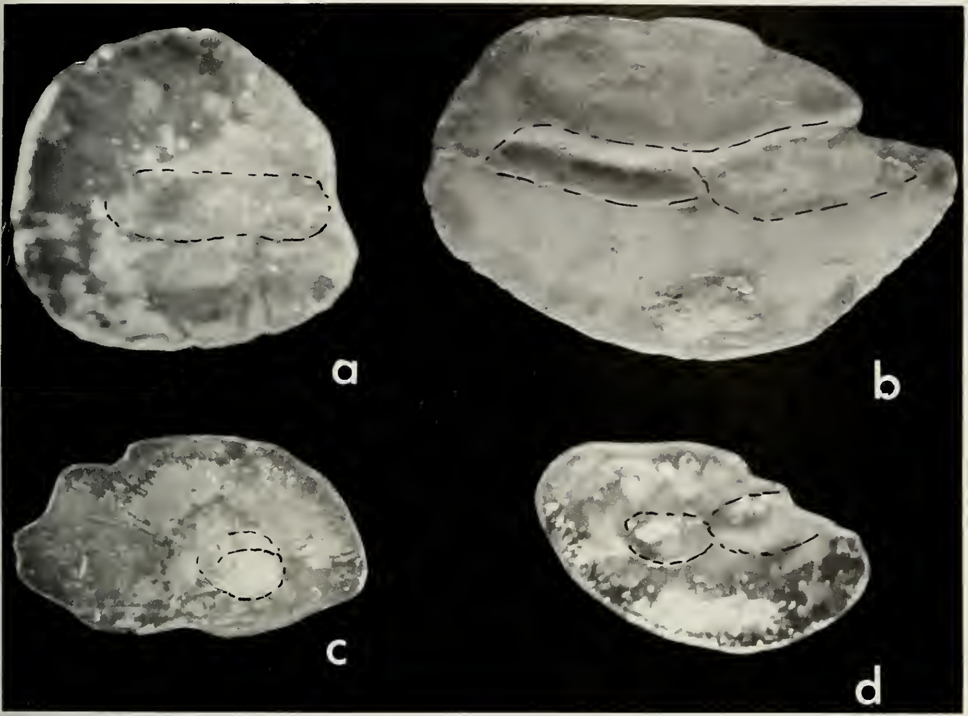

Fig. 3. Left sagittae of fish genera belonging to family Neoscopelidae (otolith lengths and fish standard lengths in mm are noted): a) *Solivomer arenidens* (1.5, 76); b) *Neoscopelus* sp. (8.0, 150); c) *Scopelengys tristis* (3.2, 172); d) *Neoscopelus* sp. (1.7, 37). Outline of sulcus has been indicated with broken, inked-in line.

In using otoliths (sagittae) as a taxonomic character, the most important feature for determining family relationships (and ancestry) is the sulcus (groove on the inner face): its position, configuration and differentiation. Although, in the Cetomimidae the sulcus is slightly excavated, it appears to be a slightly raised "blip" in the center of the otolith; it opens to the margin anterodorsally via a presulcal trough. Ostium (anterior part of sulcus) and cauda (posterior part) are undifferentiated. In *Gyrinomimus, Cetomimus* and *Ditropichthys* (Figs. 1b, c and f), the otolith has smoothly rounded margins, and appears trilobate in outline. The sulcus is encircled by a low, smooth ridge except at the point of entry for the presulcal trough. In *Cetostomus* (Fig. 1e), the otolith margin is roughened, and the sulcus is rimmed by a high, relatively sharp ridge, somewhat foliose in appearance. Otolith length in all four genera is equal to or slightly greater than otolith height.

In *Rondeletia* (Fig. 1d, Rondeletiidae), the sulcus is slightly excavated, circular in outline, and surrounded by a slightly raised rim. In contrast with cetomimid otoliths, the sagitta of *Rondeletia* is much higher than long, and the sulcus lies just inside the anterior margin. A very short presulcal trough leads to the margin, and as with cetomimid otoliths, ostium and cauda cannot be distinguished.

In *Barbourisia* (Fig. 1a, Barbourisiidae) the sulcus is elongate and deeply excavated. It is surrounded by a high, broadly rounded rim, and as in the other two whalefish families, a presulcal trough runs diagonally upwards to the anterodorsal margin of the otolith. The otolith is more than four times longer than high.

Since otoliths were on hand from all families placed in the order Beryciformes by Nelson (1973) except Korsogasteridae, and from all families placed in suborder Myctophoidei by Greenwood, Rosen, Weitzman and Myers (1966), these were examined to see if they could shed any light on the problem of whalefish relationships.

Based only upon otolith characters, the suborder Cetomimoidei of Nelson (1973:190) should be more closely allied to his suborder Stephanoberycoidei (p. 186) than Berycoidei (p. 187). Sagittae of all five melamphaid genera (Stephanoberycoidei) have a centrally located, round or oval sulcus that is surrounded by a low rim, and there is a presulcal trough leading to the anterodorsal margin (Weiler, 1968). The sagittae of *Scopelogadus* spp. (Fig. 2b) show greater similarity to whalefish otoliths than do sagittae of *Melamphaes* spp. (Fig. 2d) which are typical of the other three melamphaid genera. Otoliths of *Stephanoberyx monae* (Fig. 2a) have sulcal characters that are intermediate between those found in melamphaid genera and *Gibberichthys latifrons* (Gibberichthyidae: Stephanoberycoidei, Fig. 2c).

Only *Scopelengys* (Neoscopelidae, Fig. 3c) among myctophoid families has otoliths with sulcal characters similar to those found in whalefishes and melamphaids. Sulcal characters of *Neoscopelus* (Fig. 3b and 3d) and *Solivomer* (Fig. 3a), the other two genera in the Neoscopelidae, show closer relationships to the Myctophidae (*Neoscopelus*) and Berycidae (*Solivomer*) than they do to the whalefishes. Nafpaktitis (1977) reviewed previous research on the Neoscopelidae, but still needed is an in-depth comparison of the three neoscopelid genera to determine if the family as presently constituted accurately reflects relationships or is in fact a heterogeneous assemblage of oceanic misfits.

Acknowledgments

Special thanks go to Lawrence Quirollo, California Department of Fish and Game (DFG), Eureka, for picking up the specimen at the waterfront, for seeing that it was taken care of properly until he could send it to me, and for the many hours he subsequently put in trying to obtain capture data. Several individuals contributed otoliths that were critical to this study: Robert Lavenberg, Natural History Museum of Los Angeles County; Basil Nafpaktitis, University of Southern California; and Bruce Robison, University of California, Santa Barbara. John Paxton, The Australian Museum, and Richard Rosenblatt, Scripps Institution of Oceanography furnished information on material in collections at their institutions and elsewhere. Lillian Dempster and W. I. Follett, California Academy of Sciences supplied some much needed references and other information. Jack W. Schott, DFG, Long Beach took the excellent otolith photos, and Micaela Wolfe, DFG, Long Beach, typed the manuscript.

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The Larva of *Onthophagus medorensis* Brown with Notes on its Biology (Coleoptera: Scarabaeidae)

Onthophagus medorensis Brown (Brown, 1929) is a small, fairly common green to blue dung beetle which occurs from Kansas south to southern Texas, east to Louisiana and Arkansas and west to the edge of the shortgrass prairie (Howden and Cartwright, 1963). According to Edmonds and Halffter (1978), the larva has not been described. From data accompanying previous collections (Howden and Cartwright, 1963), it would appear that *O. medorensis* is partial to shaded, sandy areas and occurs on rotting plant material in addition to a variety of dung types. Brown (1926, 1928) indicates that most specimens have been taking during the early summer.

During the course of this study, two series containing four adult specimens each of *O. medorensis* were collected. Both series showed the metallic green phase of coloration described in Howden and Cartwright (1963). The first collection was made from human dung found near a construction site in mixed pine-oak woodland five miles south of Shreveport, Caddo Parish, Louisiana on 5 May 1977; these beetles were saved alive for rearing of the larvae. The other collection was made on 29 October 1977 from rabbit dung found in a mixed pine-oak wood on the Texas Eastern University campus, Smith County, Texas. Other dung

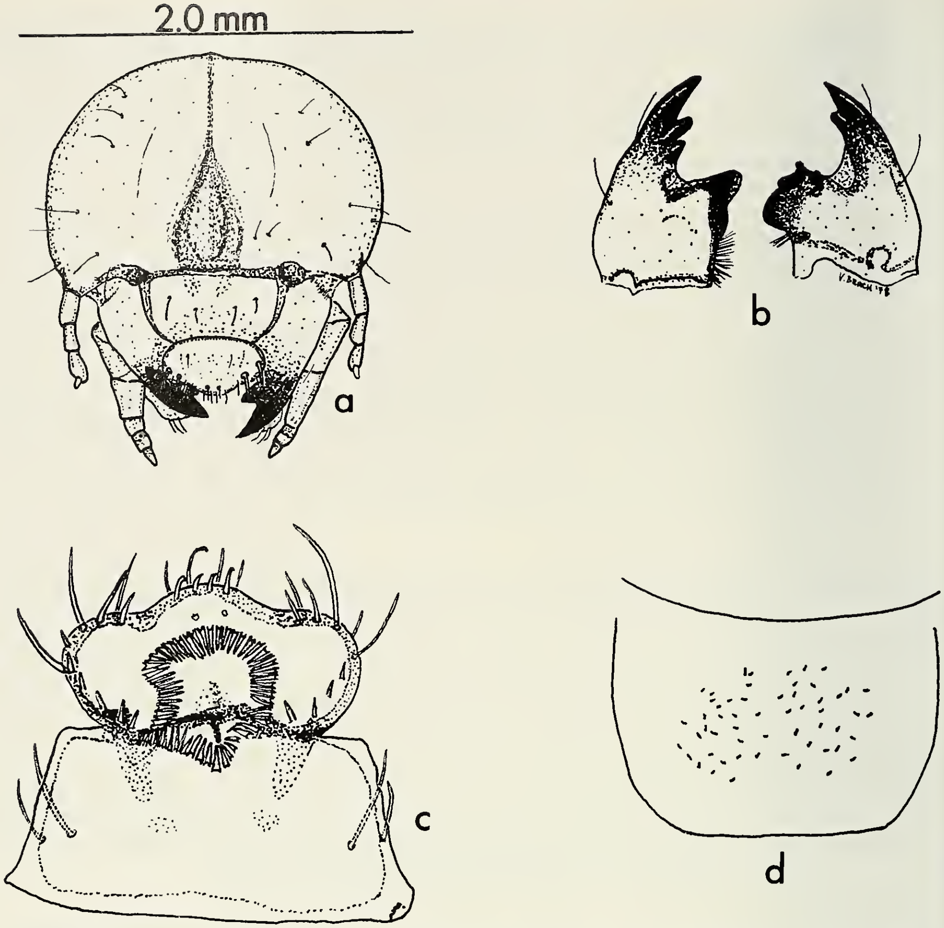

Fig. 1. Third-stage larva of *Onthophagus medorensis* Brown: a. head capsule; b. mandibles; c. epipharynx; d. arrangement of setae on venter of last abdominal segment (diagrammatic).

beetles taken with these collections were two *O. oklahomensis* Brown (Louisiana collection) and one *Canthon* sp. (Texas collection).

The specimens of *O. medorensis* from the Louisiana collection were placed in a quart rearing jar filled to within 25 mm of the top with moist sand taken from the collection site and covered with a layer of fresh human dung. On 1 June 1977, the jar was emptied and the adult beetles and brood cells retrieved. Four subspherical brood cells measuring approximately 17 mm in diameter were found; each contained a third instar larva. All four larvae were fixed and preserved in hot Ward's insect larva preservative prior to dissection and description.

The following description employs the terminology of Ritcher (1966).

O. medorensis Brown, third-stage larva (description based on four specimens; Fig. 1): Maximum width of head capsule 1.68–1.71 mm; epicranial stem deeply forked basally on frons with a prominent median hump between the fork branches; maxillary stridulatory area with 6–11 short, conical teeth ($\bar{x}$ = 8.5); gibbosity on dorsum of third abdominal segment with two irregular to subquadrate patches of 55–68 weakly curved setae; venter of last abdominal segment with two subcircular patches of 55–65 caudally directed setae; teeth of epipharyngeal phoba relatively long, coarse and very closely set; anterior epitorma very weakly sclerotized and variable in appearance; macrosensillae not evident; mandibular cusps prominent and heavily sclerotized; molar area of right mandible with a conspicuous sclerotized projection at apex.

The apparent absence of macrosensillae in the larvae of *O. medorensis* is noteworthy in that Ritcher (1966) states that the presence of a pair of macrosensillae constitutes one of the diagnostic features of larvae of this genus, although it was not used as a character in the most recent key to the scarabaeine larvae (Edmonds and Halffter, 1978). However, since larvae are known from only a small fraction of the 1500+ described species of *Onthophagus*, it is likely that this and perhaps other apparently diagnostic features will be found to have exceptions as the larvae of other species are described.

Acknowledgments

I thank James R. Green for aid in the identification of the specimens.

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OUTHERN CALIFORNIA ACADEMY OF SCIENCES

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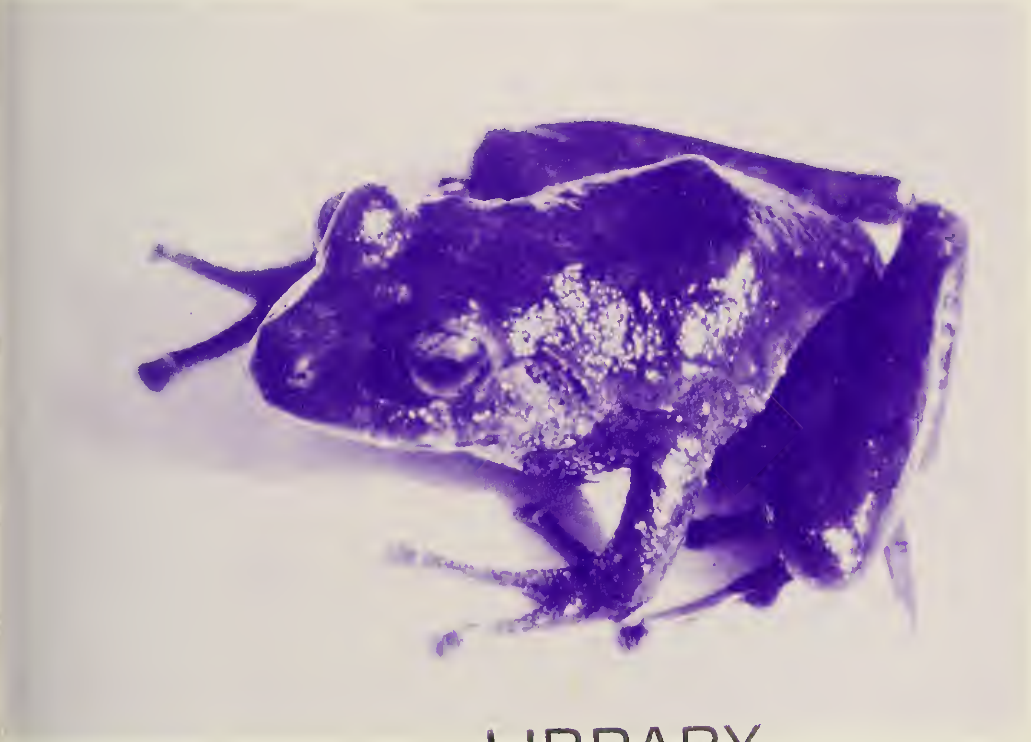

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Osprey Distribution, Abundance, and Status in Western North America: III. The Baja California and Gulf of California Population

Charles J. Henny[1] and Daniel W. Anderson[2]

Abstract.—An estimated 810 ± 55 pairs (minimum estimate) of ospreys (*Pandion haliaetus*) were nesting in the study area during our survey (24 March–1 April 1977). Approximately 174 pairs nested along the Pacific side of Baja California, 255 pairs along the gulf side, 187 pairs on the Midriff Islands, and 194 pairs in coastal Sonora and Sinaloa. Most nested on cliffs adjacent to the sea (59%); some nested on cactus in flat terrain (26%). Seven per cent nested on the ground, three percent nested in mangroves and other trees in the southern portion of the study area, and four percent nested on man-made structures. The extreme northwestern Baja California population that was extirpated early in this century has not recovered. However, several populations immediately to the south along the Pacific Coast now appear stationary. Pesticide residues in osprey eggs from Mexico were among the lowest reported for the species in North America.

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Fifty years ago the osprey was reported as a common coastal resident along both the Pacific and Gulf sides of Baja California and practically all the adjacent islands (Grinnell 1928). More recently, Friedmann et al. (1950:62) described the species as a "common resident from Baja California to Sinaloa and the Tres Marias Islands, and probably elsewhere on the Pacific Coast." Kenyon (1947) surveyed the northwest coast of Baja California in 1946 and concluded that the osprey population had declined markedly in the last 30 to 40 years except possibly at Scammon's Lagoon. Jehl (1977) updated Kenyon's work on several northwestern sites (through 1972), and concluded that the population had stabilized in the last 25 years. The historical distribution and abundance of ospreys in the remainder of Baja California and the Gulf of California is poorly understood.

The present study was designed to determine the 1977 distribution and abundance of ospreys in coastal Baja California, its adjacent islands and the coast of mainland Mexico as far south as Mazatlan (Fig. 1). Studies using the osprey as an indicator species of pollutant contamination have been conducted on nearly every nesting population in the United States (see review, Henny, 1977). These osprey studies played an important role in documenting problems associated with DDT use in the northeast (Ames and Mersereau, 1964; Ames, 1966) and elsewhere, and in documenting the recovery in productivity that followed the reduced use and the eventual ban of the product in the United States. We believe that the osprey can play a similar indicator species role in coastal Mexico. Future problems in the surveyed region may or may not be pollutant oriented, but an increase in human activity in the region is almost certain (Anderson et al., 1976). We

Fig. 1. The Baja California and Gulf of California study area for ospreys.

collected data in 1977 to form a basis for future comparisons. In addition to collecting the baseline data, it is our purpose to describe areas that we believe are critical habitat for ospreys.

Methods

We located occupied osprey nests from a fixed-wing aircraft (Cessna 210) flying 60–100 m above the shorelines and inland up to 2 km. A pilot and two observers were present in the plane, and 80 h of flying time were logged. In areas where large cactus or mangrove forests existed adjacent to the shoreline, we flew transects at increasing distances landward from the shore looking for osprey nests

Table 1. Number of occupied osprey nests (nesting pairs) seen from the air and the ground.

Location	Air n_1	Ground n_2	Both m	Tot. Est. $\hat{N}$	Visibility Rate $\hat{N}/n_1$
Los Angeles Bay (rock cliffs)	20	35	20	35.00	1.75
Midriff Islands (rock cliffs)	51	63	41	78.37	1.54
Kino Estero (cactus)	7	9	6	10.50	1.50
Islands <26° N Lat. (rock cliffs)	17	23	13	30.08	1.77
Scammon's Lagoon (small island ground nests)	26	23	22	27.18	1.05
Pooled (except Scammon's Lagoon)	95	130	80	154.38	1.63

until no more were observed. Generally, we did not search for nesting pairs more than 2 km landward from the shoreline. We made a single pass to census rocky cliffs adjacent to the shoreline or flat terrain with no cacti. It is possible that some birds nesting considerable distances from the coastline were missed during the survey. From fairly extensive surveys on the ground over the past eight years by DWA, we do not believe that any *major* osprey nesting concentrations were located outside our study area. A possible exception is near Puertecitos (northeast Baja California) which is discussed later.

Nests were located by both air and ground observers. We located nests from the air during the period 24 March to 1 April. We classified them as occupied if an adult was present on or in the immediate vicinity of the nest, or if either young or eggs were in the nest. Occupied nests were missed if a bird was not at or near a nest when surveyed, the nest was abandoned before the area was surveyed, the nest was initiated after the area was surveyed, or we failed to see the nest. The ground studies, conducted by individuals involved with other studies, were generally made by boat, although one area was surveyed on foot and from a pickup truck. The ground studies were conducted within a few days to 2 weeks of the interval for the aerial survey.

The ground studies made it possible to compare numbers of occupied nests at the time of census in various areas seen from air, ground, and both air and ground. Comparing data from both counts allowed us to obtain a visibility rate for adjusting aerial counts to the total nesting population by use of a modification of the Petersen Estimator (see Henny et al., 1978a, b; Burnham and Henny, in prep.). We sampled a finite population of size N (N unknown) by use of two methods. The data were then recorded so that we knew the number of elements n_1, observed by method 1 (aerial survey), the number of elements n_2, observed by method 2 (ground survey), and m, the number of elements observed by both methods. Then,

$$\hat{N} = \frac{n_1 n_2}{m}$$

is a reasonably good estimator of N. In this approach we assumed statistical independence of n_1 and n_2.

In sampling osprey nests, it is also necessary to assume N is not changing during the time between the ground and air survey. The ground and aerial counts

Table 2. A comparison by region and latitude of occupied and unoccupied osprey nests observed during the 1977 aerial survey (24 March–1 April).

	West Baja, L.C.		East Baja, L.C.		Midriff Islands		Mainland Mexico		Totals
Latitude	Occ.	Unocc.	Occ.	Unocc.	Occ.	Unocc.	Occ.	Unocc.	% Occ.
>27°40′	78	75	67	53	115	103	54	38	54
26°00′ to 27°40′	27	12	47	42	—	—	—	—	58
<26°00′	4	14	43	72	—	—	43	40	42
All Combined	109	101	157	167	115	103	97	78	52

The difference is not significant among locations, $\chi^2 = 11.31$, 8 d.f. ($.20 < P > .10$).

were made within 2 weeks of each other; therefore, it is doubtful that significant changes had taken place. Then $\hat{N}/n_1$ is a reasonably good estimator of the aerial visibility rate. The aerial count is multiplied by the aerial visibility rate to obtain the population estimates. Separate visibility rates were initially estimated for the nests in cacti, the nests on cliffs, and the ground nests on small islands. For this study, the nests on cliffs and cacti have been pooled because of their similar visibility (Table 1). Aerial visibility rates computed from locations with ground surveys were also utilized for similar areas, even though no ground survey was made. A comparison of the maximum number of nests seen from both air and ground with the estimated number of nests ($\hat{N}$) shows that approximately 6% of

Table 3. Distribution and abundance of nesting ospreys on the Pacific side of Baja California in 1977.

	Type of nest substrate					
Location	Cliff	Cactus	Ground	Other	Max. Observed	Total Estimate
Northwest Baja, L.C.						
Puerto Santa Catarina to Morro Santo Domingo	17.9[b]	1.6	—	—	12	19.5
Scammon's Lagoon and vicinity	—	—	27.3	22.8	41	50.1
Natividad Island	22.8	—	—	—	14	22.8
Cedros Island (west side)	19.6	—	—	—	12	19.6
San Benitos Islands[c]	26	—	—	—	23–29 (26)	26
Subtotal	86.3	1.6	27.3	22.8	105	138.0
Southwest Baja, L.C.						
Punta Eugenia to Punta Abreojos	—	—	—	1.6	1	1.6
San Ignacio Lagoon	—	—	27.3	—	26	27.3
Punta Santo Domingo to Cabo San Lucas	—	4.9	—	1.6	4	6.5
Subtotal	—	4.9	27.3	3.2	31	35.4
Grand Total	86.3	6.5	54.6	26.0	136	173.4

[b] Decimal values included to eliminate rounding errors in total estimates.

[c] Not surveyed in 1977, data are for 1971 (Jehl 1977).

Photograph 1. Occupied ground nest typical of those found in the Scammon's Lagoon and Santa Ynez areas. This nest was found on Stony Island in Scammon's Lagoon.

Note: All photographs by D. W. Anderson.

the occupied nests on cliffs and in cacti were missed in areas with both air and ground counts. Nests occupied at the time of the survey, but believed to have been missed by both surveys, are accounted for in estimates presented here. However, occupied nests abandoned before the survey, or initiated after the survey, are not included in the population estimates. No visibility rates were available for nests in mangroves; therefore, the pooled value for cacti and cliff nests was used. We believe the nests in mangroves were more difficult to locate from the air. Thus, the nesting pairs in mangroves in the Magdalena Bay area and coastal Sinaloa were probably underestimated.

Generally, in more northern latitudes where the survey has been conducted in the past (Henny et al., 1974; Henny and Noltemeier, 1975), the nesting cycle was synchronized; however, this synchrony does not occur in Mexico. Jehl's (1977:243) statement regarding ospreys in Mexico is typical, "nests there contained all stages from fresh eggs to flying young." To provide some insight into the synchrony of nesting activity among locations at the time of the survey, we used as an index the ratio of occupied to unoccupied nests recorded during the aerial counts (Table 2). Remnants of obviously very old nests were not counted. The percentage of occupied nests was lower in Baja California below Lat. 26°N, although the difference was not significant ($.20 < P > .10$). The population estimate presented in this paper for Baja California below Lat. 26°N may, in particular, be underestimated if breeding birds (possibly unsuccessful nesters) abandoned some nest sites before the survey was conducted.

Photograph 2. Nest on a beached trawler as seen from the air north of Puertocitos. It is not difficult to note the tracks around the nest made by recreationists in all-terrain vehicles.

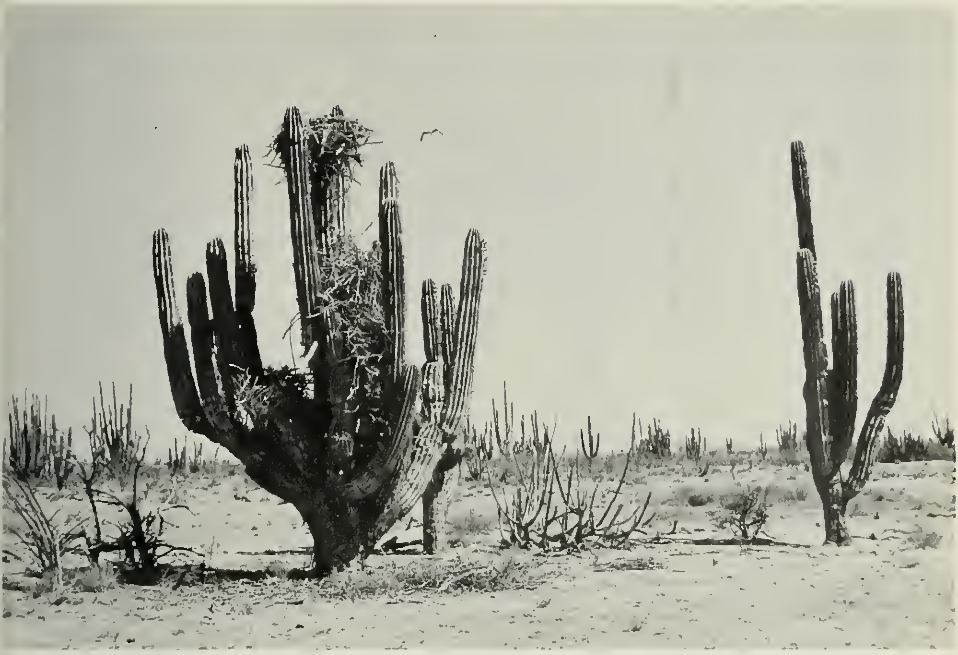
A further complication concerns the presence of nonbreeding birds. One-year olds and many of the 2-yr olds are generally not present on the breeding grounds of the more northern migratory population in the United States (Henny and Van Velzen, 1972). An attempt was made to record these birds as singles during the study; however, this was difficult where nesting was concentrated. Locations where apparent nonbreeding birds were concentrated will be discussed.

Results

Present Distribution and Abundance

To facilitate presentation of the findings, we have divided the survey into seven regions: Northwest Baja California, Southwest Baja California, Northeast Baja California, Southeast Baja California, Midriff Islands, Coastal Sonora, and Coastal Sinaloa. A minimum estimate of the total nesting population within the survey area was 810 ± 55 pairs (95% C.I.).

Northwest Baja California.—The area extends from the U.S.-Mexico border south to and including Scammon's Lagoon, and west to Punta Eugenia, including Natividad and Cedros islands. The San Benitos Islands were not surveyed in 1977, although recent population data are provided. The total nesting population in the region is estimated at 138 pairs (Table 3). No nesting pairs were observed between the border and Desembarcadero de Santa Catarina. However, from this point south to Morro Santo Domingo, an estimated 20 pairs were nesting, primarily on cliffs, although one pair nested in a yucca (*Yucca* spp.). The nesting pairs associated with Scammon's Lagoon were concentrated on three small islands (27 pairs), plus towers, platforms, pilings, channel markers, and debris that drifted ashore near the mouth of the lagoon and at Estero de San Jose (23 pairs).



Photograph 3. A typical cardon nest near Kino Bay. Note the large pile of old nesting debris below the nest and on the ground, indicating the tendency of ospreys to reuse nest sites from year to year.

Nesting pairs were not observed along Scavenger's Beach between Scammon's Lagoon and Punta Eugenia.

The rocky cliffs on Natividad Island contained an estimated 23 pairs (concentrated on the west side); the west side of Cedros Island contained an estimated 20 pairs. The east side of Cedros was not surveyed due to high wind conditions, but probably contained additional pairs. Jehl (1977) reported 23 to 29 pairs nesting on the three Benitos islands in 1971.

Southwest Baja California.—An estimated 35 pairs nested in this region that includes the coastal area between Punta Eugenia and Cabo San Lucas (Table 3). Only one pair was observed nesting between Punta Eugenia and Punta Abreojos; the nest was on a tower at Tortugas Bay. In San Ignacio Lagoon, an estimated 27 pairs were nesting on the ground on two small islands (Ballenas). South of San Ignacio Lagoon, we estimated that only seven pairs were nesting and they were concentrated in the Magdalena Bay region near Santa Margarita Island and on the mainland near San Carlos. One pair was of particular interest because it nested on the mast of a boat sunk in about 5 m of water near Santa Margarita Island.

Anderson (unpublished data) noted five or six pairs of ospreys nesting on power poles and towers in the town of San Carlos in previous years. Apparently, 20–25 birds in the town have since been shot (J. E. Mendoza, pers. comm.); and no nesting pairs were seen in San Carlos in 1977.

Northeast Baja California.—An estimated 117 pairs of ospreys were nesting along the gulf from the mouth of the Colorado River south to Santa Rosalia (Table

Photograph 4. Occupied osprey nest on a power pole near Topolobampo. Where power poles and other towers have been constructed, osprey are quick to utilize these structures as nesting platforms.

4). The terrain from the Colorado River south to Puertecitos was very flat and contained few cardon cacti (*Pachycereus* spp.) suitable for nesting sites. Only two nesting pairs were observed from the air in the extreme northern portion of the region: one nesting on a boat that was aground, and one on a cardon cactus. As mentioned earlier, we possibly missed about a dozen nests which were a

Table 4. Distribution and abundance of nesting ospreys on the Gulf side of Baja California and the Midriff Islands in 1977.

Location	Type of nest substrate				Max. Observed	Total Estimate
	Cliff	Cactus	Ground	Other		
Northeast Baja, L.C.						
Colorado River to Punta Remedios	34.2	1.6	—	1.6	23	37.4
Los Angeles Bay and Las Animas Bay	57.1	—	—	—	50	57.1
Punta de las Animas to Santa Rosalia	16.3	6.5	—	—	14	22.8
Subtotal	107.6	8.1	—	1.6	87	117.3
Southeast Baja, L.C.						
Santa Rosalia to Loreto	58.7	—	5.3	1.6	44	65.6
Loreto to Tambibiche	42.4	—	—	—	31	42.4
Tambibiche to Cabo San Lucas	27.7	1.6	—	—	23	29.3
Subtotal	128.8	1.6	5.3	1.6	98	137.3
Midriff Islands						
Guardian Angel	40.8	—	—	—	26	40.8
Tiburon	19.6	52.2	—	—	44	71.8
San Lorenzo, San Lorenzo Norte, Salsipuedes, Raza, and Partida	52.2	—	—	—	43	52.2
San Estaban, Turner, and Cholla	22.8	—	—	—	25	22.8
Subtotal	135.4	52.2	—	—	138	187.6
Grand Total	371.8	61.9	5.3	3.2	323	442.2

considerable distance inland near Puertecitos. About half of the 37 pairs estimated nesting between the Colorado River and Punta Remedios were concentrated on a group of small islands (Miramar, Lobos, Encantada, San Luis, Pumice).

The Los Angeles and Las Animas Bay vicinity between Punta Remedios and Punta de las Animas contained an estimated 57 pairs. More than half of the pairs were nesting on small islands of Los Angles Bay (Smith, la Ventana, Cabeza de Caballo, Mitlan, Islas de los Gemelos). From Punta de las Animas south to Santa Rosalia the estimated 23 pairs were scattered along the mainland on cliffs or adjacent rocks; a few pairs nested in cacti.

Southeast Baja California.—The coastal area south of Santa Rosalia contained an estimated 137 pairs (Table 4). An estimated 66 pairs nesting between Santa Rosalia and Loreto were concentrated along the coastline at Concepcion Bay and between Punta Pulpito and Loreto. Islands used in the same area included Coronado, Ildefonso, San Marcos, and Santa Ynez. Five occupied nests on Santa Ynez were on the ground, and an additional nest was on a fishing shelter. Tortuga Island was not surveyed.

Between Loreto and Tambibiche an estimated 42 pairs were nesting; an esti-

Photograph 5. Typical nest on an island in the Midriff region of the Gulf of California with feeding habitat in the background.

mated 16 pairs along mainland cliffs or on immediately adjacent rocks, and the remainder of Santa Catalina, Monserrate, Danzante, and Carmen islands. The southernmost portion of the region (Tambibiche to Cabo San Lucas) contained an estimated 29 pairs, with about half of the nests on islands and the rest along

Table 5. Distribution and abundance of nesting ospreys in coastal Sonora and Sinaloa in 1977.

Location	Type of nest substrate				Max. Ob-served	Total Estimate
	Cliff	Cactus	Ground	Other		
Coastal Sonora						
Colorado River to Punta Sargento	8.2	34.2	—	—	26	42.4
Behind Punta Sargento[a]	—	36	—	—	36	36
Punta Sargento to Guaymas	13.0	32.6	—	—	30	45.6
Subtotal	21.2	102.8	—	—	92	124.0
Coastal Sinaloa						
Sonora border to Topolobampo	—	1.6	—	4.9	4	6.5
Topolobampo to Punta Baradito	—	39.1	—	22.8	38	61.9
Punta Baradito to Mazatlan	—	—	—	1.6	1	1.6
Subtotal	—	40.7	—	29.3	43	70.0
Grand Total	21.2	143.5	—	29.3	135	194.0

[a] F. N. Hamerstrom (pers. comm.) ground count in 1977 of area not surveyed from the air.

Table 6. Locations where single ospreys were noted during in the survey in greater numbers than occupied nests.

Region	Location	Aerial Counts	
		Occupied Nests	Singles
Northwest Baja, L.C.	Scavenger's Beach	0	3
Southwest Baja, L.C.	Magdalena and Almejas bays	4	36
Coastal Sonora	Northern coast	12	20
Coastal Sonora	Guaymas to Sinaloa border	0	6
Coastal Sinaloa[a]	Topolobampo to Punta Baradito	38	14
Coastal Sinaloa	Punta Baradito to Mazatlan	1	6

[a] Possibly a more typical ratio of singles to nesting pairs, although numbers could not be determined with accuracy in high density nesting areas.

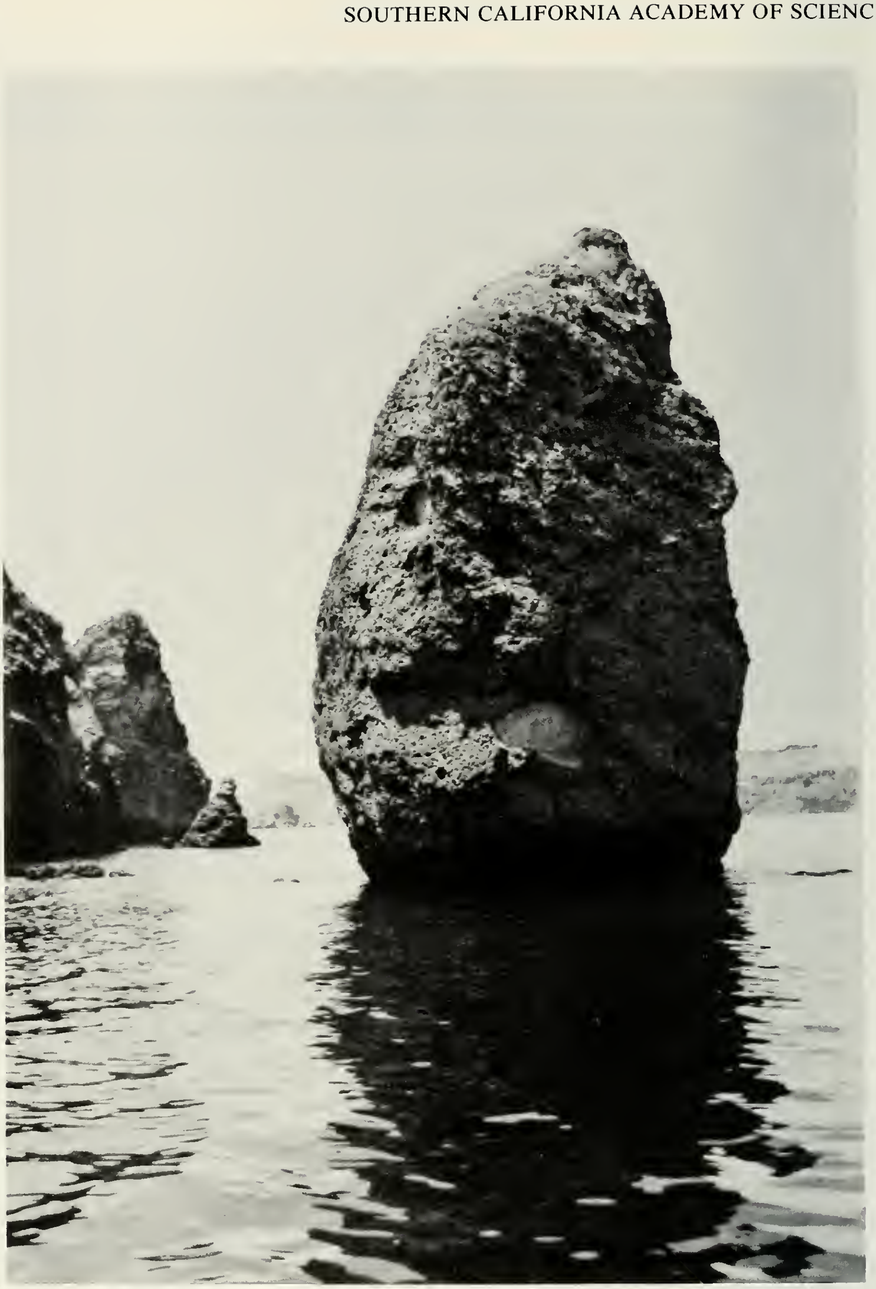
the shoreline. The more important nesting islands were Cerralvo and Espiritu Santo; a few pairs nested at San Jose and Santa Cruz.

Midriff Islands.—An estimated 188 pairs of ospreys nested on the islands located at about Lat. 29°N. in the Gulf of California (Table 4). Sixty percent of the nesting pairs inhabit Guardian Angel and Tiburon islands. Most of the ospreys on the islands nest on cliffs, but a large population nests in cardon cacti on the east side of Tiburon. The chain of islands that include Partida, Raza, Salsipuedes, San Lorenzo Norte, and San Lorenzo contained an estimated 52 pairs. An estimated 23 pairs nested on San Estaban, Turner, and Cholla, smaller islands in the vicinity of Tiburon. (Note: The air and ground counts show 25 pairs actually observed. With smaller numbers involved, occasionally the estimate is slightly smaller than the actual count.) San Pedro Martir Island was not surveyed.

Coastal Sonora.—An estimated 124 pairs of ospreys were nesting in coastal Sonora (Table 5). The extreme northern coastal area is flat with no cacti, then cardon began appearing sporadically, which attracted both nesting great blue herons (*Ardea herodias*) and ospreys. Moving south along the coast, there are a few sandy cliffs and, eventually, some rocky cliffs. An estimated 42 pairs were nesting between the Colorado River and Punta Sargento; the majority of the birds nested nearer to Punta Sargento where cardon cacti were more common. Some 36 occupied nests behind Punta Sargento in 1977 were not surveyed from the air, but ground counts were made by F. N. Hamerstrom (pers. comm.). The area behind Punta Sargento, including also the nearby flats along the eastern shore of Tiburon Island, was found to contain perhaps the greatest concentrations of breeding ospreys in the Gulf of California region.

An estimated 46 pairs nested between Punta Sargento and Guaymas, with pairs commonly found at Kino Bay, Alcatraz Island, and along the coastline from Kino to Guaymas. No nesting pairs were located in the generally flat region between Guaymas and the Sinaloa border. In the more northern portion of Sonora the cardon cacti provided suitable sites for ospreys to nest in flat country without cliffs, but the species of cactus changed below Guaymas to a type that was not suitable for nesting.

Coastal Sinaloa.—An estimated 70 pairs of ospreys nested along coastal Sinaloa (Table 5). The few ospreys nesting between the Sonora border and Topo-



Photograph 6. An unoccupied nest on a pinnacle at Puerto Refugio.

lobampo were found on the islands and peninsulas associated with San Esteban and San Ignacio bays, and on a power pole near the town of Topolobampo. South of Topolobampo to Punta Baradito, the estimated 62 pairs of ospreys were also nesting on the islands and peninsulas associated with the several large bays. Mangroves and other brushy trees were abundant and the ospreys readily nested on them. The species of cactus changed again in this area to a type that branches

Table 7. Types of nest sites selected by ospreys in Baja California and the Gulf of California in 1977.

	Type of Nest Substrate				
Location	Cliffs	Cactus	Ground	Mangroves Trees	Others[a]
Northwest Baja, L.C.	86	2	27	—	23
Southwest Baja, L.C.	—	5	27	—	3
Northeast Baja, L.C.	108	8	—	—	2
Southeast Baja, L.C.	129	2	5	—	2
Midriff Islands	135	52	—	—	—
Coastal Sonora	21	103	—	—	—
Coastal Sinaloa	—	41	—	24	5
Total No. Nests	479	213	59	24	35
Percent of Total	59%	26%	7%	3%	4%

[a] Towers, pilings, channel markers, debris washed ashore, boats (sunk and aground), fishing shelter, or power poles.

about 1.5 m above the ground. These cacti were also used by the nesting ospreys. In fact, more ospreys were observed nesting in the cacti than in the mangroves or other trees.

The southernmost nesting pair of ospreys observed during this survey was seen at Ensenada del Pabellón (Lat. 24°38′N) in a mangrove. Mazatlan was the southern terminus of the study.

Migratory Characteristics

Most Gulf of California ospreys are year-round residents, after adulthood is reached (DWA, unpublished data), a situation similar to that found in Florida at approximately the same latitude (Ogden, 1977). This contrasts with the highly migratory populations in northern latitudes of the United States, where yearlings do not return to the natal area (Henny and Van Velzen, 1972).

Single birds were observed throughout the study area and in concentrations (presumably subadults) at Magdalena and Almejas bays (Table 6). Where nesting sites were limited, there was an above-average preponderance of single birds: in northern Sonora, in extreme southern Sonora, and in southern Sinaloa which is near the southern extreme for the breeding range. Generally we believe the nonbreeding component of the population was probably scattered throughout the study area; however, the single birds were more apparent in areas with few nesting pairs. Many of these singles were apparently moulting and looked unkempt. Suitable substrates on which to build nests would not, of course, limit the distribution of nonbreeding birds.

Nesting Sites

Dead trees or trees with dead tops are the traditional sites for nesting ospreys in the western United States (Henny et al., 1978a, b); ospreys are using more and more man-made structures along the mid-Atlantic coast of the eastern United States (Henny et al., 1974; Henny et al., 1977). Trees and man-made structures were rare in the present study area, consequently the ospreys found alternative nest sites.

Numerically, the most important nesting substrate is large cliffs adjacent to the sea, both on the mainland and on the islands (Table 7). Sometimes the rocky cliffs consist of large pinnacles or stacks upon which the ospreys build their nests—some of which are of tremendous bulk. However, small sandy cliffs contain nesting ospreys in a few areas. An estimated 59% of the nesting pairs were associated with cliffs. In the flat terrain, the ospreys nest primarily in various species of tall cacti.

Nesting above ground level is critical for the ospreys on the mainland where predator access is likely. Coyotes (*Canis latrans*) are found throughout much of the study area, and it was not uncommon to see several each day during the aerial survey. Both Kenyon (1947) and Jehl (1977) mentioned coyote depredation of ground nests, even when nests were located on small islands. Coyote depredation of ground nests occurred again at Scammon's Lagoon in 1977 (Sandalio Reyes, pers. comm.). Ground nesting ospreys were restricted to very small islands at three locations: Scammon's Lagoon, San Ignacio Lagoon, and Santa Ynez Island.

Miscellaneous man-made structures were used throughout much of the study area, but the overall importance of these structures was very small (4%). Most of the pairs nesting on these structures were found at the mouth of Scammon's Lagoon. Mangroves and other trees were generally available only in the southern portion of the study area.

Status of Population

Few osprey populations in Mexico have been studied in the past; thus, it is difficult to evaluate their current status. A notable exception is northwest Baja California.

Northwest Baja California.—Jehl (1977) recently reviewed the work of Kenyon (1947) and earlier workers in northwestern Baja and a few summary statements are warranted. The findings for the islands or groups of islands from north to south may be summarized as follows:

(1) Los Coronados—no records of ospreys.
(2) Todos Santos—once common; greatly reduced by 1910 (1 pair); may have been entirely gone by 1923.
(3) San Martin—about 30 pairs ground nesting in 1913; only 3 pairs in 1946; 1 pair in 1969–71.
(4) San Geronimo—common in 1897; reduced to 1 pair by 1912; entirely gone by 1926.

We saw no ospreys nesting on any of these four northernmost islands, or groups of islands during this study.

(5) Natividad—common in 1927 (8 nests within half mile walk); some decline suggested by 1946; a minimum of 4 pairs and probably several more present in 1969–71. We saw 14 occupied nests from the air in 1977; an adjustment for aerial visibility provides an estimate in excess of 20 pairs.
(6) Cedros—very common in 1882; abundant (13 nests in short distance) 1897; abundant in 1912; the west side was not observed in recent years, although several nests were located on the east side in 1946 and 1969–71. We saw 12 occupied nests from the air in 1977 along the west side; an adjustment

for aerial visibility provides an estimate of about 20 pairs. The east side was not surveyed due to high winds.

(7) San Benitos—nested in abundance in 1896; an estimated 23–29 pairs in 1969–71. Not surveyed during this study.

In summarizing the history of the island osprey populations in northwest Baja California, we must agree with the general conclusions of both Kenyon (1947) and Jehl (1977) that the populations on the northernmost islands were decimated early in the century and have not returned. The decline probably resulted from human disturbance, including shooting of adults, and fisherman eating the eggs and "squabs" as suggested by both Kenyon and Jehl. The populations on several of the more southern islands in the region (Natividad, Cedros, and San Benitos), which are generally more distant from human populations, have not become extirpated, and appear to be maintaining themselves in good numbers.

The mainland population in northwest Baja California has been studied very little except for the small islands in Scammon's Lagoon. Kenyon (1947) reported seeing his first mainland pair of ospreys at Santa Rosalia Bay in 1946, although he could not find the nest. He stated (p. 154) "These were the only ospreys up to this point observed on the mainland, even though we had run close to shore most of the way down the coast." Rowley (1935) also recorded a recently occupied nest in a cardon cactus near San Xavier on Santa Rosalia Bay. Jehl (1977) reported observations of birds during the nesting season at several locations including a nest at Arroyo San Jose, but indicated that many of the more southern locations were inaccessible.

The first osprey that we saw along the mainland was a single bird at San Carlos Bay. We saw 12 nesting pairs from the air (total estimate 20 nesting pairs) between Desembarcadero de Santa Catarina and Morro Santo Domingo. Most of the birds were on rock, gravel, or sandy cliffs; a few pairs were nesting in cacti and one pair nested in a yucca at Santa Rosalia Bay. It has not escaped our attention that the main road in this region is away from the coastline, in contrast to the coastal road system to the north where ospreys are no longer present.

The size of Scammon's Lagoon population has been documented for a number of years. Kenyon (1947) found 27 pairs (16 at Shell Island) in Scammon's Lagoon in 1946. Jehl (1977) reported 25 nests (apparently not all occupied?) on Shell Island in 1957, 22 active nests on Shell Island in 1970; and 20 nests (17 with eggs) on Shell Island with a total population for the lagoon estimated at about 30 pairs in 1971. We located 27 pairs of ospreys nesting on three islands in the lagoon in 1977. However, 14 were observed from the air (for a population estimate of 23 pairs) nesting on man-made structures near the mouth of the lagoon and at Estero de San Jose. This portion of the lagoon has probably not been censused in the past because it can be searched efficiently only from an aircraft. Therefore, the 27 pairs on the small islands in the lagoon in 1977 compare favorably with the 27 pairs observed in 1946. Jehl (1977) also concluded that the population seemed stationary.

Other locations.—Long series of population estimates over time, from the other regions, are nonexistent to our knowledge. Most of the early workers only noted the presence or absence of the species in general terms. However, some local populations are in jeopardy. For instance, the population that nested in the town of San Carlos in Magdalena Bay a few years ago was not present in 1977. Shooting

Table 8. Eggshell thickness and pollutant residues of Gulf of California ospreys.[a]

			Pollutants (ppm)			
				Lipid-wt.		
Year (n)	Thickness (mm)[b]	% Fat	Wet-wt. Mercury	DDE	TDE	PCB
1971 (8)						
Mean ± S.D.	0.49 ± 0.05	3.27 ± 0.74	ND[c]	71.2 ± 47.3	ND	—
Range	0.43–0.59	2.3–4.8	ND	29.0–116.9	ND	0–7.4
1972 (7)						
Mean ± S.D.	0.48 ± 0.03	4.94 ± 0.50	0.2 ± 0.2	20.0 ± 7.4	<2.5	20.2 ± 11.2
Range	0.42–0.52	4.4–5.8	0.1–0.9	6.1–27.6	—	3.1–40.8

[a] Analyses conducted by Denver Wildlife Research Center according to methods described by Haegele et al. (1974); no adjustment was made for moisture or lipid loss.

[b] Normal eggshell thickness is about 0.50 mm (Anderson and Hickey, 1972).

[c] ND = no data.

probably occurs locally throughout the study area wherever the birds closely associate with man.

Pesticides.—It is now generally accepted that persistent pesticides—particularly DDE, the major metabolite of DDT—have contributed to eggshell thinning, poor productivity, and population declines in some birds of prey (Lincer, 1975). And, the osprey was among the first species of fish-eating and raptorial birds in North America discovered to show indications of a regional pattern of eggshell thinning in local populations (Hickey and Anderson, 1968; Anderson and Hickey, 1972). Local osprey population declines have been documented in many areas where production has been extremely poor (see review, Henny, 1977). Spitzer et al. (1977) presented some residue data from osprey eggs collected in three general areas of Mexico: (1) Scammon's Lagoon, (2) San Benitos Islands, and (3) Gulf of California. Additional data from the Gulf of California are presented in Table 8. One clutch of eggs from the San Benitos Islands showed moderately high DDE and PCB residues; however, generally the residues were among the lowest recorded for ospreys in North America. Eggshell thickness appeared to be about normal (Spitzer et al., 1977; Table 8).

Discussion and Recommendations

This survey yielded the first estimate of the size of the nesting osprey population in the Baja and Gulf of California area, but the survey had some limitations. Although this survey was timed to coincide with the peak of nesting activity, the lack of a highly synchronized nesting season confounds our approach. Some of the pairs may not have been associated with nests at the time the survey was conducted; therefore, our estimate of the nesting population's size is small. More research on the chronology of the nesting season is needed throughout the study area to evaluate the percent of the total breeding population that is nesting at a certain time. Additional data may allow a further refinement of the population estimate obtained from this study. Nesting chronology studies can also be combined with productivity studies which can be used to indirectly evaluate the status of the population (see Henny, 1977). Osprey eggs from only a few locations have been collected and analyzed for pesticides to date, but the residues appear to be low. In view of the general stationary populations over the last three decades (modern pesticide era) in the few areas where historical data are available, it appears likely that pesticides have not posed a threat to these segments of the osprey population. The population declines noted in extreme northwestern Baja California occurred before modern pesticides were used.

Although substantial numbers of ospreys remain today in Baja California and the Gulf of California, the extirpation of the population in the extreme northwest portion of Baja California should serve as a warning that ospreys require some protection if they are to be maintained as a part of the fauna. We know from experience in other parts of the species' range that man and ospreys can survive together, e.g., in Chesapeake Bay (the largest nesting osprey population in North America) where approximately two-thirds of the population is nesting on man-made structures and some are very close to human dwellings (Henny et al., 1974). In fact, some residents build nesting platforms for ospreys in Chesapeake Bay and consider nesting birds near their homes a status symbol.

In regard to specific management practices, we believe the potentially serious problem of coyotes depredating ground nests on the islands in Scammon's Lagoon can be solved. Apparently, strong tidal currents constantly change the configuration of the sandy islands allowing access by coyotes. Nesting platforms about 3 m above the ground could easily be built on the islands to eliminate this potential problem. We recommend initially placing platforms on only one of the islands as a test. Ospreys now nest on towers, channel markers, and pilings at the mouth of Scammon's Lagoon. Thus, they would probably accept nesting platforms on the small islands in the lagoon.

We believe the ground nesting populations in Scammon's Lagoon and San Ignacio Lagoon are the most vulnerable to human disturbance. Protective measures should be taken to limit human access to the small islands in these lagoons during the nesting season. Cliff nests, especially those on all gulf islands, are also vulnerable to the increasing human disturbance (Anderson et al., 1976).

Acknowledgments

The study was conducted under the auspices of the Migratory Bird Treaty between Mexico and the United States, and approved by Antonio Landazuri, Director General of the Fauna Silvestre. Ray Glahn, U.S. Fish and Wildlife Service pilot, guided us safely through areas where landing strips were rare, airports with gas were rarer, and radio communication was nonexistent. Ground counts were made by James Keith, Chris Mitchell, Alan Jenkins, Richard Porter, and Charles Stone of the U.S. Fish and Wildlife Service, who were in Mexico working on studies of their own; Debra Judge, graduate student at the University of California, Davis; and Sandalio Reyes, Departmento de al Fauna Silvestre, Guerrero Negro, Lower California. F. N. Hamerstrom kindly provided ground counts from the Punta Sargento region. The manuscript was reviewed by Eugene Dustman, Stana Federighi, and Lawrence Blus.

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ADDENDUM: Mazatlan Harbor was the terminus of the 1977 study; however, Morlan Nelson (pers. comm.) reported an occupied osprey nest on an island there one year later (March, 1978).

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A New Species of Leptodactylid Frog, Genus *Eleutherodactylus*, from the Cordillera de Talamanca, Costa Rica

Jay M. Savage and James E. DeWeese

Abstract.—*Eleutherodactylus rayo* a distinctive new species sharing features of the *fitzingeri* and *rugulosus* groups occurs along the Pacific slopes of the Cordillera de Talamanca of Costa Rica. Karyologically the new form most closely resembles *El. vocalis* of northwestern Mexico and certain populations of frogs from eastern Mexico, formerly referred to *El. rugulosus* but for which the name *El. berkenbuschii* W. Peters, 1870, is revived. Unlike other members of the *rugulosus* group which have 2N = 20, *berkenbuschii, rayo* and *vocalis* have 2N = 22 and approach *El. talamancae* of Coast Rica and Panama, a member of the *fitzingeri* group, in karyotypes.

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During the past 20 yr of work in Costa Rica, the University of Southern California field teams have accumulated a number of distinctive or unique frogs that appeared to be representative of species not previously known to science. In most cases formal description has been delayed pending collection of additional material. A single example of the genus *Eleutherodactylus* falling into this category was originally collected by Roy W. McDiarmid in 1964 from a remote area on the Pacific slope of the Cordillera de Talamanca. Subsequently other specimens of this form were taken from 1972–1976 in the same mountain range along the Carreterra Interamericana.

The new species belongs to the *fitzingeri* group (*sensu* Lynch, 1976) and is somewhat intermediate in characteristics between the *fitzingeri* and *rugulosus* groups as used by Savage (1975, 1976). It is called:

Eleutherodactylus rayo, new species

Fig. 1

Holotype.—LA 127669, an adult male from the second sabana on the trail from Finca El Helechales to Sabanas Esperanza, 5 km, airline, east of Finca El Helechales, Canton de Buenos Aires, Provincia Puntarenas, Costa Rica, 1640 m; collected by Roy W. McDiarmid, October 6, 1964.

Diagnosis.—The new form superficially resembles several lower Central American species of the *fitzingeri* and *rugulosus* groups. It differs from members (*andi, fitzingeri* and *talamancae*) of the former group, that share with it the feature of having the webs between toes III–IV extending at most only slightly distal to the proximal subarticular tubercle in having a well-developed calcar. All other members of the group have substantially more toe webbing, which extends nearly to distal subarticular tubercle (III) between toes III–IV and to halfway between proximal and penultimate subarticular tubercles (IV).

Fig. 1. *Eleutherodactylus rayo,* male paratype (CRE 3980) from Quebrada Fortuna at Carreterra Interamericana, Provincia de San Jose, Costa Rica, 1750 m. DeWeese photograph.

Within this cluster of slightly webbed forms it may be distinguished further by differences in posterior thigh coloration which is uniform reddish brown (*talamancae*), brown with discrete small light spots (*fitzingeri*) or dark chocolate with very large light spots (*andi*). The posterior thigh surfaces of *rayo* are essentially a uniform dark purple in life and preservative.

El. rayo is distinguished from members of the *rugulosus* group in having a well-developed calcar and in having greatly enlarged emarginate disks on fingers III–IV, while the disks are rounded, not greatly enlarged and never emarginate in the latter group. The dark purplish coloration of the hindlimb surfaces uniquely distinguishes *El. rayo* from all other known members of the *fitzingeri* and *rugulosus* groups in Central America.

Summary of characteristics.—General: Head about as wide as long. Nostril closer to tip of snout than to eye. Loreal outline slightly sloping. Snout profile, and canthus rostralis round. Dorsal outline of snout subelliptical. Choanae ovoid; vomerine teeth located between but behind level of choanae in two transverse series separated at the midline. Vocal slits and internal vocal sacs in males. Tympanum approximately ½ height of orbit; internal, indistinct; round in males oval in females. Skin of head and dorsum smooth; upper eyelid with a single tubercle. Finger II longer than I. Finger disks on I–II rounded and expanded, on III–IV emarginate; about 2 times as wide as finger on III–IV. All fingers have well developed lateral fringes. Whitish nuptial pads on thumbs of male. Subarticular tubercles flattened, round to ovoid in outline, globular; no supernumerary tubercles; thenar tubercle large, elongate; palmar tubercle large ovate; no acces-

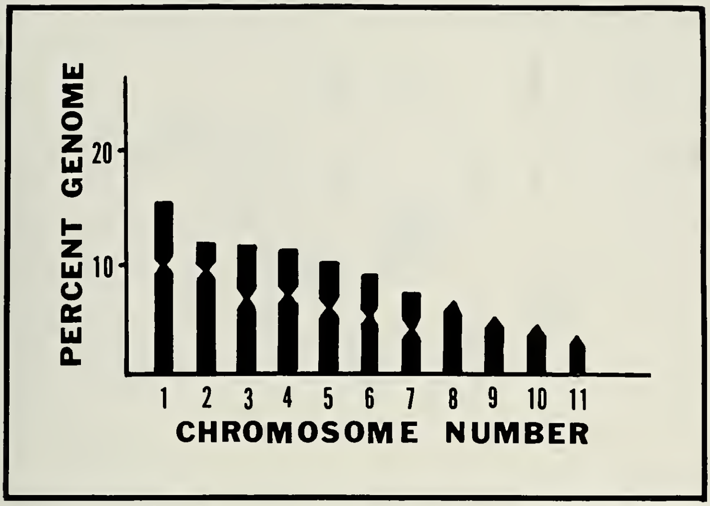

Fig. 2. An idiogram of the karyotype of *Eleutherodactylus rayo*.

sory palmar tubercles. Calcar present. Toe disks palmate on I, emarginate on II–IV and rounded and expanded on V; about 1.5 times as wide as toe on IV. Toe fringes well developed. Toes webbed only basally. Modal toe webbing formula: I 2^{-}–2^{+} II 2–3 III 3–4^{+} IV 4^{+}–3^{-} V. Subarticular tubercles projecting, ovoid in outline, obtuse to conical in profile; supernumerary tubercles lacking; outer plantar tubercle round, ¼ size of oval inner tubercle. Inner tarsal fold well developed. Venter smooth.

Coloration.—Base color of top of head, body and limbs a deep dark brown with a definite bluish purple cast; in preservative; in life deep bluish purple, adult females slightly lighter and tending toward tan as compared to the deep purple males; upper surface of snout light gray in some examples; often an interocular dark bar bordered anteriorly by a light area; upper lips with three dark bars in males; bars suggested by dark areas along mouth margin in females; a definite narrow supratympanic dark mark runs from middle of eye backward above tympanum and curves downward to shoulder. Dorsum uniform or with dark suprascapular spots or blotches in some examples; sometimes with a narrow white light line along median raphe; one adult female with a broad mid-dorsal light stripe bordered on either side by a broad dark area. Males often with some blotches of olive green in life. Dorsal and anterior surfaces of limbs uniform or with broad crossbars of dark pigment. Posterior surface of thigh dark purplish with obscure small light punctations. Throat heavily marked with dark pigment; with a narrow median light line. Venter light with a heavy mottling of dark pigment. Ventral surface of hind limbs marked like posterior thigh surface; plantar surface uniform purple. Groin and flanks similar in color to dorsum.

Measurements.—In this section the notation gives the mean followed by the range in parentheses. Standard lengths (distance from snout to vent) are given in millimeters; other measurements as percentages of standard length.

Standard length, adult males (N = 10) 40.0 (37.4–45), adult females (N = 10) 53.6 (38.2–70.9); head length, males 38.0 (34.9–41.0), females 37.3 (35.1–38.6);

Fig. 3. A representative metaphase spread (A) and karyotype (B) for *Eleutherodactylus rayo*.

head width, males 38.2 (35.8–40.5), females 41.0 (39.0–42.7); snout length, males 18.4 (17.6–19.3), females 18.6 (17.5–19.1); loreal length, males 10.6 (9.1–11.9) females 8.1 (7.4–8.9); length of orbit, males 14.7 (13.3–16.4), females 12.9 (11.7–15.2); height of tympanum, males 8.6 (7.3–9.8), females 5.9 (5.1–6.5); hindlimb length, males 210.7 (203.1–217.5), females 212.5 (209.6–215.6); tibia length, males 65.3 (62.7–66.4), females 57.4 (55.8–58.9). Note non-overlapping in tympanum height and tibia length to produce strong sexual dimorphism.

Karyotype.—Seven paratypes (CRE 3184[2], 3236–39, 9770) were examined karyologically using the technique of Patton (1967) as modified by Lowe et al. (1966). 122 spreads were counted, three were photographed and the individual chromosomes measured (Table 1), and an idiogram constructed (Fig. 2).

The diploid number (2N) is 22 and the *nombre fundamental* (N.F.) is 36. The chromosomes form a gradually descending series with no obvious size groupings. Chromosome pairs (centromere placement according to the system of Levan et al. 1964), 1, 3, 5, 6 and 7 are metacentric; 4 is submetacentric; 2 is subacrocentric and 8–11 are acrocentric (Fig. 3).

Table 1. The centromeric indices (C.I.) and percent genome values (G) for the 11 pairs of chromosomes in the karyotype of *Eleutherodactylus rayo*.

Chromosome Number	C.I.	G.
1	1.64	16.2
2	3.92	12.2
3	1.44	12.0
4	1.72	11.8
5	1.27	10.5
6	1.34	9.3
7	1.12	7.6
8	7.00	6.8
9	7.00	5.2
10	7.00	4.5
11	7.00	3.7

Habitat.—The male holotype was captured during the day while calling from a bromeliad during a heavy rain. Most of the paratypes were collected along the margins of a small stream during the daytime. They were found under debris or were apparently frightened out of their hiding places by the collector's activity and were hopping along the stream banks or across the shallows.

Distribution.—Rainforests of the upper portion of the premontane and lower portion of the lower montane slope of the Pacific face of the Cordillera de Talamanca of southwestern Costa Rica, between 1600–1850 m (Fig. 4).

Localities.—COSTA RICA: PUNTARENAS: 5 km E Finca El Helechales, 1640 m (LA 127669); SAN JOSE: Quebrada Fortuna at Carreterra Interamericana, 1750 m–1840 m (CRE 3184, 3232–33 3236–39, 3979–80, 6599, 8710–12, 9769; KU 65986); Rio Payner at Carreterra Interamericana, 1480 m (CRE 9770). All examples from San Jose Province are paratypes.

The name *rayo* is an arbitrary combination of letters that happens to mean lightning in Spanish. The name is an allusion to Roy W. McDiarmid, who first collected the species, as recognition for his work on the Costa Rican herpetofauna. Those who know Roy well will discern other reasons why this name is appropriate.

Relationships

The speciose genus *Eleutherodactylus* has always presented a serious problem to the systematic herpetologist interested in establishing relationships among morphologically similar forms. Currently about 350–400 species are recognized in the genus which ranges throughout the Neotropical region. The morphology of the group ranges from huge, stream-adapted toad-like species through moderate-sized frog-like terrestrial forms, arboreal treefrog-like species with huge finger and toe disks to large toad-like forest floor burrowers. While distantly related forms seem very distinct, the features of external morphology within the genus are recombined over and over again in a mosaic pattern that tends to make recognition of natural subdivisions difficult, while closely related forms often differ only slightly in these same features. One recourse in this situation has been to establish a series of species groups within the genus by clustering species that

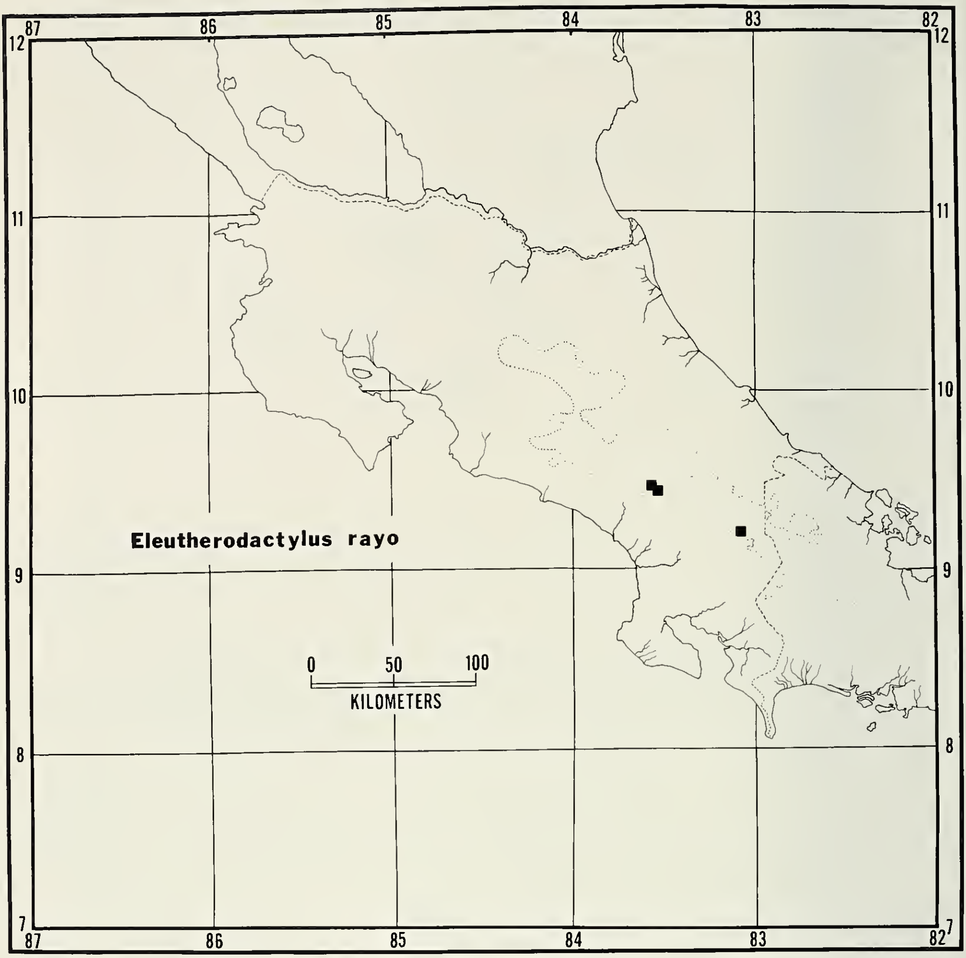

Fig. 4. Distribution of *Eleutherodactylus rayo*. The dotted line indicates the 1500 m contour.

are extremely similar morphologically and are probably phylogenetically from the same evolutionary lineage (e.g., Savage, 1976). Another alternative (Lynch, 1976) has been to group the species at a higher level (subgeneric) without giving the groups formal taxonomic status. Unfortunately the first method does not provide a sound framework for establishing the evolutionary history of the genus, while the second creates infrageneric divisions based on ''key'' characteristics of external and skeletal morphology that are of dubious evolutionary cogency.

It is clear from the study of jaw musculature (Starrett, 1968), serum proteins (Harris, 1973) and karyology (DeWeese, 1976) that a series of at least six major evolutionary lineages are subsumed under the genus *Eleutherodactylus*. In most cases these lineages do not correspond to the groupings established on external and skeletal morphologic grounds (Lynch, 1976) and suggest that the time is premature for an attempt to establish higher-level divisions based solely on traditional taxonomic (key) characters.

El. rayo morphologically is allied to the *fitzingeri* and *rugulosus* groups (Savage, 1975, 1976). Lynch (1976) proposed to place thase groups together as the *fitzingeri* group. While this is not the place to consider fully the weaknesses of Lynch's (1976) system, it must be noted that both *El. andi* of Costa Rica and *El. rayo* within this group have emarginate finger disks to negate one feature (ungual flap not indented) used to characterize this division. In addition one population referred to *El. rugulosus* (Savage, 1975) has the first finger shorter than the second, while Lynch (1976) characterizes the *fitzingeri* as having the converse situation.

Nevertheless there can be little doubt that the two groups recognized by Savage (1976) are closely allied. This relationship is further supported by the condition of the jaw muscles: depressor mandibulae with a single slip originating on the dorsal fascia but a few fibers coming from the squamosal (dfsq) or with a single slip originating on the dorsal fascia but a few fibers coming from the squamosal and annulus tympanicus (dgsqat) and adductor mandibulae externus superficialis present (e). Formulae for jaw muscles after Starrett (1968), are inadvertantly misstated for the *rugulosus* group in Savage (1975). Karyologically the two groups are also similar with the *fitzingeri* group having 2N = 22 and and N.F. = 36–40 and the *rugulosus* group with 2N = 20–22, and a N.F. = 36.

In terms of morphology *El. rayo* is distinct from all other members of the *fitzingeri* and *rugulosus* groups in having large emarginate finger and toe disks and a well-developed calcar. The only other species in these groups with similar disks, *El. andi* of Costa Rica, lacks the calcar and has a bold contrasting thigh pattern of large light spots on a dark brown background.

The jaw muscle formula for the new form is dfsqat + e. It seems likely that the differences between dfsq and dfsqat are trivial, since only a few muscle fibers are involved. The latter condition is not currently known to occur in the *fitzingeri* group while it does appear in some *rugulosus* group members (e.g., *El. brocchi* of Guatemala).

Karyologically *El. rayo* agrees in diploid number (2N = 22) and *nombre fundamental* (36) with *El. talamancae* of Costa Rica and Panama (in the *fitzingeri* group) and within the *rugulosus* group with *El. vocalis* of northwestern Mexico and the *rugulosus*-like populations of eastern Mexico (populations 1–2 of Savage, 1975). Other leptodactylids with the same numbers are: *El. decoratus* of Mexico (*alfredi* group, Lynch, 1976); and *Hylactophryne augusti*, a close *Eleutherodactylus* relative; *Leptodactylus podicipinus* and *L. wagneri* of South America. Of these forms the karyotype of *El. rayo* most closely resembles that of the *rugulosus*-like populations of eastern Mexico.

These data confirm the uniqueness of the new species, which does not appear to be closely allied to any known member of either the *fitzingeri* or *rugulosus* groups.

The Status of *Hylodes berkenbuschii*

Savage (1975:271) regarded the eastern Mexico populations (1–2) of the *rugulosus* population system as morphologically distinct from other members of the *rugulosus* stock. Nevertheless he adopted a conservative position, since the distinctive populations were allopatric to typical *El. rugulosus* (Cope, 1870) and retained them within the latter species.

Subsequently, karyologic analysis of the *rugulosus* population system (De-

Weese, 1976) discerned that the eastern Mexico populations differed significantly from all other units in the *rugulosus* population system. The eastern Mexico populations have a diploid number (2N) of 22 and a *nombre fundamental* of 36. All other known members in the system have 2N = 20. In this regard the eastern Mexico populations resemble *El. vocalis* of northwestern Mexico but differ from the latter form in chromosomal definition. These two forms are amply distinct morphologically (Savage, 1975). A more detailed discussion of karyologic features and evolution in the *rugulosus* group is in preparation by DeWeese.

The combination of morphologic differences supported by the unique karyology of the eastern Mexico populations force us to conclude that they represent a species distinct from *El. rugulosus*. The first available name for this form is *Hylodes berkenbuschii* W. Peters, 1870 (holotype: Berlin 6666; Mexico: Puebla: nr. Izucar de Matamoras). The species now to be called *Eleutherodactylus berkenbuschii* (W. Peters, 1870) is characterized by Savage (1975:270) and the distribution reviewed (pp. 271, 291–292). *El. berkenbuschii* may be most easily distinguished from *El. rugulosus* morphologically as follows (characteristics of the latter form in parentheses): canthus rostralis sharp (rounded) and first finger usually shorter than second finger (first finger usually longer than second).

Synonyms of *El. berkenbuschii* include *Eleutherodactylus natator* Taylor, 1939 (holotype: CM 1000014; Mexico: Veracruz: Tlilapam) and *Eleutherodactylus vulcani* Shannon and Werler, 1955 (holotype: Mexico: Veracruz: Volcan San Martin.)

Conventions and Acknowledgments

In order to reduce the number of times the long name *Eleutherodactylus* is spelled out in this and subsequent papers and to clearly distinguish it from other anuran groups when the generic name is abbreviated, we have adopted the form *El.* to represent the generic name. Those who know Spanish will note that this also provides an euphonious neatness to discussions of species in the genus since *el* is the Spanish definite article meaning "the." We have eschewed the use of diacritical marks on Spanish localities for the reasons given by Stuart (1963).

Material used in this study has been made available through the kindness of the authorities at the Museum of Natural History, University of Kansas (KU) and the Los Angeles County Museum of Natural History (LA). Field assistance was provided by several workers from the University of Southern California: Rosemarie DeWeese, Ronald T. Harris, Carl S. Lieb, Sandra Limerick, James J. Talbot and Nancy D. Savage. Dr. P. H. Starrett examined the jaw area of the new form to establish its jaw muscle formula. Our work in Costa Rica was expedited by aid from the Organization for Tropical Studies and the Facultad de Biologia, Universidad de Costa Rica. To all of the above we express our deep appreciation.

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New Species and Records of Polychaetous Annelids from the *Tetraclita* (Cirripedia: Crustacea) Zone of the Northern Gulf of California, Mexico

Jerry D. Kudenov

Abstract.—Two new species of polychaetes belonging to the families Phyllodocidae and Nereidae are described from the *Tetraclita* zone of Bahía Cholla, Puerto Peñasco, Sonora, Mexico. The ranges of *Syllis elongata* (Johnson, 1901), *Typosyllis fasciata* (Malmgren, 1867) and *Perinereis monterea* (Chamberlin, 1918) are extended into the Gulf of California.

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Over 500 species of polychaetes are currently known from the Gulf of California (Reish, 1968; Fauchald, 1972; Kudenov, 1975a, b, c and in press). A small collection of polychaetes was kindly made available by Prof. J. R. Hendrickson, University of Arizona. These were collected during 10–24 October 1976 by his student, Mr. R. Dougherty, from under the tests of *Tetraclita squamosa* (Bruguiere) at Bahía Cholla, Puerto Peñasco, Sonora, Mexico. This collection site is hereafter referred to as the "study area." *T. squamosa* occurs in the high intertidal zone and is rather common in the Gulf of California (Brusca, 1973). The ecological succession and distribution of invertebrate species in vacant tests of *T. staliactifera panamensis* was investigated in Panama by Reimer (1976a, b). The entire collection and types are lodged at the Allan Hancock Foundation, University of Southern California.

Family Phyllodocidae

Eumida uschakovi, n. sp.

Fig. 1

Material examined.—Study area, Holotype, AHF POLY 1217.

Description.—Holotype complete, with 256 setigers, measuring 25 mm long, 1 mm wide with parapodia, 0.6 mm wide without. Body elliptical in cross section, lacking midventral groove; uniformly pale rose in color in alcohol with traces of dark dorsolateral pigmentation.

Prostomium elliptical, longer than wide, with 5 conspicuous antennae (Fig. 1a). Anterior dorsal pair of antennae conical, longer than wide; ventral pair cirriform, about 2 times longer than dorsal pair; median antenna inserted on anterior prostomium, well ahead of eyes. One pair of dark, circular, lenticulate eyes present middorsally; nuchal papilla absent. Proboscis not everted, not examined.

First segment reduced, not visible dorsally. Tentacular formula of $1 + S_1^1 + S_N^1$ with tentacular cirri cirriform; with dorsal cirri of segments 2 and 3 longest, and ventral cirrus of segment 2 shortest; ceratophores of each tentacular cirrus with 3–4 annuli.

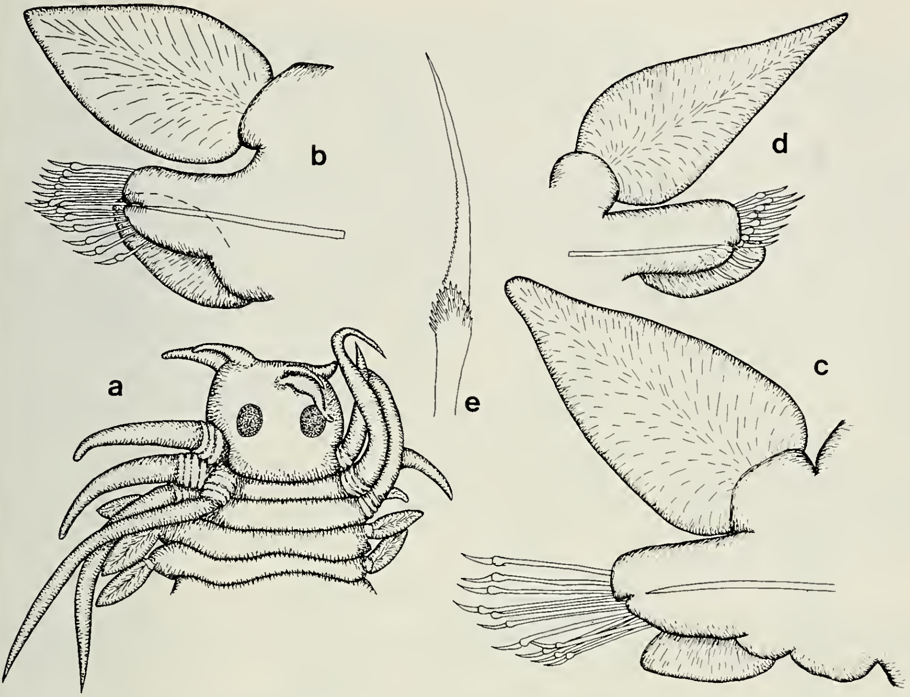

Fig. 1. a–e. Holotype, AHF POLY 1217, *Eumida uschakovi*. a. anterior setigers, dorsal view, ×27; b. right parapodium, setiger 10, anterior view, ×70; c. same, setiger 75, anterior view, ×70; d. left parapodium, setiger 125, ×70; e. composite spiniger, ×340.

Dorsal cirri 2–3 times longer than wide; broadly lance-shaped, distally blunt in anterior, medial setigers; becoming narrow, distally pointed in posterior setigers (Fig. 1b–d). Dorsal cirri of anterior, posterior setigers oval in cross section; those of medial setigers flattened. Ventral cirri distally rounded, projecting beyond parapodial lobes only of anterior, posterior setigers. Parapodial lobes distally notched, with aciculum penetrating notch in anterior setigers (Fig. 1b–d).

All setae as composite spinigers with spinous distal shafts and short appendages (Fig. 1e). Appendages obliquely sculptured, with a row of denticles on cutting edge becoming indistinct distally; number of setae gradually decreasing from 16 in setiger 10; 13 in setiger 75; 10–11 in setiger 125.

Pygidium with 1 pair of stout, distally blunt anal cirri equalling length of last 5–6 prepygidial setigers.

Discussion.—*Eumida uschakovi* is similar to *E. fusigera* (Malmgren) *sensu* Uschakov (1972), *E. parva* St. Joseph and *E. granulosa* (Verrill) in having dorsal cirri at least 2 times longer than wide. *E. uschakovi* differs from these species in having inflated, instead of flattened dorsal cirri; in having the median antenna inserted on the anterior prostomium, instead of between the eyes; and in lacking both prolonged superior parapodial processes and pointed ventral cirri. This species is named in honor of Prof. P. V. Uschakov in recognition of his monographic study of phyllodociform polychaetes.

Family Syllidae

Syllis elongata (Johnson, 1901)

Pionosyllis elongata Johnson, 1901:403–404, pl. 6, figs. 67–70.
Syllis elongata. Hartman, 1968:461–462, figs. 1–3; Banse and Hobson, 1974:61.

Material examined.—Study area, 2 specimens, AHF 000366-0.

Description.—These specimens generally agree with the original description, but differ in the segmental distribution of the pharnyx and proventriculus, and in the number of articles per dorsal cirrus. The pharynx extends through setigers 13–14, while the proventriculus is present in setigers 14/15–22. The long and short dorsal cirri of setigers 10 and 11 have 45 and 26 articles, respectively; those of setigers 190 and 191 with 15 and 12.

Discussion.—*S. elongata* normally has the pharynx and proventriculus through setigers 11, and setigers 11–19/20, and dorsal cirri with 16–20 articles anteriorly, and 14–15 posteriorly. The mexican specimens differ, and may represent a new subspecies, which I hesitate doing until additional materials are available.

Distribution.—Western Canada to southern California; newly reported from the Gulf of California, Mexico.

Typosyllis fasciata (Malmgren, 1867)

Typosyllis fasciata. Berkeley and Berkeley, 1948:74–75, fig. 109; Hartman, 1968:485–486, figs. 1–3; Banse and Hobson, 1968:64.

Material examined.—Study area, 2 specimens, AHF 000366-02.

Discussion.—These specimens agree well with previous descriptions.

Distribution.—Western Europe; western Canada to southern California; newly reported from the Gulf of California, Mexico.

Family Nereidae

Perinereis monterea (Chamberlin, 1918)

Perinereis monterea. Hartman, 1968:557–558; Banse and Hobson, 1974:71.

Material examined.—Study area, 2 specimens, AHF 000366-03.

Discussion.—These specimens agree well with previous descriptions.

Distribution.—British Columbia to western Mexico; newly reported from the Gulf of California, Mexico.

Neanthes cortezi, n. sp.

Fig. 2

Material examined.—Study area, Holotype, AHF POLY 1218; 20+ Paratypes, AHF POLY 1219.

Description.—A small species up to 25 mm long, 1.5 mm wide with parapodia, 1 mm wide without, for 80 setigers. Body elliptical in cross section, midventrally grooved; prostomium, palps, palpistyles, antennae with brown pigment.

Prostomium longer than wide, distally rounded, with conical frontal antennae (Fig. 2a). Palpi very large, about as long as prostomium; palpistyles nearly spherical. Two pairs of eyes present with anterior pair farthest apart, crescent-shaped; posterior pair elliptical.

Proboscis with dark brown, conical paragnaths on both rings as follows: I,

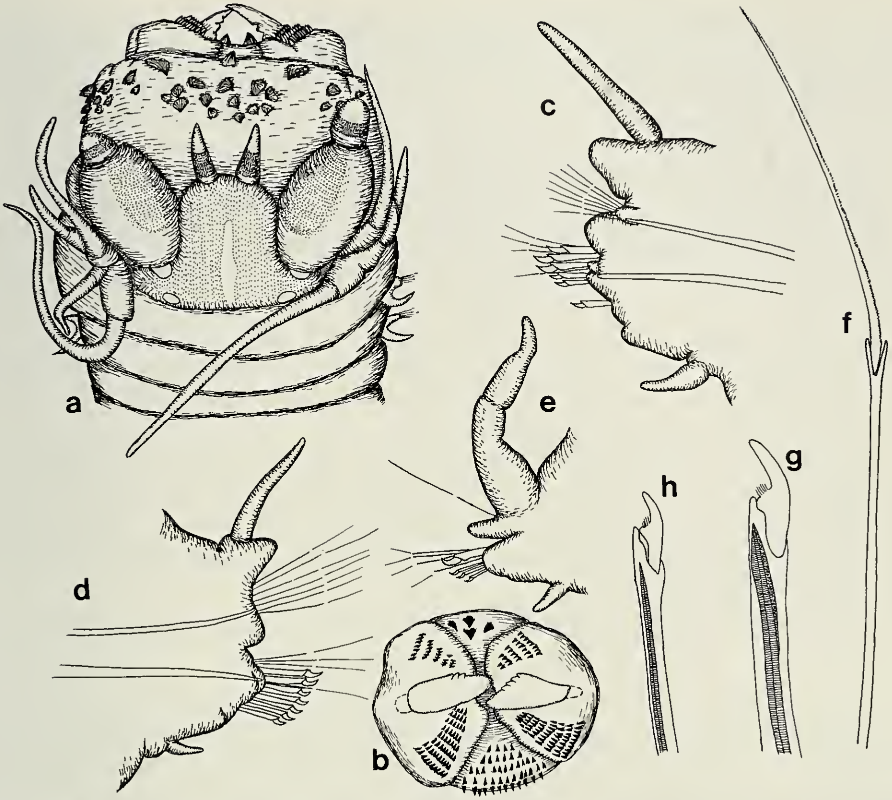

Fig. 2. a–h. Holotype, AHF POLY 1218, *Neanthes cortezi*. a. anterior segments, dorsal view, ×27; b. maxillary ring, pharynx, frontal view, ×27; c. right parapodium, setiger 10, anterior view, ×70; d. left parapodium, setiger 40, anterior view, ×70; e. right parapodium, setiger 70, anterior view, ×70; f. homogomph spiniger, ×250; g–h. superior and inferior heterogomph falcigers, ×340.

diamond patch of 4 cones; II triangular patch of 25 cones in 5 rows; III, oval patch of 45 cones in 5 rows; IV, trapezoidal patch of 56 cones in 8 rows; V, diamond patch of 14 cones; VI, single high conical paranath; VII–VIII, 91 large, small cones in 3 continuous rows (Fig. 2a, b). Jaws dark brown in color each with 11 triangular teeth.

Peristomium ⅓ as long as prostomium, with 4 pairs of cirriform tentacular cirri; anterior and posterior ventral pairs extending to setiger 1; anterior dorsal pair extending to setiger 3; posterior dorsal pair extending to setigers 7–8.

Anterior biramous parapodia with trilobed noto- and neuropodia (Fig. 2c); rounded pre- and postsetal lobes, a small round intermediate lobe plus a rectangular inferior lobe. Ventral cirri clavate in all setigers, decreasing in length posteriorly (Fig. 2c–e). Dorsal cirri finger-like, inserted on superior notopodial lobe.

Posterior parapodia with bilobed noto- and neuropodia. Dorsal cirri becoming reduced; situated distally on elongated superior notopodial lobes (Fig. 2e).

Notosetae all composite homogomph spinigers with denticulate appendages

(Fig. 2f). Neuropodia include composite homogomph spinigers in superior positions; composite heterogomph spinigers in intermediate positions; and thick and thin shafted heterogomph falcigers in intermediate and inferior positions. Superior heterogomph falcigers with shafts 2 times wider than inferior ones (Fig. 2g, h), each with 5–6 hairs on cutting margin of a short falcate appendage.

Discussion.—Neanthes cortezi belongs to group IIB2c (Fauchald, 1972) to which the following species are assigned: *N. noodti* Hartmann-Schröder, *N. seridentata* Hartmann-Schröder, *N. ruficeps* (Ehlers) and *N. pseudonoodti* Fauchald. Fauchald (1977) compared the latter 4 species. *N. cortezi* is most closely related to *N. noodti* and *N. pseudonoodti* in having paragnaths present in all pharyngeal regions. *N. cortezi* differs in having a patch of 14 cones in area V while the other 2 species each have a single cone. *N. cortezi* and *N. noodti* each have a single cone on area VI, but the paragnaths differ greatly in size; *N. pseudonoodti* has 2 cones on area VI.

N. cortezi, N. noodti and *N. pseudonoodti* are also related ecologically and zoogeographically in that all are associated with barnacles in rocky intertidal habitats in the eastern Pacific. It is probable that *N. cortezi* evolved from a widespread ancestor of both *N. noodti* and *N. pseudonoodti* through isolation in the Gulf of California.

Distribution.—Bahía Cholla, Puerto Peñasco, northern Gulf of California.

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A Survey of the Littoral and Sublittoral Ascidians of Southern California, Including the Channel Islands

Rimmon C. Fay and James A. Vallee[1]

Abstract.—The ascidian populations of the eight Channel Islands, as well as three islets, the Cortez Bank and the Coronado Islands were surveyed. Thirty-eight species were found offshore compared to the 48 identified species which have been found above a depth of 60 m in southern California. It was observed that viviparous ascidians are specifically more abundant than oviparous ascidians on the Channel Islands and the possible significance of this mode of reproduction is discussed as an explanation for their local distribution. The habitat preference of southern California ascidians is presented. Nine species of ascidians of unresolved identification are compared to the most closely related, described North American species.

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The ascidians of southern California have been surveyed by Ritter and Forsyth, 1917; Van Name, 1945; and Fay and Johnson, 1971. Those reported by Ritter and Forsyth were collected intertidally, while those listed by Van Name were collected by dredge as well as intertidally. Those reported by Fay and Johnson, 1971, were collected primarily with the aid of SCUBA, although some intertidal and trawl sampling was conducted.

The present study is a continuation of Fay and Johnson's 1971 report on the ascidians of the mainland coast of southern California and extends the study area to the Channel and Coronado Islands.

Little has been reported on the ascidians of the Channel Islands. Van Name, 1945, summarizing information to that date, noted the occurrence of *Trididemnum opacum, Pyura mirabilis,* and *Molgula pugetiensis* at or near San Nicholas Island, and the occurrence of *Clavelina huntsmani, Archidistoma psammion, Ritterella aequalisiphonis, Styela truncata, Molgula regularis,* and *Eugyra arenosa* around Santa Cruz Island. He also reported that *Halocynthia hilgendorfi igaboja* was found around Santa Catalina Island. Given and Lees, 1967, reported that *Euherdmania claviformis, Diplosoma macdonaldi, Metandrocarpa taylori,* and *Styela plicata* also occur around Santa Catalina Island. With these few exceptions the distribution of ascidians of the Channel Islands is unreported in the literature and the present study is the first attempt to provide specific information about the ascidians of all the Channel Islands. To the best of the authors' knowledge this is the first comprehensive survey of any hard bottom invertebrate group in southern California including collecting sites on all of the Channel Islands.

Methods

Collection sites were usually visited using 18′ and 24′ dive boats, however, occasionally commercial dive boats were used. Trawling was conducted from the 26′ F/V PISCES using a 2 m beam trawl. Collection sites included the north,

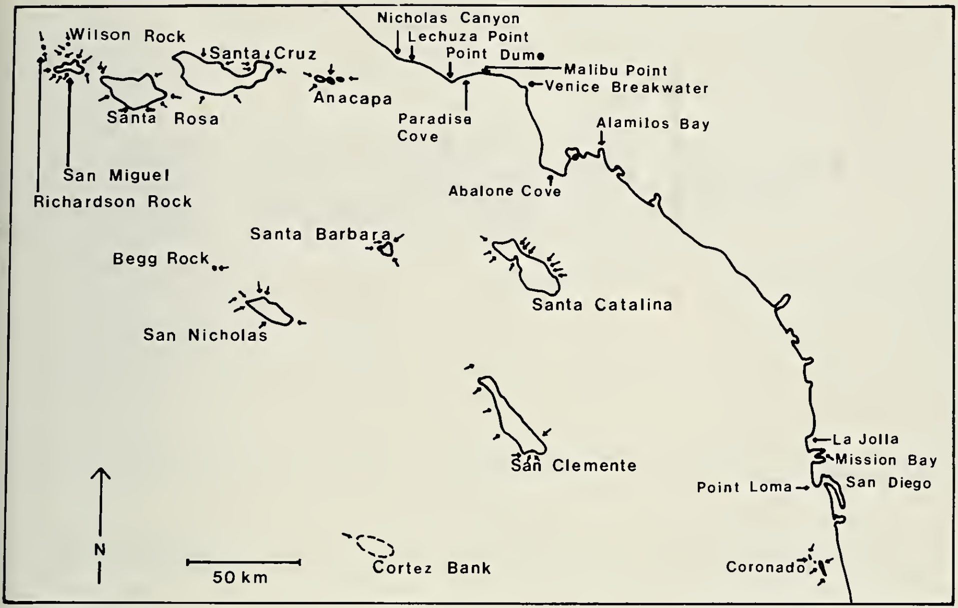

Fig. 1. Southern California Channel Island Collection Sites. Arrows around islands and rocks indicate collecting sites.

east, south and west sides of each of the islands. In addition to the Channel Islands, sites on Richardson Rock, Wilson Rock, Begg Rock, the Coronado Islands and Cortez Bank were surveyed to a depth of about 30 m with the aid of SCUBA (Fig. 1).

The period of study extended from 17 August 1972 to 11 February 1979. Detailed records of the dates and locations of the collection sites are maintained at Pacific Bio-Marine Labs, Inc.

Specimens collected were placed in 15% magnesium sulfate sea water along with a few crystals of menthol for 12 to 16 h to narcotize them. They were then transferred to 5% sea water formalin. Zooids were examined under a dissecting microscope and identifications were made using Van Name, 1945; Berrill and Abbott, 1949; and Abbott, 1975.

Results and Discussion

The mainland, island, and bank distribution of each species of ascidian collected is listed in Table 1. This table also indicates those species which brood their tadpoles (viviparous species) and those which release their gametes into the water (oviparous species). This distinction in mode of reproduction is noted because the Channel Islands appear to have a higher percentage of viviparous species when compared with the ascidian biota of the mainland (Table 2). No oviparous species were found on the three rocks visited. This suggests that the short larval period of the viviparous ascidians is essential to the maintenance of these species at the isolated island collection sites where active current movement is observed. Viviparous ascidians usually produce tadpoles which are able to settle and metamorphose within minutes to a few hours after being released from

Table 1. The distribution of the ascidians of the Channel Islands and the mainland coast of southern California from Santa Barbara to San Diego.

Species / Island Rock Bank	Richardson Rock	Wilson Rock	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	Begg Rock	San Nicholas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Cortez Bank	Coronado Islands	Mainland
*Aplidium californicum**	X	X	X	X	X	X	X	X	X	X	X	X	X	SB to SD
*Aplidium solidum**	X	X	X	X	X			X	X					SB to SD
*Aplidium propinquum**				X	X	X					X			PD
*Aplidium arenatum**		X	X	X	X	X		X	X	X	X		X	SB, PD, LJ, LP
*Euherdmania claviformis**			X***	X	X	X		X	X	X	X		X	SB to SD
*Polyclinum planum**		X	X	X				X	X					COP to SD
*Polyclinum laxum**								X	X					
*Synoicum parfustis**		X	X	X	X			X						COP to PL
*Didemnum carnulentum**	X	X	X	X	X	X	X	X	X	X	X	X	X	SB to SD
*Trididemnum opacum**		X	X	X	X	X		X	X	X	X			SB to SD
*Diplosoma macdonaldi**	X	X	X	X	X		X			X***	X			SB to SD
*Lissoclinum caulleryi**		X	X	X	X	X		X	X		X			PD to SD
*Clavelina huntsmani**	X	X	X		X	X			X	X	X	X		SB to SD
*Cystodytes lobatus**		X	X	X	X	X		X	X	X	X	X	X	SB to SD
*Distaplia occidentalis**	X	X	X	X	X		X	X***		X	X			SB to SD
*Archidistoma psammion**			X	X	X	X		X	X	X	X	X	X	SB to SD
*Archidistoma diaphanes**			X	X	X			X						COP to SD
*Archidistoma ritteri**		X	X	X	X	X		X	X		X	X	X	SB to SD
*Archidistoma molle**			X	X										
*Pycnoclavella stanleyi**		X	X	X	X	X		X	X				X	PD, MP, LP
*Ritterella aequalisiphonis**			X			X		X	X***					SB, PD, NC
*Ritterella pulchra**		X									X			SB, NC
*Ascidia ceratodes***			X	X	X	X		X	X		X			SB to SD
*Ascidia vermiformis***										X				PD
*Chelyosoma productum***														SB to SD
*Corella willmeriana**														3 mi S. Pt. Fermin
*Ciona intestinalis***										X				SB to SD
*Perophora annectens**								X						SB to SD

Species	Island Rock Bank													
	Richardson Rock	Wilson Rock	San Miguel Island	Santa Rosa Island	Santa Cruz Island	Anacapa Island	Begg Rock	San Nicholas Island	Santa Barbara Island	Santa Catalina Island	San Clemente Island	Cortez Bank	Coronado Islands	Mainland
*Polyzoa translucida**														VB, AB
*Botryllus tuberatus**			X	X				X	X	X	X			SB to SD
*Botrylloides diegense**														SB to SD
*Metandrocarpa dura**														PD
*Metandrocarpa taylori**			X		X	X		X	X	X	X	X	X	PD to PL
*Stylela montereyensis***				X	X			X					X	SB to SD
*Styela plicata***														SB to SD
*Styela clava***														SB to SD
*Styela truncata**					X									SB to SD
*Styela gibbsii***			X		X			X	X	X	X	X		SB to SD
*Styela partita***														SD
*Styela coriacea***									X	X				SMB
*Pyura haustor**		X	X	X	X			X		X	X	X	X	SB to SD
*Pyura mirabilis***				X	X							X		PL, LP, MB, PC
*Halocynthia hilgendorfi igaboja***										X				AC
*Boltinia villosa***			X	X				X			X			COP to SD
*Bathypera ovoida***										X				SMB
*Molgula regularis**			X	X		X			X	X	X		X	SB to SD
*Molgula pugetiensis***			X	X				X						SMB
*Eugyra arenosa***														SMB

* = viviparous.
** = oviparous.
*** = Roger Seapy, personal communication.
Abbreviations used:

AB	—Alamitos Bay
AC	—Abalone Cove
COP	—Coal Oil Point
LJ	—La Jolla
LP	—Lechuza Point
MB	—Mission Bay
MP	—Malibu Point
NC	—Nicholas Canyon
PC	—Paradise Cove
PD	—Point Dume
PL	—Point Loma
SB	—Santa Barbara
SD	—San Diego
SMB	—Santa Monica Bay
VB	—Venice Breakwater

Table 2. The number and percentage of oviparous and viviparous species.

	Viviparous		Oviparous	
	#	%	#	%
All of Southern California	32	67	16	33
Island, Islet or Bank				
Richardson Rock	6	100	0	0
Wilson Rock	16	100	0	0
San Miguel	22	85	4	15
Santa Rosa	20	80	5	20
Santa Cruz	20	83	4	17
Anacapa	15	94	1	6
Santa Barbara	17	85	3	15
Begg Rock	4	100	0	0
San Nicholas	21	81	5	19
Santa Catalina	15	75	5	25
San Clemente	18	86	3	14
Cortez Bank	9	82	2	18
Coronado	11	92	1	8

the parent. This greatly reduces the chances of their being swept away from suitable habitats by currents. The eggs and larvae of oviparous ascidians on the other hand, must develop in the plankton for a day or more before they are able to settle and metamorphose; during this time they would be subject to transport away from isolated habitats thereby making it difficult to maintain stable populations of oviparous species at small isolated sites. The channel rocks are examples of this circumstance.

The very short larval period that characterizes most of the ascidian populations of the Channel Islands and rocks, as well as their isolation, suggest that these populations are self dependent for their larval recruitment and therefore are endemic.

Nine species of ascidians known to occur along the mainland of southern California were not found on the Channel Islands by the authors, five of these are oviparous. Seven species, all viviparous, were found on all of the Channel Islands (Table 1). These observations again suggest that viviparity is of advantage at the island habitats.

Some Channel Island ascidians seem to be quite restricted in their distribution. Ten species have been collected on only one or two of the islands by the present authors (Table 1). It should be pointed out that *Styela coriacea, Halocynthia hilgendorfi igaboja,* and *Bathypera ovoida* from Santa Catalina Island were collected with a beam trawl which was not used around the other islands.

Since the publication of Fay and Johnson in 1971, the present authors have gathered additional information on the distribution of ascidians on the mainland coast of southern California. This is summarized in Table 1. Noteworthy additions include the occurrence of *Pyura mirabilis* at Point Loma, Lechuza Point, Mission Bay and Paradise Cove; *Molgula regularis* (=*M. verrucifera,* in Fay and Johnson, 1971) from Santa Barbara to San Diego; *Molgula pugetiensis* and *Bathypera ovoida* in Santa Monica Bay; *Polyzoa translucida* (=unidentified Styelid in Fay d Johnson, 1971) on the Venice breakwater, off San Pedro, and in Alamitos y; *Corella willmeriana,* three miles south of Point Fermin; and *Ascidia ver-ormis* at Point Dume. Recently (February, 1977) *Styela partita* has been col-ted in San Diego Bay (C. Lambert, pers. comm.).

t should be noted that several specimens of *Mogula regularis* were observed have tadpoles in their atrial chambers. This is of importance because Van me (1945) indicated that a closely related ascidian, *Mogula cooperi* (Hunts-n, 1912) from off British Columbia is distinguished from *M. regularis* (Ritter, 7) only because *M. cooperi* broods its tadpoles while *M. regularis* does not. e brooding of tadpoles by *M. regularis* reported here suggests that *M. cooperi* uld be synonymized with *M. regularis.*

During this and earlier work, it was subjectively observed that many of the idians were associated with protected waters or vigorous wave and current ion. For example, *Styela plicata, S. clava,* and *Ciona intestinalis* are found he calm waters of protected bays while *Clavelina huntasmani* is found at sites osed to vigorous currents or wave action. Table 3 lists the ascidians of south- California subjectively according to the relative vigor of water movement in habitats where they are found. Some of them, such as *Distaplia occidentalis* l *Pyura haustor* were found in all three types of circulation: calm water, mod-te exposure to currents and wave action, and exposure to vigorous currents l/or wave action.

t may be noted, except for the ascidians discussed in the introduction, the tribution of Channel Island ascidians reported in the present study all consti-e range extensions. The following are of particular interest. *Polyclinum laxum,* ich was previously reported only from the Gulf of California by Van Name in 5, is here reported from Santa Barbara and San Nicholas Islands. The previous thernmost occurrence of *Archidistoma molle* was Pacific Grove (Van Name, 5). In the present study it was found at Santa Rosa and San Miguel Islands. n Name also noted that only one specimen of *Pyura mirabilis* had been col-ted off southern California. It is here reported from Santa Rosa Island, Santa iz Island and Cortez Bank, as well as on the mainland coast. Van Name also e only one collection site for *Bathypera ovoida* (1000 fathoms, 22 miles south San Nicholas Island). It is here reported to be rather common at Santa Catalina ind. *Corella willmeriana* was reported by Van Name to occur as far south as day Harbor, Washington. It is apparently also found off central California ce it is listed in Abbott's key to the ascidians of central California in Light's nual (Abbott, 1975); this report extends its range to 3 mi south of Point Fermin, s Angeles County.

n addition to the 48 species of southern California ascidians listed above, we e collected nine species which cannot be identified as species of ascidians wn from southern California.

o describe and name these species is a task beyond the scope of the present dy, however, they may be characterized as follows:

Aplidium sp. A

The colony consists of sand-covered, club-shaped heads similar to *Aplidium pinquum* and *A. arenatum.* The branchial sac has 8 to 13 rows of stigmata npared to 5 rows in *A. arenatum* and up to 21 in *A. propinquum.* The stomach

Table 3. Water surge association of southern California ascidians.

Species	Calm Water	Moderate Water Movement	Vigorous Water Movement
Aplidium californicum	X	X	X
Aplidium solidum		X	
Aplidium propinquum		X	
Aplidium arenatum		X	
Euherdmania claviformis		X	X
Polyclinum planum			X
Polyclinum laxum			X
Synoicum parfustis			X
Didemnum carnulentum		X	X
Trididemnum opacum		X	X
Diplosoma macdonaldi	X	X	
Lissoclinum caulleryi		X	X
Clavelina huntsmani			X
Cystodytes lobatus	X	X	X
Archidistoma diaphanes		X	
Archidistoma psammion		X	X
Archidistoma ritteri		X	X
Archidistoma molle			X
Distaplia occidentalis	X	X	X
Pycnoclavella stanleyi		X	X
Ritterella aequalisiphonis		X	
Ritterella pulchra		X	
Ascidia ceratodes	X		
Ascidia vermiformis		X	
Chelyosoma productum		X	
Corella willmeriana		X	
Ciona intestinalis	X		
Perophora annectens		X	X
Polyzoa translucida	X	X	X
Botrylloides diegense	X		
Metandrocarpa dura		X	X
Metandrocarpa taylori		X	
Styela plicata	X		
Styela clava	X		
Styela truncata	X	X	
Styela gibbsii		X	
Styela coriacea	X		
Styela partita	X		
Styela montereyensis			X
Botryllus tuberatus	X	X	
Pyura haustor	X	X	X
Pyura mirabilis		X	
Halocynthia hilgendorfi igaboja		X	
Boltenia villosa		X	
Bathypera ovoida	X		
Molgula regularis		X	X
Molgula pugetiensis		X	
Eugyra arenosa	X		

usually has five to eight folds compared to five folds for *A. arenatum* and 18 to 21 for *A. propinquum*. *Apildium* sp. has been found at San Nicholas, San Clemente, Santa Catalina, San Miguel, and Anacapa Islands, at Wilson Rock, and off Nicholas Canyon, Los Angeles County.

Rhopalaea sp. A

This species attains a height of 25 mm and has about 80 rows of stigmata. The arrangement of the muscle bands in the mantle differs from that reported for *R. abdominalis* by Van Name (1945) and for *R. birkelandi* by Tokioda (1971), both from American waters. The species has been taken in Santa Monica Bay by trawl and by SCUBA at Point Dume.

Trididemnum sp. A

This species is very similar to *T. opacum*. It differs in that there are so few spicules that the test is very soft and translucent as compared to the tough, opaque test of *T. opacum*. *Trididemnum* sp. has been found at Santa Rosa and San Miguel Islands, Begg Rock, and off Nicholas Canyon, Los Angeles County.

Botryllus sp. A

This species is similar to *B. tuberatus* but the branchial sac has eight rows of stigmata instead of four. The systems are round or oval and usually consist of 6 to 14 zooids. *Botryllus* sp. occurs in Mission Bay on floats and on *Styela clava*.

Botrylloides sp. A

The zooids of this species appear to be very similar to those of *Botrylloides diegense*, however, the tadpoles are distinctively different. The body of *B. diegense* tadpoles is about 1.2 mm long and has about 32 ampullae, while the body of *Botrylloides* sp. tadpoles is about 0.6 mm long and has eight ampullae. The colony tends to mass and fold in a golden yellow complex larger than *B. diegense*. *Botrylloides* sp. has been found at San Nicholas, Santa Cruz, Santa Rosa, and San Miguel Islands.

Ascidia sp. A

This species is similar to *A. ceratodes*. However, unlike *A. ceratodes*, the present species has a thick, opaque, cartilaginous test, and is not laterally flattened. Five specimens 4.0 to 4.5 cm tall were collected in San Diego Bay.

Styela sp. A (probably *partita*)

One individual has been collected from Los Angeles Harbor, and a few from San Diego Bay.

Styela sp. B

This is a very contractile form. When fully extended the internal body structures, especially the two pairs of gonads, are similar to *S. gibbsii*. However, externally the posterior portion of the test is covered with a dense mat of branching papillae, similar to *Styela hemicaespitosa* described by Ritter in 1913, and synonymized with *Styela coriacea* by Hartmeyer in 1923. However, the present species is distinct from *S. coriacea*, which has only one pair of gonads. *Styela* *hemicaespitosa* should probably be re-established for it. This species has been trawled from Santa Monica Bay in 24–35 fathoms.

Polyclinum sp. A

This is an encrusting species of *Polyclinum*. The colony examined was about 45 cm long, 30 cm wide and 2–3 cm thick, with a smooth upper surface lightly coated with sand. It was collected from San Nicholas Island, where it was found living under a rocky ledge at a depth of 35 ft.

In addition to the above species, there is also a form of *Polyclinum* that is egg-shaped and has a slender stalk. This form of *Polyclinum* has been taken several times in the Point Dume area. It is here included as a form of *Polyclinum planum*, which is usually laterally flattened, and has a thick peduncle.

During the course of this and previous studies it was recognized that there is a need for a key to the Southern California ascidians. Therefore the following artificial key was prepared. It is based upon preserved material and zooid characteristics are used extensively, thus a dissecting microscope will be required. Zooid size, gonad description and the characteristic number of rows of stigmata described in the following key refer to adult zooids only.

A Preliminary Artificial Key to the Ascidians Found in Southern California

1. Simple ascidians 33
– Colonial ascidians 2
2. Body entire, not divided into 2 or 3 regions 26
– Body divided into 2 regions 14
–. Body divided into 3 regions 3
3. Atrial languet present 7
– Atrial languet absent 4
4. Each zooid with its own test (although sharing a common base) 5
– Zooids embedded in a common test, colony composed of lobes or club shaped heads 6
5. Twelve or thirteen rows of stigmata, zooids up to 35 mm tall, color in life, translucent grey to slightly greenish .... *Euherdmania claviformis*
– Seven rows of stigmata, zooids up to 30 mm tall, color in life, golden yellow .... *Pycnoclavella stanleyi*
6. Lobes incrusted with sand, and up to 20 mm tall, color in life, transparent encrusted with sand .... *Ritterella aequalisiphonis*
– Lobes incrusted with sand, up to 25 mm in height, color in life, transparent test with red zooids .... *Ritterella pulchra*
7. Colony composed of distinct lobes or club shaped heads 8
– Colony surface rather even, not composed of distinct lobes or club shaped heads 11
8. Branchial sac with 5 rows of stigmata, lobes of the colony up to 25 mm tall, sand encrusted .... *Aplidium arenatum*
– Branchial sac with 8 or more rows of stigmata 9
9. Stomach smooth, without distinct longitudinal folds (except for typhlosole), lobes of the colony up to 11 cm tall, color in life, salmon .... *Synoicum parfustis*

– Stomach with 5 to about 20 distinct longitudinal folds 10
10. Branchial sac with 8 to 13 rows of stigmata, lobes of the colony up to 35 mm tall, sand encrusted .... *Aplidium* sp.
– Branchial sac with 16 to 21 rows of stigmata, lobes of the colony up to 5 cm in height, sand encrusted .... *Aplidium propinquum.*
11. Entire colony supported by a distinct peduncle, colony may be up to 20 cm tall, color in life, red wine to yellow .... *Polyclinum planum*
– Entire colony attached by a broad base, not supported by a distinct peduncle 12
12. Stomach wall with many (8–23) longitudinal folds 13
– Stomach wall smooth, without many longitudinal folds, colony up to 8 cm across, mahogany colored in life .... *Polyclinum laxum*
13. Eight to twelve rows of stigmata, colony up to 20 cm across, ½ to 3 cm thick, color in life, white to salmon pink .... *Aplidium californicum*
– Thirteen to fifteen rows of stigmata, colony up to 16 cm across and 3½ cm thick, color in life, white .... *Aplidium solidum*
14. Each zooid with its own test (although sharing a common base) 15
– Zooids embedded in a common test 16
15. Zooids with about 80 rows of stigmata, zooids (including test) up to 35 mm tall, color in life, jade green .... *Rhopalaea* sp.
– Zooids with 16 to 20 rows of stigmata, zooids (including test) up to 40 mm tall, color in life, white or vivid pink .... *Clavelina huntsmani*
16. Atrial siphon present and tube-like 17
– Atrial siphon absent, atrial aperture an opening on the dorsal surface .. 23
17. Spicules present in the test 18
– No spicules present in the test 20
18. Spicules disk-shaped, or occasionally in the form of amorphous calcareous deposits, colony may be 25 cm or more across and up to 2 cm thick, color in life, orange-tan, whitish or grayish ...... *Cystodytes lobatus*
– Spicules stellate 19
19. Surface of test completely opaque due to the abundance of spicules, zooids not visible through the test, colony up to 15 cm across and 4 mm thick, flesh color in life .... *Trididemnum opacum*
– Surface of test transluscent due to the scarcity of the spicules, zooids clearly visible through the test, colony up to 8 cm across and 3 mm thick, color in life, brown .... *Trididemnum* sp.
20. Test tough and hard, upper surface even, without lobes, colony up to 15 mm thick, color in life, burgundy .... *Archidistoma psammion*
– Test soft with even surface, or with projecting lobes 21
21. Colony soft, with an even surface, without projecting lobes 22
– Colony with projecting lobes or elongate heads which may be up to 40 mm tall, color in life, turquoise .... *Archidistoma ritteri*
22. Zooids average about 3 mm long or less, colony about 1 cm thick color in life, white to pale vermillion .... *Archidistoma diaphanes*
– Zooids 5 to 8 mm long, colony about 2 cm thich, color in life, light grey .... *Archidistoma molle*
23. Minute spicules present in the test 24
– Minute spicules absent 25

24\. Atrial aperture a plain round opening restricted to the dorsal surface, with no languet, colony up to 4 mm thick, color in life, white to orange .... *Didemnum carnulentum*

– Atrial aperture very large, extending around to the sides of the branchial sac, atrial languet present, colony about 3 mm thick, color in life, grey .... *Lissoclinum caulleryi*

25\. Atrial aperture with a languet, each row of stigmata crossed by a transverse vessel, colony flat and about 1 cm thick or club shaped and up to 3½ cm tall, color in life, variable: white, grey, green, brown, and mixed .... *Distaplia occidentalis*

– Atrial aperture without a languet, the rows of stigmata not crossed by a transverse vessel, colony about 2 mm thick, gelatinous, color in life, tan .... *Diplosoma macdonaldi*

26\. Four to 8 rows of stigmata 27

– Nine to 13 rows of stigmata 29

27\. Each zooid with its own test or zooids fused, but not arranged in systems, atrial siphon tube-like, and opening directly to the outside, maximum height (including test) about 3 mm, color in life, emerald green .... *Perophora annectens*

– Zooids arranged in systems, atrial aperture opening into a common cloaca 28

28\. Four rows of stigmata, colony up to 2 mm thick, color in life, dark grey .... *Botryllus tuberatus*

– Eight rows of stigmata, colony up to about 2 mm thick, colorless, has the appearance of fish eggs .... *Botryllus* sp.

29\. Zooids in systems, atrial aperture provided with a languet and opening into a common cloaca, colony up to about 5 mm thick 30

– Zooids not in systems, atrial aperture without a languet, and opening directly to the outside 31

30\. Tadpoles with about 32 small papillae surrounding the anterior end of the body, color in life, orange, purplish .... *Botrylloides diegense*

– Tadpoles with 8 large papillae surrounding the anterior end of the body, color in life, golden yellow .... *Botrylloides* sp.

31\. Branchial sac with 3 longitudinal vessels, zooids up to 6 mm in height, color in life, grey .... *Polyzoa translucida*

– Branchial sac with 5 longitudinal vessels 32

32\. Zooids close together in a common test, colony up to about 4 mm thick, color in life, crimson .... *Metandrocarpa dura*

– Zooids separated, each with its own test, but interconnected with at least a film of test, zooids up to 5 mm tall, color in life, crimson .... *Metandrocarpa taylori*

33\. Branchial sac with internal longitudinal folds 39

– Branchial sac flat, without internal longitudinal folds 34

34\. Anterior end of the test a flattened disk provided with thin horny plates, reaches a maximum height of 50 mm, color in life, jade green, yellowish or brownish .... *Chelyosoma productum*

– Anterior end not flattened nor provided with thin horny plates 35

35\. Ascidian resembling a ball of mud, stigmata arranged in perfect double spirals, maximum test diameter about 15 mm color in life, muddy grey .... *Eugyra arenosa*

– Ascidian not resembling a ball of mud, stigmata not arranged in perfect double spirals 36

36\. Branchial sac extends posteriorly beyond the stomach in a long narrow pouch which is as long or longer than the distance from the stomach to the branchial siphon, maximum test length 14 cm, appearance in life, transluscent, tinged with green .... *Ascidia vermiformis*

– Branchial sac does not extend posteriorly in a long narrow pouch 37

37\. Stigmata spiral, stomach on the right side of the body, intestine curves ventrally under the stomach, maximum length of the test 45 mm, color in life, jade green to yellowish .... *Corella willmeriana*

– Stigmata straight, stomach on the left side of the body, intestine curves dorsally over the stomach 38

38\. Atrial siphon located on the dorsal side near, or posterior to the middle of the body 39

– Atrial siphon located near the anterior end of the body, maximum test length 25 cm usually 10 cm or less color in life, yellowish green .... *Ciona intestinalis*

39\. Test transparent or transluscent, flexible, laterally flattened, test up to 50 mm long, color in life, jade green .... *Ascidia ceratodes*

– Test opaque, rigid, cartilaginous, not laterally flattened, up to 45 mm long, color in life, jade green .... *Ascidia* sp.

40\. Large tentacles branched 41

– Tentacles always simple 47

41\. A closed renal sac on the right side of the body 42

– No renal sac present on the right side of the body 43

42\. An "S" shaped ovary on each side of the body, maximum test diameter 4 cm, usually 15 mm or less sand encrusted .... *Molgula regularis*

– An oblong ovary on each side of the body, maximum test length 15 mm, sand encrusted .... *Molgula pugetiensis*

43\. Test provided with precisely intersecting rows of small papillae, maximum diameter 4 cm, usually 2 cm or less, color in life, pearly white .... *Bathypera ovoida*

– Test not provided with precisely intersecting rows of small papillae (but may be provided with spines exhibiting no precise pattern) 44

44\. Body of test provided with spines, and usually relatively free of encrusting debris or organisms 45

– Body of test lacking spines (although minute spines may be present on the siphons), test may or may not be covered with debris or encrusting organisms 46

45\. Body supported by a stalk, total length of the test up to 9 cm, color in life, dull rose red .... *Boltenia villosa*

– Body attached directly by the posterior end, no stalk present, up to 10 cm in diameter, but usually 3 cm or less, color in life, reddish about the apertures, otherwise brown .... *Halocynthia hilgendorfi igaboja*

46\. Siphons located at opposite ends of an elongate body and directed in nearly opposite directions, test free of encrusting debris or organisms,

up to 65 mm long, color in life, dull white .... *Pyura mirabilis*
- – Both siphons directed upwards, test usually encrusted with debris or organisms, up to 120 mm long, color in life, rose red at ends of siphons .... *Pyura haustor*

47. Body supported by a narrow stalk, the upper part of which is hollow and contains a tubular prolongation of the mantle 48
- – Body attached directly by the posterior end, no hollow narrow stalk present 49

48. Conspicuous tubercles anteriorly, longitudinal folds of the test restricted to the posterior body and stalk, 4 or more ovaries on the right side of the body, test up to 20 cm tall, color in life, rose brown to brown .... *Styela clava*
- – Tubercles few and inconspicuous, longitudinal folds extend anteriorly nearly to the siphons, 3 or fewer ovaries on the right side of the body, test up to 30 cm tall, color in life, tan to reddish brown .... *Styela montereyensis*

49. Branchial sac with only one internal longitudinal vessel between the branchial folds, test up to 30 mm tall, color in life, reddish brown .... *Styela truncata*
- – Branchial sac with 2 or more internal longitudinal vessels between the branchial folds 50

50. Two ovaries on each side of the body 51
- – Other than 2 ovaries on each side of the body 53

51. Posterior region of the test provided with slender branching papillae which are usually obscured by silt, test up to 25 mm in height, color in life, greyish yellow .... *Styela* sp.
- – Test not provided with such papillae 52

52. Ovaries clearly sinuously curved, test up to 30 mm tall, color in life, yellow posteriorly, purplish anteriorly .... *Styela partita*
- – Ovaries only slightly sinuously curved, nearly straight, test up to 40 mm tall, color in life, reddish brown .... *Styela gibbsii*

53. One ovary on the right side of the body, test up to 20 mm long, color in life, reddish brown .... *Styela coriacea*
- – At least three ovaries on the right side of the body, test up to 10 cm tall, color in life, white and brown .... *Styela plicata*

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A Redescription of *Pettiboneia sanmatiensis* Orensanz (Polychaeta: Dorvilleidae) and a Revised Key to the Genera of the Dorvilleidae

James A. Blake

Abstract.—Pettiboneia sanmatiensis Orensanz originally described from Argentina, has been discovered in California and British Columbia. The new specimens are compared with the type collection and the species is redescribed. The jaw apparatus consists of seven pairs of denticle rows and is unique to the family Dorvilleidae. A new key to the genera of the Dorvilleidae is provided which includes *Pettiboneia*, but excludes *Apophryotrocha* Jumars which has been found to be a juvenile onuphid and not a dorvilleid.

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During the course of intertidal surveys in the White Gulch area of Tomales Bay, California, a small meiofaunal dorvilleid was discovered which appeared to be identical to *Pettiboneia sanmatiensis* Orensanz, 1973, from Argentina. The species had not been reported since its original description. The identification was confirmed following a comparison of the Tomales Bay specimens with the type collection from Argentina. Two additional specimens from British Columbia also proved to be the same species. Study of these materials has revealed that *P. sanmatiensis* possesses a unique jaw apparatus, unlike any other known for the Dorvilleidae. A complete redescription of the species is provided herein along with a revised key to the genera of the Dorvilleidae.

I am grateful to Prof. Elena Martinez Fontes of the Museo Argentino de Ciencias Naturales (MACN), Buenos Aires for the loan of the type collection and to the late Katharine D. Hobson for the specimens from British Columbia. The Tomales Bay specimens were collected by Debrah L. Armitage and are deposited in the National Museum of Natural History, Smithsonian Institution (USNM).

Pettiboneia Orensanz, 1973

Type-species.—Pettiboneia sanmatiensis Orensanz, 1973, by original designation.

Diagnosis.—Palps well developed, biarticulate; antennae simple, clavate, dorsal cirri small, elongated, bearing notoaciculum; ventral cirrus present; setae including serrated capillaries, furcate and composite setae; jaws including a pair of mandibles and seven pairs of denticle rows, carriers lacking.

Remarks.—Pettiboneia is monotypic and appears to be most closely related to *Schistomeringos* Jumars (=*Stauronereis* Verrill) in having an elongated dorsal cirrus, a notoaciculum and furcate setae. *Pettiboneia,* however, has small, simple antennae and 14 denticle rows while *Schistomeringos* has long, multiarticulate antennae and the typical dorvilleid arrangement of four denticle rows. Jumars (1974) and Oug (1978) have reported the presence of extra denticle rows in some

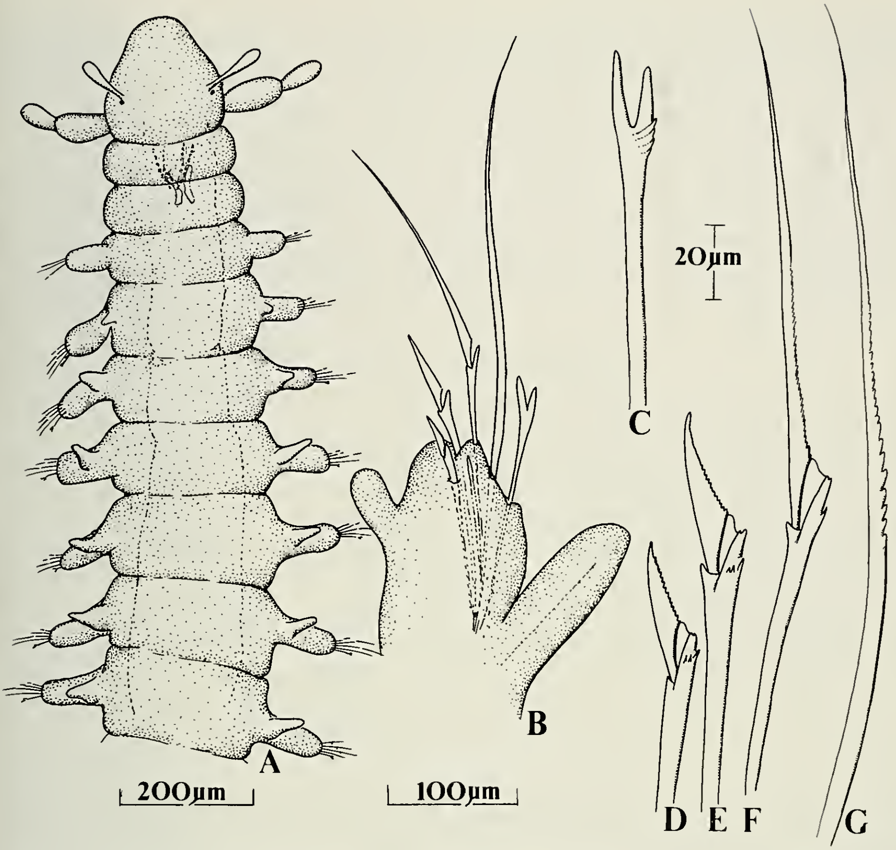

Fig. 1. *Pettiboneia sanmatiensis*: A. Anterior end in dorsal view; B, Middle parapodium in anterior view, dorsal cirrus to the right, ventral cirrus to the left; C. Furcate seta; D–F. Composite setae; E. Serrated capillary seta.

of their species of *Schistomeringos*. These authors consider them to be replacement maxillae since they are located directly under the ordinary set. The extra 10 denticle rows found in *Pettiboneia*, on the other hand, are located well forward of the first four rows and show no evidence of being superimposed by them.

Pettiboneia sanmatiensis Orensanz, 1973
Figs. 1–2

Pettiboneia sanmatiensis Orensanz, 1973: 338–339, pl. 5, figs. 1–8.

Material examined.—ARGENTINA: N.W. Golfo San Matias, 15–16 m, sand and gravel, Campaña exploratoria, SAO-1/71 Sta. 22 and 24, SAO-V/73, Sta. 228, five paratypes and holotype (Type series number, MACN 27818), one paratype on two slides (USNM 56509). CALIFORNIA: Tomales Bay, White Gulch, intertidal, sand-mud, 18 March 1974, coll. D. L. Armitage, five specimens (USNM 56498), three specimens on five slides (USNM 56510-1). BRITISH COLUMBIA: Chemainus Bay, subtidal, 11–12 m, sand-gravel, 30 September 1974, coll. K. D. Hobson, two specimens (USNM 56498).

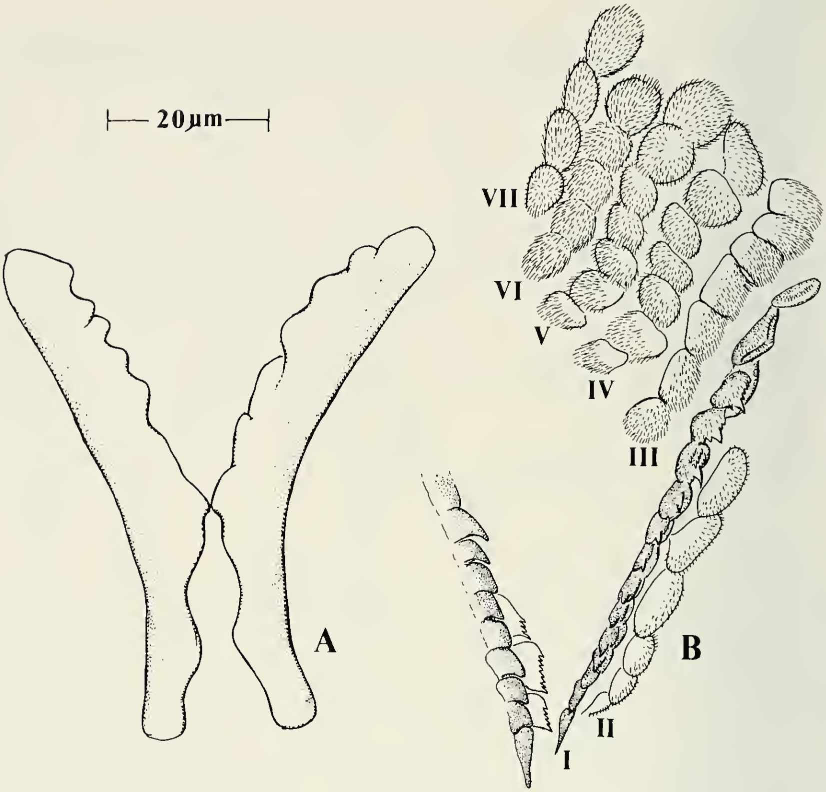

Fig. 2. *Pettiboneia sanmatiensis*: A. Mandibles; B. Maxillary apparatus consisting of seven pairs of denticle rows. Left side mostly omitted. Each pair denoted by numerals I–VII.

Description.—A small, slender, thread-like species, measuring up to 7.0 mm long and 0.4 mm wide for 55 setigers. Color in life: tan with brown granular spots scattered over cuticle; color in alcohol: opaque white.

Prostomium pear-shaped, broadly rounded on anterior margin, bluntly truncated on posterior margin; one pair of black granular eyes located at bases of antennae (Fig. 1A); antennae small, simple, clavate; palps well developed, biarticulate. Segments 1–2 achaetous; setiger 1 lacking dorsal cirrus, this beginning on setiger 2, small at first, increasing to full size by setiger 4 (Fig. 1A–B); dorsal cirri elongated, each bearing a thin notoaciculum; ventral cirri short, stubby; neurosetae including a thick neuroaciculum, sometimes protruding through cuticle, a single furcate seta (Fig. 1C), a single long serrated capillary seta (Fig. 1G), and 3–4 heterogomph composite setae grading in a series from short falcigers to long spinigers (Fig. 1D–F); each composite seta with finely serrated cutting edge on blade, small spinelets on end of shaft and a thin membrane connecting shaft and blade. Body terminating in four short anal cirri, each weakly clavate.

Jaw apparatus consisting of a pair of mandibles (Fig. 2A) and seven pairs of denticle rows (Fig. 2B); carriers lacking. Basal denticles of pair I not fused, narrow pointed with a single tooth gradually developing over subsequent denticles, distal denticles with smaller spines and spinelets; pair II with 6–11 denticles, each covered with numerous spinelets; pairs III–VII with numerous spinelets on denticles; pair I: dark brown; pairs II–VII: light tan.

Ecology.—*Pettiboneia sanmatiensis* occurs in coarse intertidal sands in Tomales Bay and is associated with dense populations of *Pygospio elegans* Claparède. In life, the specimens coil in a corkscrew fashion when removed from the sand. This behavior is similar to that of some archiannelids and demonstrates their dependence upon the sand grains for adhesion. In British Columbia this species was taken on a sand-gravel bottom in 11–12 m and in Argentina was taken on a sand-gravel bottom in 15–16 m.

Distribution.—Argentina, California, British Columbia.

Remarks.—The systematics of the genera of the Dorvilleidae have been confused in the past owing to several problems of nomenclature and varying interpretation of the weight of taxonomic characters used by different workers. As a result of revisions by Pettibone (1961), Fauchald (1970) and Jumars (1974) most of these problems would appear to be resolved. Oug (1978), however, has described new species of *Schistomeringos* and *Ophryotrocha* which differ from Jumars' (1974) definitions, and may eventually require further revisionary work on the genera. Until such time, the generic arrangement proposed by Jumars is, with one exception, accepted. An examintion of the holotype (AHF Poly 1081) and paratype (AHF Poly 1082) of *Apophryotrocha mutabiliseta* Jumars, 1974, has revealed that the species is actually a post-larval onuphid and not a dorvilleid. These juveniles possess five occipital tentacles or their scars and are similar in many respects to the larvae of *Nothria elegans* Johnson as described by Blake (1975). *Pettiboneia* was not included in the generic keys provided by Jumars (1974) and Fauchald (1977). A revised key to the genera of the Dorvilleidae is presented (see below).

No differences have been detected between the specimens of *Pettiboneia sanmatiensis* from Argentina, California and British Columbia. The first two pairs of denticle rows (I–II) approximate those observed in most other dorvilleid genera, except that maxillary carriers are lacking. In each of the slide preparations, the basal denticles of the first two pairs have separated easily, suggesting that there is no fusion of these parts. Denticle rows III–VII are more distally positioned and widely separated basally. The possible function of such a large number of denticle rows in *P. sanmatiensis* is probably related to a meiofaunal mode of life. When protruded, these numerous denticles could provide a broad rasping surface to work on the coarse sand grains and gravel found in its habitat. Diatoms and other small microflora are probably removed by their action.

The lack of meiofaunal collecting along the Pacific Coast of North and South America may account for the apparent disjunct range of *P. sanmatiensis*. Very fine mesh screens are necessary to retain this species, and despite a thorough survey of the White Gulch area of Tomales Bay by Dr. Ralph Johnson in the 1960's (Pacific Marine Station, unpublished data), this species was not found. Very small cores, individually sorted alive were required before the species was discovered. It is probable that *P. sanmatiensis* will be found elsewhere when such methods are employed.

Key to the Genera of the Dorvilleidae

1. Parapodia uniramous, without elongate dorsal cirri and notoacicula 4
– Parapodia sub-biramous, with elongate dorsal cirri and enclosed notoaciculum 2
2. Furcate setae present 3
– Furcate setae absent .... *Dorvillea*
3. Antennae small, simple; jaw pieces with 14 denticle rows ..... *Pettiboneia*
– Antennae long, multiarticulate; jaw pieces with 4 denticle rows .... *Schistomeringos*
4. Furcate or geniculate setae present 5
– Furcate and geniculate setae absent 6
5. Palps well developed, with at least one article; jaws with four denticle rows .... *Protodorvillea*
– Palps very small, simple or biarticulate; jaws with two denticle rows ... . *Meiodorvillea*
6. Setae all simple, acicular .... *Parophyrotrocha*
– Setae include both simple capillaries and composite setae 7
7. Setiger 1 modified, with two types of large specialized setae: (1) a simple recurved spine, (2) a large, thick, sharpely recurved composite falciger; antennae and palps biarticulate .... *Exallopus*
– Setiger 1 not modified; antennae and palps reduced, papilliform .... *Ophryotrocha*

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Research Notes

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New Mammalian Records from the Late Pleistocene of Rancho La Brea

Procyonids, talpids, or chiropterans have not previously been recorded from the late Pleistocene Rancho La Brea asphalt deposits in Hancock Park, Los Angeles, California (Stock, 1956). Re-examination of the existing collection and continuing excavation have produced specimens referrable to *Bassariscus astutus, Procyon lotor, Scapanus latimanus,* and *Lasiurus cinereus*; all of which have modern distributions including the Rancho La Brea area.

The authors recently located an isolated upper left first molar referrable to *Bassariscus astutus* (Fig. 1B) stored with the Ranch La Brea collections of the Los Angeles County Museum of Natural History (LACM). The specimen was in a homemade Riker mount type of box together with isolated teeth of other small mammalian taxa common in the La Brea fauna such as *Microtus californicus, Neotoma* sp., *Spermophilus beecheyi, Sylvilagus auduboni, ?Lepus californicus,* and *Mephitis mephitis.* The label on the outside of the box was destroyed by silverfish but the contained specimens are undoubtedly from Rancho La Brea. The preservation of all specimens in the box is typical of La Brea materials, and we know of no Riker boxes in the LACM collections which contain fossil vertebrate materials from other sites. Most of these homemade Riker type boxes in the La Brea collection contain specimens from pit A (the various excavations at La Brea are commonly called "pits"). The remnants of the original label and its position on the box are the same as was used for labelling other Riker boxes from pit A. The history and nature of pits A, B, C, and D remain somewhat enigmatic. These excavations were begun in the spring of 1929 by field parties from the LACM and continued perhaps to 1931, but only fragmentary records can be located. The excavations were disrupted in the early summer of 1929 when the field parties were sent to the newly discovered late Pleistocene Conkling Cavern site in eastern New Mexico. The age and stratigraphic relationships of pit A with other La Brea pits are uncertain but the avian assemblage appears to indicate a later period of accumulation than the typical late Pleistocene pits (Howard, 1962).

The tooth, LACM V-5205, is that of a young adult animal. The root canals are hollow and the cusps are sharp and little worn. V-5205 agrees in every detail with the left M/1 of living *Bassariscus astutus.* Measurements: greatest anterior-posterior diameter measured parallel to labial margin of tooth is 5.6 millimeters (mm); transverse diameter measured at right angles to above is 6.5 mm. It appears to be closest in both morphology and measurements to *B. astutus willetti* but adequate series of modern subspecies were not examined.

In June of 1969, the LACM, supported by grants and monies from the LACM Foundation, National Science Foundation (GB 24819), Los Angeles County, and numerous private corporations together with volunteer assistance, embarked on a long-range excavation program at pit 91, Rancho La Brea. The remaining new mammalian records from Rancho La Brea come from pit 91. On the basis of the

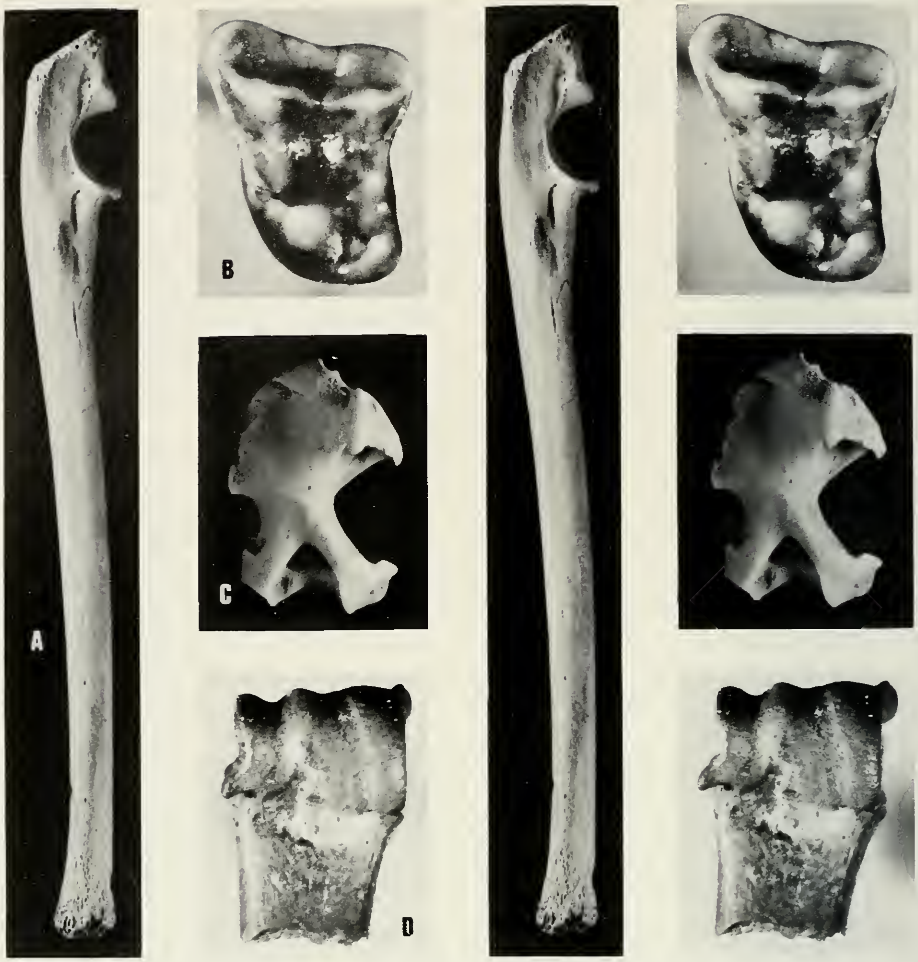

Fig. 1. A, LACM R-36926, *Procyon lotor* left ulna ×1. B, LACM V-5205, *Bassariscus astutus* left M/1 ×5. C, LACM R-21363, *Scapanus latimanus* right humerus ×2.5. D, LACM R-18437, *Lasiurus cinereus* distal left humerus ×9. All stereographic pairs. A and D coated with ammonium chloride and photographed with a Baird Stereo-Bar. B and D photographed with a Nikon SMZ-10 trinocular microscope.

few preliminary radiocarbon dates, pit 91 seems to be well stratified and has a late Pleistocene history from about 25,100 years before present (B.P.) to greater than 33,000 years B.P. Detailed stratigraphic data for the following specimens are on file at the George C. Page Museum.

LACM R-36926 is the left ulna of a large juvenile raccoon lacking proximal and distal epiphyses (Fig. 1A). Although immature, the diaphysis and semi-lunar articulation are fully formed and comparable with adult specimens of *Procyon lotor*. Measurements: midshaft antero-posterior diameter 6.7 mm; midshaft transverse diameter 4.4 mm; length of semi-lunar notch 12.0 mm; width of upper portion of semi-lunar notch 8.9 mm.

A complete right humerus, LACM R-21363, of an adult mole (Fig. 1C), agrees in details and measurements with modern specimens of *Scapanus latimanus*. The measurements for R-21363 are: Total length (distance from most proximal point on the humerus to the center of a line connecting the two most distal points)—13.3 mm; proximal width (greatest distance between the teres tubercle and the greater tuberosity, measured at right angles to long axis)—9.7 mm; minimum shaft width (narrowest mediolateral distance across the shaft of humerus, measured at right angles to the long axis)—3.9 mm; shaft thickness (antero-posterior distance from surface to surface, measured at same level as, and at right angles to, the shaft width)—3.7 mm.

LACM R-18437 is an incomplete left distal chiropteran humerus (Fig. 1D). Part of the spinous process and much of the posterior surface are missing. The fossil was compared with a number of modern specimens and the illustrations of J. D. Smith (1972). The tubercle on the proximal anterior margin of the lateral epicondyle is well developed and sharp; the distal spinous process is well developed and closely appressed to the medial epiconcdyle. These features appear to be characteristic only of *Lasiurus*. The relatively large size (2.6 mm across the most distal portion of the articulation) is comparable only to *L. cinereus* of the genus. The preserved portions of the fossil are identical to a modern specimen of *L. cinereus*, 46147, in the mammalogy collections of LACM.

Acknowledgments

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Post-larval Polychaetes in Sandy Beaches of Tomales Bay, California

Although many macrobenthic organisms spend part of their lives as transient members of the meiofauna (Thorson, 1966), relatively little quantitative data are available on their interactions in the meiobenthos. For example, Muus (1973) presents data on macrobenthic larval settling and mortality rates, and the duration of their stay in this habitat.

This paper presents preliminary quantitative data on the distribution and settling rates of post-larval polychaetes from sandy beaches of Tomales Bay, California. Research was conducted at the Pacific Marine Station, Dillon Beach, California, from 18 February to 18 May 1970. Sediment samples were collected along transects in Tomales Bay at Lawsons Flat, White Gulch and Walker Creek delta, and were taken either with a core (5.4 cm dia) or a petri dish (10 cm dia). Core samples were taken to a depth of 4 cm; dishes to 1.5 cm. In the laboratory, samples were divided into 4 subsamples which were not preserved or anaesthetized. A modified Boisseau apparatus was used in which a standard distillation flask was substituted for the cylinder (see Hulings and Gray, 1971). Filtered sea water was used throughout this experiment. Organisms were retained on a 70 μm mesh which was examined for entangled animals after each elutriation. Eight control samples were examined for post-larval polychaetes in which the number of larvae was known prior to elutriation. All control polychaetes were removed from the sediment after 9 min.

A total of 11 species of polychaetes belonging to 7 families was found: *Anaitides williamsi* Hartman; *Platynereis bicanaliculata* (Baird); *Nephtys caecoides* Hartman; *Hemipodus borealis* Johnson; *Glycinde armigera* Moore; *Lumbrineris ?zonata* Johnson; *Polydora socialis* (Schmarda); *P. caulleryi* Mesnil; *Pseudopolydora kempi* (Southern); *P. paucibranchiata* (Okuda) and *Pygospio californica* Hartman. The overall mean larval density for the entire sampling period was 468.7 ± 377.8 worms$\cdot$m^{-2}, and ranged from 56.8 to 1055.8 worms$\cdot$m^{-2} (N = 36 samples). Periods of heaviest settling occurred during late March and late April (Fig. 1). Species settling heavily during the first period are *H. borealis, P. kempi* and *N. caecoides*; those of the second period are *G. armigera, A. williamsi* and *N. caecoides*. Settling data for all species are presented in Table 1. *Pseudopolydora kempi* had the highest settling rate (103.67 ± 15.45 individuals$\cdot$m$^{-2}\cdot$ day), followed by *G. armigera, H. borealis, N. caecoides, A. williamsi* and *P. bicanaliculata*. Habitat partitioning is shown by *H. borealis* and *G. armigera* where dense settling periods were temporally separated.

All of these polychaetes were taken within the upper 2 cm of the sediment column. Two transects parallel to the shoreline at Lawsons Flat revealed a density of 488.3 worms$\cdot$m^{-2} above and 233.5 worms$\cdot$m^{-2} below the waterline. *A. williamsi, N. caecoides* and *G. armigera* were generally taken on the exposed beach, while*P. bicanaliculata* was collected below the waterline.

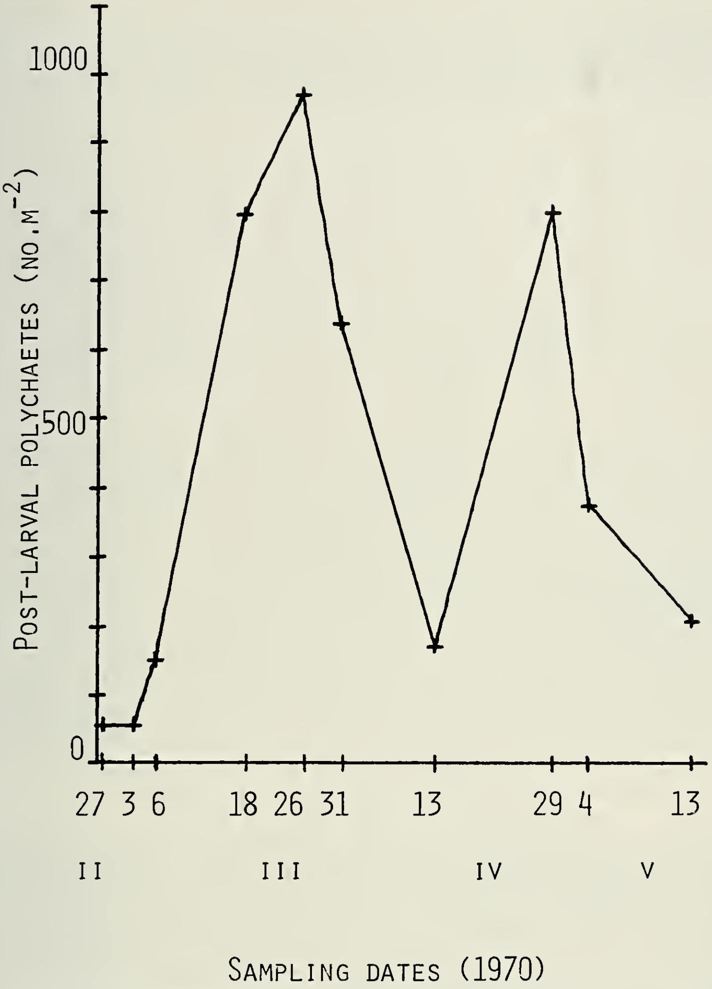

Fig. 1. Settling trends for all species of post-larval polychaetes from Tomales Bay, California.

The temporally most widespread species was *Nephtys caecoides*, which had a mean density of 97.1 individuals·m^{-2}. I calculated that this species had a combined summer density of 21.2 adult worms·m^{-2} at White Gulch and Lawsons Flat (see Johnson, 1967, data for 1963). Although these data are restricted in time, the mortality rate of *N. caecoides* must be substantial.

The presence of certain post-larval polychaetes in beach sediments corresponds well to their periods of reproduction (see Blake, 1975; Blake and Woodwick, 1975). All sampling for this experiment was performed in regions where adult populations of these species were low (see Johnson, 1970). Muus (1966) states that, "vast numbers of larvae settle where they do not belong." This is apparently reflected in the patchy settling pattern of *Pseudopolydora kempi*. It is well known that many larvae can postpone settling and metamorphosis. However, when such delays are coupled with adverse climatic conditions, for example, massive mor-

Table 1. Densities (no·m^{-2}) and mean settling rates (no·m^{-2}·day^{-1}) for post-larval polychaetes from Tomales Bay, California.

DATE	*A. williamsi*	*P. bicanaliculata*	*N. caecoides*	*H. borealis*	*G. armigera*	*L. ?zonata*	*Ps. kempi*	*Ps. paucibranchiata*	*P. socialis*	*P. caulleryi*	*Py. californica*
27 Feb	—	28.4*	28.4*	—	—	—	—	—	—	—	—
3 Mar	—	—	28.4	28.4	—	—	—	—	—	—	—
6 Mar	—	—	38	56.6	—	—	—	—	38	19	—
18 Mar	—	171	227	397.5	—	—	—	—	—	—	—
26 Mar	86	29	142	28.4	—	—	742	—	—	—	28.4
31 Mar	—	—	—	63.6	—	—	573	—	—	—	—
13 Apr	86	43	—	—	128	—	—	—	—	—	—
29 Apr	171	114	172	—	513	—	—	—	—	—	—
4 May	125	—	125	—	250	—	—	—	—	—	—
18 May	—	—	16	—	95.3	80	—	16	—	—	—
$\bar{x}$	93.6	48.2	97.1	114.9	246.6	—	657.5	—	—	—	—
±s	62.9	62.3	79.9	158.8	189.7	—	119.5	—	—	—	—
no·m^{-2}·day^{-1}											
×	12.8	8.7	14.7	15.1	24.5	—	103.7	—	—	—	—
±s	8.6	8.5	9.7	11.6	20.4	—	15.5	—	—	—	—

* Data not included in computation of mean.

talities may be inevitable. The increased density of worms on an exposed beach is probably a behavioral adaptation by raptorial feeders, rather than being the result of prevailing climatic conditions. The species typically encountered in this habitat may gain a feeding advantage through decreased motility of prey species. The nereid species typically collected below the waterline is basically omnivorous, and may be disadvantaged in exposed habitats.

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The Calcanea of Members of the Hyaenidae

The calcanea of all currently recognized species of living members of the Hyaenidae were examined. These are the calcanea of *Crocuta crocuta* (15 specimens), *Hyaena brunnea* (2 specimens, 1 malformed), *H. hyaena* (5 specimens), and *Proteles cristatus* (4 specimens). All calcanea of hyaenas have the same articular surfaces: posterior (PAS), medial (MAS), anterior (AAS), and cuboid (CAS) (Fig. 1); the proximal end of the medial articular surface folds over the proximal end of the sustentaculum astragali (SA); and the outline of the outer surface lacks a distinct trochlear process (TP) and tends to dip inward near the cuboid facet (Fig. 1). See Stains (1959, 1962, 1973) or Robinette and Stains (1970) for terminology.

Genera and Species of the Family Hyaenidae

Crocuta crocuta—Spotted Hyaena

Specimens examined.—American Museum of Natural History (AMNH) 21542, 27767, 35358, 36390, 163101, 163105; U.S. National Museum of Natural History (USNM) 161909, 162920, 163100, 163102-4, 163299, 163344, 164506, 164834, 172685 (USNM 163344 illustrated, Fig. 1a).

Crocuta crocuta has the largest calcaneum of modern hyaenas; more than 55 mm long and 25 mm wide (Table 1). The body of the calcaneum is robust and the greater tuberosity (GT) is twisted toward the inner side (Fig. 1a). The anterior articular surface is large and distinct, and is separated from the medial articular surface. A ridge of unarticulated bone sometimes connects the two surfaces (in 2 of 15 specimens examined).

Hyaena spp.

Calcanea next in size to those of *Crocuta*, but slightly smaller, are those of the genus *Hyaena* which range between 45 to 54 mm long and 22 to 25 mm wide (Table 1). The anterior articular surface is more elongate in the proximo-distal direction than in *Crocuta* and, in most cases, is joined with the medial articular surface.

Hyaena brunnea—Brown Hyaena

Specimens examined.—AM 83690; USNM 221088 (deformed) (AM 83690 illustrated, Fig. 1c).

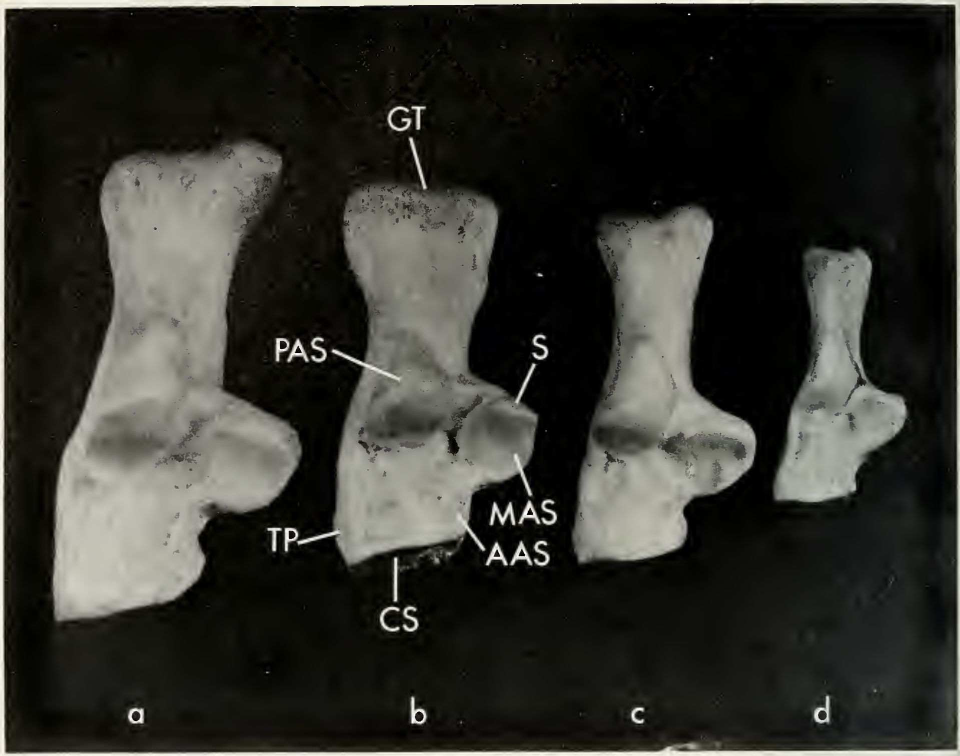

Fig. 1. Calcanea of the Hyaenidae. a. *Crocuta crocuta,* b. *Hyaena hyaena,* c. *Hyaena brunnea,* d. *Proteles cristatus.* GT—greater tuberosity, S—sustentaculum, TP—trochlear process, CS—cuboid surface, AAS—anterior articular surface, MAS—medial articular surface, PAS—posterior articular surface.

The shape of the greater tuberosity of *H. brunnea* is closer to that of *C. crocuta* than to other hyaenas. The junction of the anterior and medial articular surfaces is more obvious in *H. brunnea* than in *H. hyaena* (Fig. 1) although the young of *H. hyaena* also show a distinct connection.

One specimen of *H. brunnea* is malformed (USNM 221088). The malformation appears to be a deletion of part of the main distal dorsal surface of the one opposite the anterior articular surface and just above the cuboid facet. Examination of the calcaneum from the opposite foot in the same specimen, reveals an exact copy of the malformation indicating that the condition is genetic and not due to some previous injury.

Hyaena hyaena—Striped Hyaena

Specimens examined.—AMNH 54512; USNM 14403, 99626, 155455, 163111 (USNM 14403 illustrated, Fig. 1b).

Calcanea of adults of *H. hyaena* show a slight separation of the anterior and medial articular surfaces. *H. hyaena* calcanea are most easily distinguished from *H. brunnea* by the greater width of the greater tuberosity of *H. hyaena* when viewed from the dorsal aspect. The calcanea of *H. hyaena* are larger (52 mm

Table 1. Measurements and Indices for Calcanea of Species of the Family Hyaenidae.

Hyaenid Species	No.	Length (mm) Range	Length (mm) Avg	Width (mm) Range	Width (mm) Avg	W/L Index Range	W/L Index Avg
Crocuta crocuta	15	56.5–62.2	58.9	26.9–33.9	29.5	.46–.56	.50
Hyaena hyaena	3	50.2–53.9	51.8	23.1–25.0	23.9	.45–.52	.48
Hyaena brunnea	1		44.6		22.1		.50
Proteles cristatus	3	29.0–31.9	30.2	14.1–16.3	15.5	.49–.54	.51

length, 23.9 mm width than those of *H. brunnea* (44.5 mm length, 22.1 width). Table 1 gives additional measurements.

Proteles cristatus—Aardwolf

Specimens examined.—AMNH 27768, 70261; USNM 164503, 181523 (USNM 181523 illustrated, Fig. 1d).

Proteles cristatus possesses the smallest calcaneum (total length 30.2 mm, width 15.5 mm), and resembles *H. brunnea* (Fig. 1c) most closely in shape than other members of the family. In most respects, the calcaneum of *P. cristatus* (Fig. 1d) is a miniature of *H. brunnea*. The cuboid facet is nearly oval in shape medio-laterally in *P. cristatus*; more circular in shape in other hyaenas. In addition, the more proximal half of the posterior articular surface is sigmoid in *P. cristatus*; in other hyaenas this surface is slightly sigmoid to rounded. In this feature, *H. brunnea* again approaches *P. cristatus* more closely than do the other hyaenas.

Conclusions

H. brunnea and *P. cristatus* have calcanea with joined anterior and medial articular surfaces and similar shapes. Calcanea of *C. crocuta* are the most distinct with an inward flaring of the greater tuberosity.

The hyaenas are regarded as being offshoots of viverrid ancestors according to the fossil evidence (Beddard, 1902; Romer, 1966; Simpson, 1945). Of all calcanea examined (Stains, 1959) in other familes of the Carnivora, some members of the Viverridae (Stains, J. Morph.) show the closest resemblance to the hyaenas. Within the viverrids, calcanea of the Herpestinae resemble the hyaenas in shape of the greater tuberosity in particular. In viverrids, the trochlear process s usually distinct and often well above the distal end of the calcaneum. However, n the Herpestinae this process is slight and at the distal end of the calcaneum.

Most dogs (Stains, 1975) and cats also lack a distinct trochlear process although here is usually an enlargement near the distal end of the bone. In general, a feature of the calcaneum such as the trochlear process remains rather uniform hroughout members of a family such as the bears and procyonids (Stains, 1973), mustelids (Stains, 1976a, 1976b), sciurids (Stains, 1962) and viverrids (Stains, J. Morph.). Robinette and Stains (1970) discuss terminology in seals. Of all the iving genera of carnivores I have examined, the cheetah of the Felidae has a calcaneum with an outline closest to the hyaenas. The cheetah has a small trochear process near the distal end of the bone, an elongation of the calcaneum, a mall swelling between the minute trochlear process and distal to the posterior articular surface, a smooth curved posterior articular surface, and a grooved greater tuberosity in which it differs from the hyaenas.

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INSTRUCTIONS FOR AUTHORS

e BULLETIN is published three times each year (April, August, and November) and includes articles in English any field of science with an emphasis on the southern California area. Manuscripts submitted for publication ould contain results of original research, embrace sound principles of scientific investigation, and present data clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, ieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous erence of pronouns, and logically placed modifiers.

MANUSCRIPT PREPARATION

t is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The hor is requested to submit *at least two additional copies with the original,* on 8½ × 11 opaque, nonerasable er, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the manuscript.*** otnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to author.**

n abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* ompany a *feature article. Abstract should not exceed 100 words.*

feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, and rature cited. Avoid using more than two levels of subheadings.

research note is usually one to six typewritten pages and rarely utilizes subheadings. Consult a recent issue he BULLETIN for the format of *notes*. Abstracts are not used for notes.

bbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the LLETIN. **Omit periods after standard abbreviations:** 1.2 mm, 2 km, 30 cm, but Figs. 1–2. Use numerals *before* ts of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of ghts and measurements should be used wherever possible.

axonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the International le of Botanical Nomenclature (Lawjouw *et al.*, 1956), the International Code of Nomenclature of Bacteria and uses (Buchanan *et al.*, 1958), and the International Code of Zoological Nomenclature (Stoll *et al.*, 1961). cial attention should be given to the description of new taxa, designation of holotype, etc. Reference to new a in titles and abstract should be avoided.

he literature cited: Entries for books and articles should take these forms.

IcWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.
Iolmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54: 452–458.
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ables and figures (line drawings, graphs, or black and white photographs) **should not repeat data contained in text.** The author must provide *numbers* and *short legends* for tables and figures and place reference to each hem in the text. Legends should be typed on a separate sheet of paper and placed at the end of the manuscript. **strations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size;** inarily they should be no more than twice the size of intended reduction and should not exceed 8½ by 11 inches ize. Photographs *must* be printed on glossy paper. Submit one photoduplicated copy of each illustration. All strations accompanying **Research Notes** will be reduced to one column width. **All half-tone illustrations will have t screen (grey) backgrounds. Special handling such as dropout half-tones, special screens, etc., must be requested nd will be charged to authors.**

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ll manuscripts should be submitted to the Editor, Jeffrey I. Chapman, School of Public Administration, Uni- sity of Southern California, Los Angeles, California 90007. **Evaluation of a paper** submitted to the BULLETIN ins with a critical reading by the Editor; several referees also check the paper for scientific content, originality, clarity of presentation. Judgments as to the acceptability of the paper and suggestions for enhancing it are sent he author at which time he or she may be requested to rework portions of the paper considering these rec- nendations. The paper then is resubmitted and may be re-evaluated before final acceptance.

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UTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

me 78 Number 3

S-A78(3) 151–206 (1979) DECEMBER 1979

Southern California Academy of Sciences

Founded 6 November 1891, incorporated 17 May 1907

Membership is open to scholars in the fields of natural and social sciences, and to any pers interested in the advancement of science. Dues for membership, changes of address, and requests f missing numbers lost in shipment should be addressed to: Southern California Academy of Science the Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 900

Annual Members	$ 12.
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The Bulletin is published three times each year by the Academy. Manuscripts for publication shou be sent to the appropriate editor as explained in "Instructions for Authors" on the inside back cov of each number. All other communications should be addressed to the Southern California Acader of Sciences in care of the Natural History Museum of Los Angeles County, Exposition Park, L Angeles, California 90007.

Date of this issue 7 March 1980

Bull. Southern California Acad. Sci.
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Seventieth Anniversary of Academy Excavations at Rancho La Brea

Gretchen Sibley

Los Angeles County Museum of Natural History, 900 Exposition Blvd., Los Angeles, California 90007.

The Southern California Academy of Sciences was one of the early organizations permitted to collect fossil material from the Pleistocene beds at Rancho La Brea in Los Angeles, California. The Academy work began in June, 1909, though the first recognition of the importance of the fossils had come 34 years before. In 1875 William Denton visited Major Henry Hancock at the rancho, collected a few fossil bones and, two years later, published a description of them in the Proceedings of the Boston Society of Natural History. The article apparently created no appreciable notice and was soon forgotten (Stock, 1956).

It was not until 1901 that a sustained interest brought effectual activity. Mr. W. W. Orcutt, while studying the geology of the area for the Union Oil Company, found a number of bones which he transferred to his office. In 1905 Mr. F. M. Anderson, a geologist with the Southern Pacific Company, noticed the material and realized its importance. He contacted his friend, Prof. John C. Merriam of the University of California, who immediately obtained permission from Mrs. Henry Hancock to excavate at the ranch during the years 1906 to 1913. Merriam made a fine collection for the university and published the first public announcement in the Sunset Magazine, October, 1908. He carried on the work with some of his colleagues and students but was never able to finance an extensive project.

Shortly after Merriam began his work, both Occidental College and the Los Angeles High School were granted permission to collect the fossil material. James Zacchaeus Gilbert, professor of biology at Los Angeles High School, became intensely interested, headed up the dig and made a small collection for the high school. The bones remained at the school until the late sixties when they were given to the Los Angeles County Museum of Natural History.

Gilbert used interested students to help excavate, but he realized the importance of the fossils and the necessity for securing money to carry on the work on a larger scale. He turned to the Southern California Academy of Sciences of which he was a long-standing member and fellow. The progress can be followed from the excellent minutes and editorials provided by Holdridge Ozro Collins, secretary, and editor of the Bulletin. The first mention of the work at Rancho La Brea appears in the minutes of a meeting of the directors held on Wednesday, March 17, 1909.

"A communication was received from Mr. Samuel Fox, relating to a proposed excavation in the Rancho La Brea, west of the City of Los Angeles, which is owned by Mrs. Ida Hancock, and the Secretary was instructed to inform Mr. Fox that while the directors are in full sympathy with this project, there are no funds subject to their control which are available for this purpose."

April and May passed with no further information, but Gilbert's enthusiasm began to kindle interest. At a section meeting held at the residence of Mr. S. J. Keese on Monday, June 12, 1909, "Prof. Gilbert gave a statement of the progress in the excavations at the Rancho La Brea, made immediately possible by means of the generous donation to the Section by Mr. John D. Hooker. He placed upon exhibition several fossils, in excellent condition of preservation, of long-extinct animals, which he had excavated at this place, and he outlined the plan for future work under the auspices of the Academy."

On June 28 the project was continued by the directors. "Professor J. Z. Gilbert was authorized to organize a Zoological Section, and the Secretary was instructed to communicate with Mrs. Erskine M. Ross [formerly Mrs. Henry Hancock], and request from her an allotment in her Rancho La Brea for excavation under the auspices of this Academy, in a search for fossil and geological specimens."

It is interesting to note that the work was under the new zoological section though there was a geological section in the Academy.

Mrs. Ross allowed the Academy to begin excavation near the old Hancock home. Following John D. Hooker's initial donation, Los Angeles City also contributed to the fund, and the Academy canvassed members to take care of other expenses.

Holdridge Collins published the details in the following editorial in the Bulletin of July, 1909.

> The organization of a Section of Zoology marks a new era in the life of the Academy. Professor James L. [sic] Gilbert, Chairman of the Section, well known in this community for his scientific attainments, is at the head of the Biological Department of the Los Angeles High School, and during the short period of the life of this Section he has accomplished wonders. It has been known for some time that in a depression on the Rancho La Brea, are buried the remains of early fauna of California. A communication from the Academy to Mrs. Erskine M. Ross, owner of the rancho, requesting permission to excavate at this place, brought a most gracious consent, and, owing to the liberality of Mr. John D. Hooker, Prof. Gilbert was able to proceed at once with the work. An opportunity so rare comes but once, and we are fortunate that we have been able to delve in so rich a bed of extinct fauna at the very door of the Academy.
>
> On Monday, July 26, 1909, Prof. Gilbert placed upon exhibition in the City Hall the results of his work since the commencement of the public school summer vacation. A Buffalo skull, with a sweep of horns of 31 inches from tip to tip, the largest ever found; the bones of the Camel, Horse, Antelope, Sloth and Elephant in their most gigantic forms; a skull of the sabre-toothed tiger, complete in all its parts; the head and part of the bones of a huge lion—not the mountain lion of California, but of the African type; smaller cats, rodents and a large variety of birds, great and small, were shown in an unusually excellent state of perfection. None of these are petrified, and their preservation from a time before man made his appearance is explained by their burial in a grave of brea.
>
> This exhibit was inspected by the Mayor and the gentlemen of the City Council, who were so impressed with the value of these discoveries and fear

James Z. Gilbert (black hat and beard) explains fossils to visitors and student workers in the Academy dig at Rancho La Brea, 1909.

that the numerous foreign Scientific Bodies, which have applied for permission to excavate in this wonderful deposit, will carry away fossils which should forever remain in a home Museum, that, on the same day an appropriation of five hundred dollars was made to the Academy for the continuance of this work.

Academy members received their first detailed account of the work in October. A summary is given in the minutes.

The first lecture of the season of 1909–1910 was given by Professor James Z. Gilbert on Monday evening, October 4, 1909, in Symphony Hall.

His subject was "The extinct fauna of the Southwest, as represented by numerous fossils of extinct animals discovered at La Brea Rancho.

A large attendance was in presence and a very pleasant episode of the evening was the music of the young ladies' Glee Club of the Los Angeles High School.

In introducing his subject, Prof. Gilbert paid a tribute of thanks to Mrs. Erskine M. Ross for her gracious allotment of a tract on her ranch, and the

> liberality of Mr. John D. Hooker and the Council of Los Angeles, which had enabled him to carry on the excavations without cessation throughout the entire summer.
>
> Upon the screen he presented views of the small lake in the eucalyptus grove and explained the geological and paleontological conditions of the district surrounding this unique deposit of fossils.
>
> The ancient spring of water, gushing through a bed of asphaltum, was a fatal trap to hold to their death the numerous animals of earth and air, which resorted to this place to quench their thirst.
>
> A most interesting collection, in an excellent condition of preservation, of the fossils of the lion, the sabre-toothed tiger from infancy to old age, the wolf, mastodon, giant sloth, camel, horse, antelope, small rodents of numerous species, the peacock, the great condor, and the ancestors of the eagle, and many other animals whose descendants are now found only in tropical lands, was placed upon exhibition, and their characteristics explained by the Professor, and at the close of the address these remains were examined by the intensely interested audience.

Later in the month, "The Secretary was instructed to extend to Professor W. H. Housh, Principal of the High School, an expression of the appreciation of this Board for his kindness in furnishing room in the High School building for the work of cleaning the fossils lately excavated and giving them a secure place for storage."

At the director's meeting on October 15, the following was recorded. "In view of the valuable acquisition of fossils from Rancho La Brea; the tender of geological and zoological collection; the necessity for the proper housing and care of these valuable contributions to science, and the increasing needs of the Academy, it was resolved to place before the members and the public generally, a formal statement of the financial requirements of the Academy, and solicit subscriptions, to enable us to continue a work which has been so fruitful of results.

"A note of thanks was unanimously given to Mr. John D. Hooker for an additional gift of $500.00 for the prosecution of the excavations in Rancho La Brea."

Collins reported later in the year. "The work of cleaning and mounting the fossils from Rancho La Brea is proceeding with gratifying success, under the direction of Professor Gilbert. At this writing, a sabre-tooth tiger and a giant wolf stand in all the perfection of their skeleton ferocity, and bones of a giant ground sloth have been assembled, and work has been commenced on their mounting. A finely mounted and perfect skull of a sabre-tooth tiger, with sabres, eight inches in length, has been placed in the office of the Secretary where it can be seen at any time by members of the Academy and their friends."

At this time the Academy had been in existence for eighteen years. On November 6, 1891 it was established as the Southern California Science Association by an enthusiastic group of men and women interested in science. Five years later the rapidly growing organization adopted its present name. By 1909, when excavations at La Brea were undertaken, the membership had grown to around one hundred and eight (Howard, 1957). And the decision to aid Gilbert at Rancho La Brea led the Academy into a period of its greatest activity. The new Hall of

Records had just been completed and it was hoped that an area might be secured in the new building for a display of La Brea fossils. Hector Alliot, Academy member, met with the County Board of Supervisors and reported to William Spalding, president of the Academy.

> Following our recent conversation I met the county Supervisors, by appointment, this morning and (unofficially) [sic] explained to the board the civic importance of the work of the Academy of Science [sic] of Southern California in various fields, particularly that of paleontology.
>
> The necessity of their recognizing the efforts of the Society in preserving the valuable specimens from the La Brea ranch deposits, by providing a suitable space for exhibition purposes in the new Hall of Records building was urged upon them.
>
> While unwilling to bind themselves by a resolution, the Supervisors unanimously agreed that they would see that an exhibition room, or rooms, for the display of zoological and other collections owned by the Academy of Science [sic] would be provided in the projected Museum Building at Agricultural Park. The first installment of county funds will be forthcoming in September, and the architects will be able to commence work on this Museum in a short time.
>
> Pending the completion of the Museum, Supervisor Eldredge has kindly offered the Academy of Science space for the public exhibition of their collections in the County Court House, when certain portions of that building shall have been vacated by departments which are to move to the new Hall of Records. The entire space in the latter building has already been apportioned.
>
> The Academy of Science can therefore feel certain that in the near future temporary rooms will be at their disposal for public exhibition purposes in the County Court House; and that they are assured permanent quarters in the Museum, when it shall have been erected in Agricultural Park.

The ''projected Museum Building at Agriculture Park'' would become the Los Angeles Museum of History, Science and Art (now the Los Angeles County Museum of Natural History), and the park would soon be named Exposition Park. This cultural area was the dream of Judge William M. Bowen. In 1898 he had become interested in the park then given over to rabbit coursing, gambling, drinking and related activities. When he discovered the land belonged to the State of California, he spent years in the courts clearing title to the property which had fallen into private hands. He was convinced that the park was to become a cultural center for the City and County of Los Angeles. The new museum, state exposition building (now the State Museum of Science and Industry), the armory (now the Space Museum), the new race track (later replaced by the Memorial Coliseum) and the gardens and lawns, were a part of his general plan for the park (Sibley, 1978). His friend, Howard Robertson (1953) shared his dream and recalled Bowen's first plan made in the fall of 1908: ''We spread out a piece of wrapping paper on the desk, sketched in the park boundaries, and began laying plans for putting the land to good use as a cultural center. At last, here was the place for a museum!''

Several organizations were interested in a building in which they might exhibit their collections. On January 16, 1910, the board of directors of the Historical Society of Southern California met with Judge Bowen who showed them preliminary plans for a museum. They decided to invite several groups to meet with the Board of Supervisors to request room to house their collections (Guinn, 1909–10).

On February 7, 1910, representatives from the Historical Society, the Southern California Academy of Sciences, the Fine Arts League and the Cooper Ornithological Club, Southern Division, met with the County Board of Supervisors to discuss the proposed museum. Judge Bowen outlined an agreement that was drawn up and signed by the supervisors and representatives of each of the organizations.

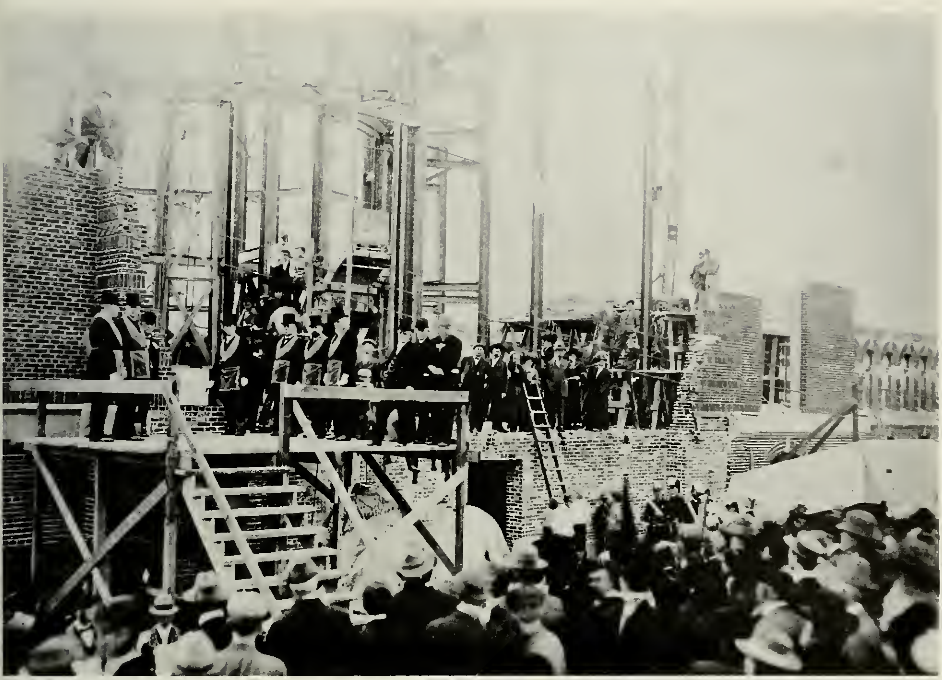
According to the contract—from the Academy files—the County agreed "to erect at Agricultural Park a Historical Museum and Art Gallery for the purpose of collecting and exhibiting therein a collection of fine arts, specimens, and data of biology and zoology, and historical matter relative to the Pacific Coast, more particularly Southern California, with a view of promoting and encouraging scientific art and historical education and investigation;" It would also maintain and operate the building, handle the exhibits and pay salaries of employees. The four organizations "shall have the care, supervision, control and management of said building and the collection, installation and supervision of said exhibits therein, for a period of fifty years, from and after the 7th day of February, 1910, through a Board of Governors."

The Board was set up as follows on the next day:

Chairman of the Board of Supervisors:
  Mr. C. J. Nellis
Two representatives from the Fine Arts League:
  Mrs. Henrietta House
  Mr. T. E. Gibbon
Two representatives from the Historical Society:
  Dr. George Bovard
  Mr. J. M. Guinn
Two representatives from the Southern California Academy of Sciences:
  Mr. William A. Spalding
  Dr. Anstruther Davidson
One representative from the Cooper Club:
  Mr. Howard Robertson
One representative selected at large:
  Judge William M. Bowen

To the members on December 5, 1910, Collins reported in the Bulletin, "The President, Mr. Spalding, reported progress the erection of the new County Museum Building in Agricultural Park, and, in a view thrown upon the screen, he pointed out the wing which will be the home of this Academy, and explained the conveniences which will be placed at our disposal. He invited all present to attend the ceremonies of the laying of the Corner Stone on the afternoon of December 17, 1910."

At the Academy Director's meeting five days later,



The cornerstone of the Museum was laid on November 17, 1910.

The Secretary reported that he had been requested to take charge of the selection of records to be sealed in the Copper Box which will be deposited in a cavity of the Corner Stone of the new County Museum Building, to be laid by the Most Worshipful Grand Master of Ancient, Free and Accepted Masons of California, on Saturday, December 17, 1910, and he asked for instructions from the Directors as to what documents of this Academy should be selected for that collection.

He was directed to have the Articles of Incorporation, Certificate of the Secretary of State and List of Members of the Academy, printed in a suitable form, and with Volumes VIII and IX of the Bulletin and a short typewritten History of the Academy, to be prepared by Mr. Knight, placed in the Box. The Secretary was also instructed to send to all members, a circular, informing them of the time and place of the ceremonies connected with the laying of the Corner Stone and to include with said Circular a silk badge upon which shall be printed the words "Academy of Sciences."

The secretary must have had a busy six days accomplishing so much. Today there would not be a printer available to set all the material in type on such short notice.

As scheduled, the cornerstone was laid on December 17, 1910 and the park was christened Exposition Park. After the ceremony Collins wrote at the bottom of the list of contents placed in the cornerstone: "The box containing the above temized documents was retained in my possession and by me placed in the

Cavity of the Corner Stone as it was sealed and laid by the Grand Lodge F. and A.M. of California.'' It would have been interesting to have the full account of happenings at the ceremony because on December 22 Collins wrote to Spalding: ''I hereby tender my resignation as Secretary of the Southern California Academy of Sciences.'' The letter was filed with a notation by Collins at the bottom: ''The resignation was tendered by reason of certain transactions connected with the laying of the Corner Stone of the County Museum Building in Agricultural Park on Saturday, December 17, 1910. The Board of Directors refused to consider it and it was returned to me. December 24, 1910, Holdridge O. Collins.''

Apparently members of the Academy were working diligently on their collections for the following editorial appeared in the Bulletin in January, 1911:

> The Directors are particularly gratified in being able, at this early date, to inform our members that immediately upon the completion of that Building, most valuable, interesting, beautiful and, in some respects, unique collections in Geology, Ichtheology [sic], Conchology, Ethnology, Ornithology, Botany, Entomology and Zoology will be speedily placed in position in the large exhibition room, for inspection by the curious and examination by the student. Some of these collections have been purchased, some have been gathered at the expense of the Academy, some have been presented and a few have been loaned. Professor Gilbert has been most assiduous in his labor of cleaning and mounting the fossils from Rancho La Brea, and he reports that he now has enough skeletons to occupy the space of one side of the hall. Among them are two complete giant ground-sloths, several sabre-tooth tigers, a lion, giant wolf, foxes, coyotes, probably a complete mastodon and camel, a turtle, deer, the giant ox; and, of the creatures of the air, numerous skeletons of the giant condor, vultures, hawks, eagles, owls, herons, geese, peacocks and an innumerable quantity of creeping, crawling, walking and flying smaller fry, which possessed this region as least two hundred thousands of years ago, and which nature has embalmed and preserved in their air tight graves.

The Museum building was completed early in 1912 and exhibits were quickly moved in. Art occupied the west wing and rotunda, history was assigned the north wing and science was installed in the south wing. By July the following description of science exhibits appeared in the Bulletin:

> The progress made in cleaning, assembling and mounting the fossils from La Brea Rancho is most gratifying, and by September of this year we expect to present for public inspection an exhibit, which will surprise even those who have followed our work and which will convince the public of the great treasures we have exhumed from the zoological graves of the antiduluvium [sic] past.
>
> Mr. Raymond D. Jewett and Mr. Eugene J. Fischer have devoted most faithful, conscientious and skilled labor to the mounting of these fossils and the excellent taste and supervision of Mrs. Daggett have furnished most appropriate and beautiful desks, standards and cases for the mounts.
>
> At the present time, there stands in all its skeleton ferocity a sabre-tooth tiger six feet two inches in length by three feet in height; the gigantic ground

The Museum was finished and opened in November, 1913.

sloth measuring fourteen feet from its snout to the end of its tail standing over nine feet high; a mastodon, thirteen and one-half feet long and eight feet high with the cores of its tusks complete, its skull being seven and one-half feet in circumference; a female bison eleven feet two inches in length and five and one-half feet high; a giant wolf, about the size of the present Alaska timber wolf and resembling in its general build the German and Russian wolf; the skeleton of an African lion of the present day standing close to the sabre-tooth and showing by comparison the great size and strength of the latter. Work upon the male bison is progressing rapidly and, at this time, the spinal column is mounted thirteen feet in length, and with ribs eighteen inches longer than those of the female. Its skull measures forty-two inches between the cores of the horns, from which an estimate may be made of the enormous spread of these weapons of offense and defense as they once were in all their glory. The elephantus imperialis or imperiator, which exceeded in size the Mastodon and Mammoth, is represented by an enormous humerus and femur, and hopes are entertained that among the tons of unassorted fossils remaining to be examined, enough of the other parts will be found to furnish an entire skeleton.

In the cases are displayed the complete skeletons of a sabre-tooth tiger and giant wolf articulated, with the bones spaced and labelled for examination, and a series of wolf bones of adults and young for study of comparative anatomy.

There are also to be seen the humerus and pelvis of an extinct lion of the

La Brea fossils dominated exhibits in the science wing of the Museum, 1913

> African type and we did have the skull, excavated from our concession in the Brea beds, but it has mysteriously disappeared.
>
> It would be tedious to enumerate everything now shown in our Exhibition room, but the cases contain several skulls of the sabre-tooth, the giant wolf, four distinct species of the extinct coyote, skulls and bones of birds and fowls of the air and water and parts of the camel and giant horse.
>
> Although this hall has not been thrown open to the public, Mr. Daggett, the general superintendent, is always glad to welcome any member of our Academy for an inspection of these treasures.

Science and History wings of the Museum were opened in March, 1913, but the gala opening was on November 6. A great parade of city officials, marching bands and industrial floats slowly passed through the flower strewn streets of central Los Angeles and traveled to Exposition Park. Both the Museum and State Exposition Building were officially opened, the cornerstone for the Armory was laid and water from the new Owens River Aqueduct rose thirty feet in the air from the pipe that would soon supply the fountain in the sunken garden. That evening the Museum was filled with important citizens invited to a private opening (Los Angeles Times and Los Angeles Tribune, 1913; Sibley, 1978). This was the climax of many months of hard work by the Academy, begun in a tar pit at Rancho La Brea.

On October 17, 1914 a gavel made from La Brea fossils was presented to President Arthur B. Benton, Dr. Astruther Davinson, second president of the Academy, designed the gavel using a ground sloth vertebra for the head, and

Since 1976, re-mounted fossils, such as the saber-tooth cat, have been housed in Hancock Park in the new George C. Page satellite of the Natural History Museum.

wood from the fossil McNab Cypress for the handle. And because the Academy had been so closely associated with Rancho La Brea, in 1915 the skull of the saber tooth cat was included in the seal of the organization.

As the years passed the Academy continued its work at the Museum through representatives on the Board of Governors. However, curators and preparators took over the work of developing collections and exhibits.

Two additions were added to the Museum in the twenties and then The Depression arrived. The Academy suffered but survived with a membership reduced to less than 50 (Howard, 1957).

Beginning in the early forties, meetings were held at the Museum on the ground floor beneath the old science wing. Here a potluck dinner preceded each monthly gathering. In the early sixties the growing Academy moved into the new Auditorium where it met for a number of years before adopting its present pattern of meetings.

In all those years few changes were made in the old Rancho La Brea exhibit in the south wing. Numerous plans were made for a museum to house the animals in Hancock Park. Allan Hancock had deeded the fossil bearing area to the County to preserve the animals and he hoped for a small museum in which to exhibit the fossils. Bond issues and budget requests failed so many times that the project seemed hopeless. Finally in the late sixties the fossil exhibit at the Museum was modernized with what little money was available.

In 1973 Mr. George Page, a wealthy philanthropist, offered to build a museum at Hancock Park. The County accepted his gift and today an unique building stands in the midst of the area where struggling animals once died and early Academy members excavated for their remains. The Museum presents the story with film, paintings and reconstructions (Sibley, 1978). But the important exhibits are the skeletons—many are the same collected and mounted by the Academy for the first Museum exhibits. Now the animals stand in more natural positions and the remounting has removed most of the old iron bars and pipes. Thus the work of the Academy remains, evidence of the foresight of the early scientists, men and women who realized the significance of the fossils and secured public support for their preservation.

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The Salt Marsh and Transitional Vegetation of Bahia de San Quintin

Leon F. Neuenschwander, Ted H. Thorsted, Jr., and Richard J. Vogl

Abstract.—This study describes a relatively pristine salt marsh and ecotones that could serve as a comparison for understanding disturbed West Coast marshes. The salt marsh and terrestrial transitional vegetation of Bahia de San Quintin is composed of a low number of species with only a few dominants, and it is similar to southern California marshes. Species react to minor elevational differences to create vegetation patterns or gradients, with each species reaching its highest frequency in the higher drier portions in a particular part of the marsh. *Salicornia virginica* has the broadest amplitude of occurrence. Plant cover increases with elevation which corresponds to decreases in tidal inundation, saturated soils, and salinity. Frequencies of species were low and variable in the marsh-upland transitions, but were high and consistent in the marsh proper. The presence of capillary extensions of tidal waters appears to be a critical factor in controlling the distribution of species in the ecotone areas. The establishment of submerged *Zostera marina* beds blocks the open body of water and initiates successive development that may culminate in terrestrial vegetation by contributing to its stabilization and sedimentation. Piles of detached *Zostera* mat down the emergent vegetation which results in open pockets that are eventually revegetated.

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In general, enclosed bays and lagoons of semiarid eastern Pacific regions between Pt. Conception, California and Acapulco, Mexico have not been extensively studied (Johnson, 1958; Barnard, 1961; Mudie, 1970).

California salt marshes are concentrated around San Francisco, Los Angeles, and San Diego where human population expansion has caused an alteration, rapid destruction (Darby, 1964; Anonymous, 1971), or pollution (Barnard, 1961; Vogl, 1966). Around 1900 there were 28 sizeable estuaries between Morro Bay, California, and Ensenada, Mexico (Orme, 1973). Since then, 15 have been modified either slightly or moderately, 10 have been altered drastically and 3 have been destroyed (Speth, 1969; Macdonald, 1977a). Remaining marshes are threatened by highways or development in the U.S., and farming or settlement in Mexico, and the alterations of natural drainages and tidal prisms. Intact undisturbed salt marshes complete with their transition zones do not exist in southern California.

The closest undisturbed salt marsh with an intact transitional vegetation to the southern California marshlands is Bahia de San Quintin. This extensive bay (Fig. 1) is located at 116°00′ longitude and 30°31′ latitude which is approximately 273 km (170 miles) south of the U.S. border on the Pacific side of Baja California, Mexico (Fig. 2).

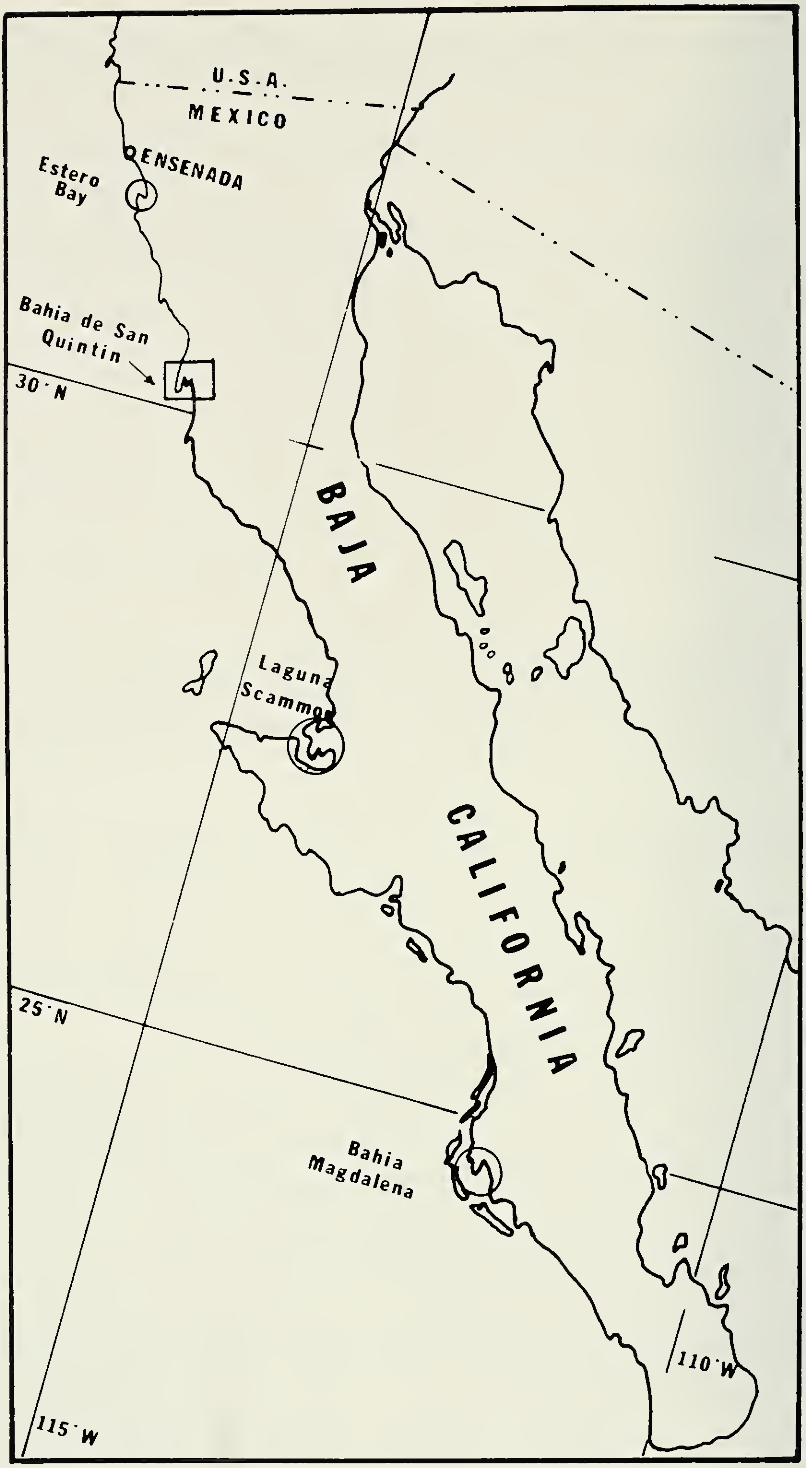

Fig. 1. Location map showing Bahia de San Quintin, Baja, California.

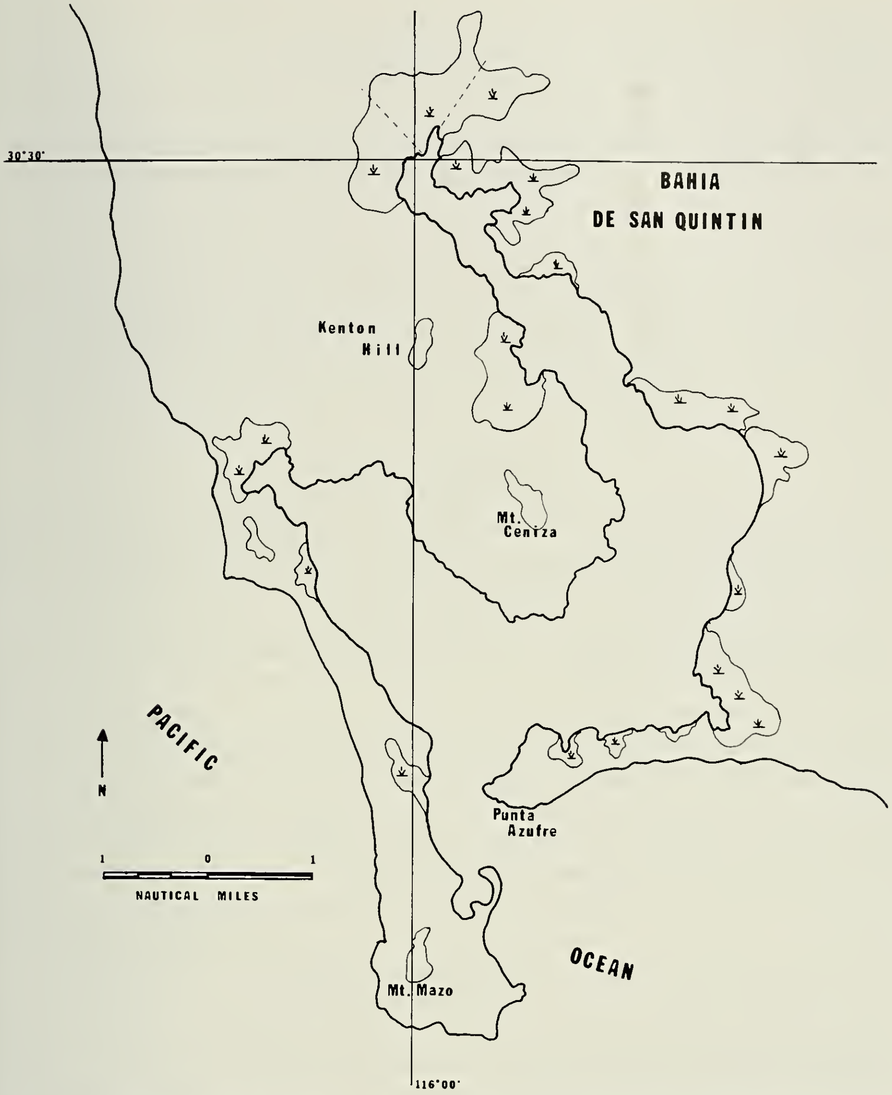

Fig. 2. Map of Bahia de San Quintin. Local landmarks are given their Spanish names. Dotted areas represent the marsh and/or the transition areas studied.

The primary objective of the study of Bahia de San Quintin was to provide the baseline information to make possible the comparisons with disturbed salt marsh ecosystems. Hence, this study could be of use in understanding and countering problems that arise from disturbance and pollution.

The invertebrates of Bahia de San Quintin have received considerable attention (Barnard, 1962, 1964; Keen, 1962; King, 1962; Menzies, 1962; Reish, 1963; Macdonald, 1967), but the emergent vegetation has been only briefly described (Dawson, 1962). Vonder Haar (1972) studied the evaporite environment at Laguna Mormona adjacent to Bahia de San Quintin. Rundel et al. (1972) reported on the upland lichen community surrounding the Bay. Barnard (1962) and Dawson (1962) described the benthic flora of Bahia de San Quintin.

Salt marshes located south of Bahia de San Quintin remain largely unstudied. The salt marsh vegetation of Laguna Guerro Negro and Ojo de Liebo has been briefly described by Phleger and Ewing (1962). An overview of Pacific Coast salt marshes (Macdonald and Barbour, 1974; Macdonald, 1977b; Breckon and Barbour, 1974) includes some general information regarding these Baja California salt marshes.

Of all the studies mentioned, only those done in Newport Bay (Vogl, 1966) and Tijuana Marsh (Zedler, 1977) utilized quantitative methods (Thorsted, 1972). The remaining studies are based largely on partial floral lists or general observations of the vegetation. Except for Newport Bay (Vogl, 1966), the peripheral or transitional vegetation bordering West Coast salt marshes has not been published (Neuenschwander, 1972).

Description of Area

Two types of salt marshes occur in Bahia de San Quintin: 1) extensive littoral marshes occurring in bay cul-de-sacs, large coves, and silted shallows, and 2) limited shoreline marshes occupying eroded shoreline edges, minor bay indentations, and the wet fringes of small valleys (Fig. 1).

Littoral marsh physiography.—The large marshes are fairly level and characterized by extensive drainage channels that dissect the marshes in a snake like fashion with numerous sharp bends and oxbows. The meandering main channels or tidal cuts are usually 2 m or more deep and range from 3–10 m wide. The vertical mud banks are honeycombed with crab (*Hemigrapsus* sp.) burrows and the lower portions support small yellow sponges. The larger channel bottoms are flat and covered with firm muds that support vigorous stands of *Zostera marina.* Water remains in these channels during normal low tides, and crabs, small fishes, and bubble snails are abundant. The outside banks of channel curves are often undercut by tidal flow, and short sections of bank are frequently slumped with the marsh vegetation intact. Just offshore the emergent vegetation forms large areas. Extensive mud flats occur in a few of the marshes.

The smaller, higher elevation channels are up to 3 m wide and 2 m deep and also meander dramatically. Bank sides are similar to those of main channels, but the bottoms tend to be U-shaped and consist of soft gray-brown muds and black ooze with a strong hydrogen sulfide odor. These channel bottoms are exposed during low tides and are generally devoid of vegetation but support numerous California horn snails (*Cerithidea californica*). Some secondary channels in the shallow marshes at the base of Punta Azufre have completely slumped banks and support stands of *Spartina foliosa,* a condition not found elsewhere in the study area.

Primary and secondary channel banks have shoulders that are usually elevated a few cm above the adjacent marsh surface. These mud levees are usually 0.25–1 m in width and are apparently produced as waterborne silts and clays precipitate in the dense *Spartina foliosa* stands that typically line the raised banks.

In some marshes, channel curves have occasionally been cut off, forming shorter channels and leaving dead slough curves and oxbow bends, which appear to remain devoid of vegetation for long periods before being invaded by *Batis maritima*, *Spartina*, and *Salicornia virginica*.

The uppermost drainage channels are shallow, short, and fairly straight. These vary from just a few cm to about 30 cm in depth and are completely vegetated. These tertiary drains usually enter the secondary channels at right angles and at some height above the secondary channel bottoms.

The lower and middle elevations of the marshes contain occasional ''rotten'' spots, small open pockets in the otherwise dense vegetation usually created by suffocating mats of detached *Zostera*. These ''rotten'' spots are most abundant in the Punta Azufre marshes which are downwind from the prevailing northwest winds that push huge drifting quantities of *Zostera* into these marshes. Small vegetation free depressions or salt pans with impaired drainage are less common, being widely scattered in the middle zone of the most extensive marshes.

Exposed mudflats (Doty, 1946) amidst *Zostera* beds and the emergent *Spartina* are usually covered with dense green algal mats composed of species of *Cladophora, Enteromorpha, Vaucheria,* and patches of *Ulva*. Large numbers of California horn shells were observed on and beneath the extensive algal mats. These algae extend throughout the lower littoral and into the middle littoral zone wherever the emergent vegetation is not dense.

The large littoral marshes have eroded mud banks along their open-water edges. In places these mud banks rise vertically 1.5–2 m above the open bay mudflats. They contain numerous invertebrate burrows, often worn smooth by tides and waves, and occasional slumped bank sections. In other places extensive bank erosion has taken place, resulting in *Spartina* covered banks that slope sharply or more gently toward open water. In the shallow marshes at the base of Punta Azufre, these open-water ledges are the lowest, consisting of a hard clay curb averaging about 30 cm in height. These clay banks are devoid of invertebrate burrows and are often free of plant life for 3 m or more inland, whereas other marshes support dense *Spartina* or, less commonly, *Salicornia* to the immediate edges of the eroded banks.

The large marshes are underlain by muds that contain varied mixtures of clay, silt, volcanic ash, sand, and organic matter that are at least 2 m or more deep. The marsh surfaces are firm, except for ''rotten spots,'' salt pans, and channel bottoms, and can be traversed on foot with ease during low tides. The marshes backed by playas and the shoreward portions of marshes contain particularly stable substrates.

An exception to the firm substrates was found in the lava cove marsh in the north end of Bahia Falsa, the west bay arm. Portions of the middle zone of this marsh support sparse and chlorotic stands of annual *Salicornia bigelovii* plants and abundant ''rotten spots'' and shallow salt pans covered by dark platelets of salt and algae underlain by a spongy substrate. These peat like muds remain saturated or charged with water even when the tides have dropped the surrounding water levels.

The ever wet soil surface is firm enough to support the weight of a man, but quakes with each step. A stake can be plunged into the substrate 1–2 m and removed with ease, a feat that cannot be accomplished elsewhere. These boggy sites might relate to subterranean lava dikes that impair drainage, water blockage

Fig. 3. Bahia de San Quintin showing the typical littoral zones of the salt marsh.

created by offshore mud flats, a particularly peaty substrate that has a high water retaining capacity, or to the subsurfacing of fresh waters draining the adjacent volcanic cone and lava beds.

Shoreline marsh physiography.—The fringe marshes are discontinuous and limited to shoreline edges. They tend to be less than 25 m wide and are generally devoid of tidal channels, although they are readily inundated during high tides. Some of the marshes are level, others grade gently toward the Bay, and still others are somewhat terraced. The mud and silt substrates are shallow and firm, usually less than 25 cm thick, and are often overridden by erosional deposits of sand, loam, volcanic ash, and lava from adjacent uplands. In many places these marshes have become established on inundated upland soils.

The bayward edges of these narrow marshy strips are abrupt and consist of water worn clay ledges, exposed sand bars or lava rock rubble, stratified beach rock created by the freshwater deposition and lamination of calcium carbonate in sand and loam, or in a few places, beaches stabilized by accumulations of mollusk shells. Shoreline marshes which are exposed to constant wave action or strong tidal currents along the open water edges and generally lack *Spartina.*

Transition zone physiography.—The most common ecotones between marshlands and upland vegetations occur on variable slopes in stabilized sandy loam hills. A few marshes are backed by abrupt aa′ lava flows or sand dunes. Recently disturbed dunes have spread directly into the marshlands as a result of strong northwest winds. Most of the transition zones occur on relatively steep slopes, and vegetation changes are abrupt.

The transition in Punta Azufre marsh extends onto a salt playa. The slope is nearly level and the transition zone is about 50 m wide. This transition is underlain, at about 21 cm depth, with a salt layer or pan.

Fig. 4. Bahia de San Quintin showing the typical transitional vegetation with the capillary fringe and upland influence.

Geology and climate.—The marine and quaternary geology of Bahia de San Quintin has been reported by Gorsline and Stewart (1962).

A dry Mediterranean climate characterizes most of Baja California, but the presence of cold upwelling water along the coast (Dawson, 1951) results in a high frequency of fog (Meigs, 1966). Few climatic records are available, but temperatures at Santa Maria del Mar, just inland from the Bay, range from 13°–23°C annually (Hastings, 1964, 1965; Hastings and Humphrey, 1969). The annual rainfall is reported by Gorsline and Stewart (1962) to be between 5–10 cm per year, usually occurring in the winter.

The wind is generally present in the mornings and early evenings, and is predominantly from the northwest. These winds often move offshore fog clouds rapidly over the Bay. Winds peak from March through June with 20–30 knot velocities (Barnard, 1961). Tropical hurricanes occasionally make their way up the coast from the southwest during late summer and produce unusual amounts of rainfall.

Methods

The vascular plants present in the salt marshes of Bahia de San Quintin were identified according to Munz (1959) and Shreve and Wiggins (1964). Voucher specimens are on file in the California State University, Los Angeles (CSULA) herbarium.

Seven littoral salt marshes and 14 upland transition zones were selected for quantitative study. Each of the selected marshes was divided into three littoral (Fig. 3) or marsh zones and one transitional zone (Fig. 4). Seven additional transition zones were sampled to include the variability of the upland vegetation. The lower littoral zone is characterized by alternating periods of daily inundation and exposure and is always bound on the bayside by open water. The middle littoral zone is slightly higher and drier than the lower zone, but has characteristically soggy or water logged soils due to capillary action from tidal waters. It is inundated regularly during neap tides, storms, and windy weather. The upper littoral zone borders the uplands and is flooded only by unusually high or storm tides and lies above mean high tide. Soils are wetted during the higher tides, and soils and plants are subject to salt spray during rough weather. The transition or maritime zone (Vogl, 1966) is the ecotone between the upland vegetation and the lowland littoral zone vegetation. This zone is not inundated by tidal or storm waters. The lower limits of this zone are clearly delimited by a line of debris, flotsam, and dead *Zostera marina* deposited by the highest water of the year (referred to as the debris or storm line). The transition zone was arbitrarily limited to a 30 m wide perimeter inland of the debris line or the salt marsh edge.

Each zone in each study marsh was sampled with 160 (25×25 cm^2) quadrats. This quadrat size was found to be the maximum usable to obtain meaningful frequencies (less than 100%) for the common salt marsh species (Vogl, 1966). Percent plant cover was visually estimated for 16 quadrats in each zone.

Transition zones were sampled differently to help determine the vegetation position and zonation within each transition zone, four representative line intercepts were taken on different slopes. The line intercept samples were obtained by placing a 30 m tape at right angles to the shoreline, starting at the debris line. The horizontal distance each species occurred above this high tide mark, the amount of the line covered by each species, and the slope angle was recorded.

Depth to soil moisture was taken in each transect of the transition zone. Depth to the capillary fringe of the salt marsh water table was obtained by boring soil cones at 1 m intervals along 30 m lines placed at right angles across the transition zone. Each hole was dug to a maximum of 2 m.

Water retaining capacities were obtained for the various transitional soil types using the method presented in Curtis and Cottam (1962).

Results

The phytogeographic area of Bahia de San Quintin (Wiggins, 1960) encompasses coastal salt marsh, alkali flat, coastal strand, and coastal desert scrub (Shreve and Wiggins, 1964; Munz, 1968). The last two communities comprise the upland vegetation around the Bay. The transition zone between the salt marsh and the surrounding uplands contains floral elements of all four communities.

The marsh flora is composed of only 17 emergent phanerogam species (Table 1). All of the species, with the possible exception of *Mesembryanthemum nodiflorum,* are indigenous (Moran, 1950). The transitional flora is represented by 33 species from 28 genera and 19 families. Of these species, 12 are characteristically found in salt marsh, and 21 are normally associated with desert and coastal uplands.

Frequency·Cover.—Average frequency and cover values (Table 1 and 2) show that only eight species are common in the marshes. *Salicornia virginica, Spartina foliosa, Batis maritima,* and *Monanthochloe littoralis* are dominants, with *Frankenia grandifolia, Salicornia subterminalis, Suaeda californica* and *Salicornia bi-*

Table 1. Average percent frequencies for all species in each zone. Frequency range for the seven stands for the littoral zones and 14 stands in the transition zone are in parentheses.[1]

	Littoral			
Species	Lower	Middle	Upper	Transition
Spartina foliosa	90.8% (86–97)	6.9% (0–21)	—	—
Salicornia bigelovii	0.8% (0–6)	21.5% (0–96)	0.1% (0–1)	—
Triglochin concinna	0.8% (0–6)	9.5% (0–33)	0.1% (0–1)	—
Salicornia virginica	34.4% (20–65)	86.7% (71–93)	52.2% (20–86)	3.7% (0–21)
Batis maritima	27.0% (13–36)	55.2% (9–86)	4.9% (0–16)	0.0% (0–0)
Frankenia grandifolia	6.8% (1–16)	29.0% (14–46)	43.3% (24–84)	4.6% (0–16)
Suaeda californica var. *californica*	4.1% (1–8)	20.4% (5–31)	25.8% (9–50)	1.4% (0–8)
Jaumea carnosa	1.3% (0–5)	3.3% (6–18)	6.3% (0–28)	0.2% (0–2)
Salicornia subterminalis	0.1% (0–1)	0.9% (0–4)	46.5% (5–81)	38.7% (13–74)
Monanthochloe littoralis	—	27.4% (0–12)	75.1% (22–97)	42% (7–49)
Limonium californicum var. *mexicanum*	—	4.0% (0–12)	13.7% (0–34)	7.3% (0–62)
Cressa truxillensis var. *vallicola*	—	—	3.5% (0–16)	0.9% (0–7)
Atriplex watsonii	—	—	1.5% (0–4)	3.9% (0–18)
Cuscuta salina	—	0.4% (0–3)	0.1 (0–1)	—
Mesembryanthemum nodiflorum	—	—	0.1% (0–1)	2.6% (0–25)
Frankenia palmeri	—	—	—	31.7% (4–68)
Lycium brevipes	—	—	—	6.2% (3–11)
Atriplex julacea	—	—	—	8.8% (1–24)
Haplopappus venutus	—	—	—	0.1% (0–1)
Euphorbia mesera	—	—	—	0.7% (0–4)
Dudleya brittonii	—	—	—	0.4% (0–2)

Table 1. Continued.

Species	Littoral Lower	 Middle	 Upper	Transition
Aesculus parryi	—	—	—	0.1% (0–1)
Distichlis spicata	—	—	—	0.4% (0–5)
Juncus acutus	—	—	—	0.1% (0–1)
Allenrolfea occidentalis	—	—	—	0.3% (0–3.2)
Mammillaria dioica	—	—	—	0.1% (0–1)
Machaerocereus gummosus	—	—	—	0.1% (0–1)
Echinocereus maritimus	—	—	—	0.1% (0–1)
Lichens	—	—	—	6.9% (1–17)
Green algae mat	67.8% (6–90)	48.6% (0–94)	—	—
Bare ground	0.6% (0–3)	0.6% (0–1)	0.2% (0–1)	10.4% (3–26)

[1] Each value in the littoral zones is based on 1120 quadrats and each value in the transition zone is based on 2240 quadrats.

gelovii less frequent. Frequency Cover of the common species varied in the different zones within the marsh zonation.

The lower littoral zone contains only 9 species, and is dominated by *Spartina* (90.8%·47.0%), *Salicornia virginica* (34.4%·33.1%), and *Batis* (27.0%·6.4%). *Spartina* characterizes the lower littoral zone. Its growth is particularly green and robust in comparison to stands farther north, perhaps indicating the absence of toxic pollutants in the Bay (Mobberley 1956). *Spartina* pioneers the algae covered mudflats and extends to the upper or landward limits of daily inundation. *Salicornia virginica* and *Batis* also occur throughout this zone. Sometimes they are thinly dispersed throughout the understory of the uniformly tall (1–1.35 m) *Spartina* grass stems, but they may occur in localized dense colonies where the *Spartina* is sparse or they may grow on the open mudflats beyond the typically dense band of *Spartina*.

The middle littoral zone contains 12 species. *Salicornia virginica* (86.7%·22.7%) dominates, with lesser amounts of *Batis* (55.2%·16.8%) (Table 1 and 2). These most widespread littoral species transcend the middle zone in both directions. *Salicornia virginica* dominates this zone with its robust and dense clonal growth. *Batis* typically pioneers poorly drained pans and occupies low flats, slight depressions, and old drainage channels.

Table 2. Average percent cover for the common species in each zone. The range for all seven stands is given in parentheses.[1]

	Littoral			
Species	Lower	Middle	Upper	Transition
Spartina foliosa	47.0% (42–53)	1.0% (0–4)	—	—
Salicornia virginica	20.2% (6–43)	33.1% (27–61)	22.7% (5–58)	2.5% (0–21)
Batis maritima	6.4% (4–8)	16.8% (3–35)	1.2% (0–6)	—
Frankenia grandifolia	2.3% (0–5)	9.9% (2–17)	13.8% (0–35)	1.5% (0–7)
Jaumea carnosa	1.1% (0–8)	1.0% (0–4)	4.3% (0–24)	—
Suaeda californica var. *californica*	1.0% (0–3)	6.9% (3–11)	8.3% (0–22)	—
Triglochin concinna	—	5.2% (0–25)	—	—
Limonium californicum var. *mexicanum*	—	2.1% (0–6)	6.0% (0–17)	1.6% (0–13)
Salicornia bigelovii	—	6.9% (0–41)	—	—
Monanthochloe littoralis	—	1.0% (0–8)	45.7% (1–81)	22.0% (0–55)
Salicornia subterminalis	—	—	22.7% (0–45)	20.5% (6–62)
Atriplex watsonii	—	—	1.6% (0–7)	2.2% (0–16)
Frankenia palmeri	—	—	—	19.0% (6–30)
Lycium brevipes	—	—	—	2.7% (0–6)
Atriplex julacea	—	—	—	2.0% (0–6)
Lichens	—	—	—	2.2% (0–9)
Green algae mat	81.8% (59–100)	22.4% (0–56)	—	—
Bare ground	3.0% (0–11)	14.0% (3–30)	8.7% (0–24)	29.2% (12–42)
Zostera litter	3.0% (0–10)	—	1.2% (0–9)	—

[1] Each value is an average based on 1120 quadrats for the littoral zones and 2240 quadrats in the transition zone.

Of the less frequent species, *Frankenia grandifolia* occurs in almost pure stands in soggy areas, while *Monanthochloe littoralis* and *Suaeda californica* are most frequent on slightly higher and drier ground. *Salicornia bigelovii* is confined to low, wet flats and "rotten spots," sometimes occurring in pure stands or sharing the sites with *Triglochin concinna* and *Batis*. *Salicornia virginica* often occurs on the edges of, or occasionally within, these poorly drained flats. *Cuscuta salina* parasitizes *Salicornia virginica* in this zone, particularly, growing on drier sites. Green algae have a frequency of occurrence of nearly 50% (Table 1).

The upper littoral zone has 14 species, with *Monanthochloe* (75.1%·45.7%) dominant (Table 1 and 2). *Salicornia subterminalis* (46.5%·2.7%) attains its highest frequency cover in the upper and drier sections, while *Salicornia virginica* is most common in the lower and more moist regions. *Frankenia* frequently occurs in pure aggregations on slight rises, or intermingles with *Monanthochloe* and *Salicornia virginica* in wetter areas. *Suaeda* and *Limonium californicum* occur as scattered individuals throughout this zone, particularly on drier sites. *Jaumea carnosa* occurs in wet and dry areas, spreading by vegetative runners with weak upright branches. Exceptionally dense and vigorous aggregations of *Jaumea* grow on rough lava sites overlain with sandy silt. *Cressa truxillensis* mixes with *Monanthochloe* on the driest places. *Cuscuta* parasitizes *Cressa* and *Salicornia virginica* growing on dry sites, but was not observed on any other species. *Atriplex watsonii* and *Mesembryanthemum nodiflorum* were only rarely encountered along the extreme landward edge of this zone. The upper limits of this zone are marked by a band of debris and decomposing *Zostera* litter.

The transition zone is dominated by *Salicornia subterminalis* (38.7%·20.5%) and *Monanthochloe* (42.7%·22.0%). Nine other salt marsh species have frequencies of occurrence of less than 8% (Table 1), and are concentrated in the lowest portions of this ecotone zone near the debris line. *Salicornia subterminalis* also occurs in alkaline substrates around the Bay and in alkali flats near the coast.

The dominant species in the upland parts of the transition zone are *Frankenia palmeri* (31.7%·19.0%), *Atriplex julacea* (8.8%·2.0%), and *Lycium brevipes* (6.2%·2.7%). *Frankenia* is the most widespread species, and consistently occurs lower in the transition zone than the other upland species. An additional 13 upland species have frequencies less than 2% (Table 1). *Mesembryanthemum nodiflorum* (2%) only occurs in the disturbed portions of upper sandy loam transitions. The coastal scrub species *Euphorbia mesera,* is found in ash, cinder, and sandy loam substrates associated with volcanic outcrops. Lichens are attached to rocks, soils, and some plants in the upper portions of the transition zone (Rundel et al., 1972).

Average percent cover values generally correspond to frequency values in the littoral and transition zones. Total cover is 74.5% in the transition zone, 78.0% in the lower littoral zone, 83.9% in the middle littoral zone, and 126.3% in the upper littoral zone. Both cover and the number of species increased from the lower or wetter to the higher or drier portions of the marsh, as found in Newport Bay (Vogl, 1966). However, in the transition zone, cover decreased from the lower portion near the marsh toward higher elevations. Combined salt marsh species account for 48.3% of the cover in the lower part of the transition which is more than the cover of the combined upland species (25.8%).

The dominant upland species are scattered throughout the upper portion of the transition. *Frankenia palmeri* extends the lowest toward the marsh (Fig. 5). *Fran-*

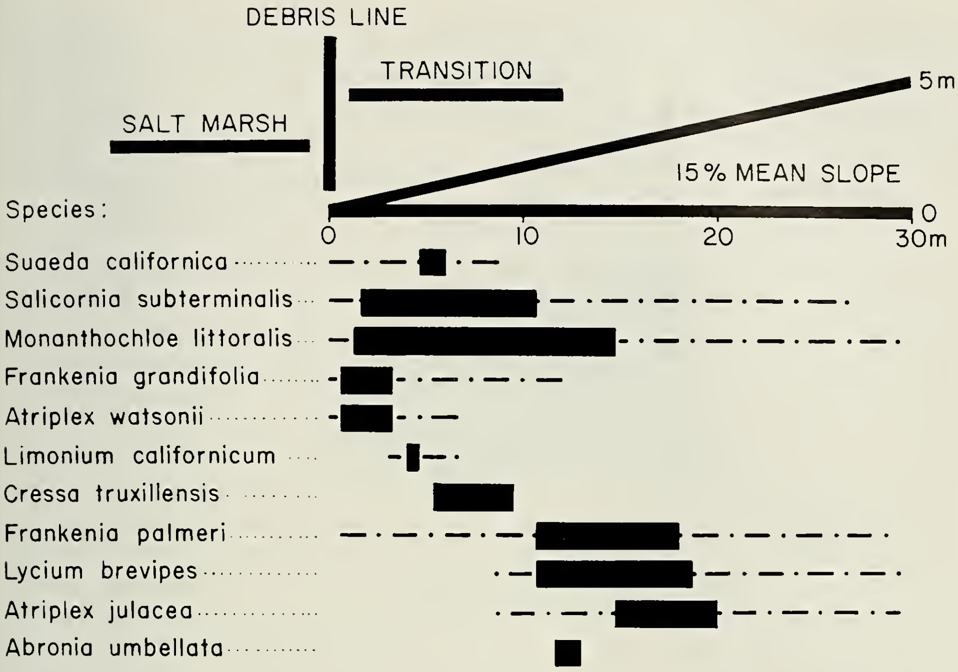

Fig. 5. Dominant position for each species within the transition zone (30 m) on the mean slope. Cover is expressed by standard error of the mean as a solid bar and the ranges are the dotted lines.

kenia palmeri and *Lycium* have approximately the same range (10.5–18.0 m from debris line) and approximately the same cover (15.8%). *Atriplex julacea*'s cover (7.3%) is about half that of *Frankenia palmeri* and *Lycium*. *Atriplex julacea* ranges higher in the transition zone (15.9–19.8 m) than the other upland dominants.

The line intercept cover in the transition zone is graphically represented in Figure 5. Species cover, composition and vertical stratification vary with the slope. Slopes on sandy loam substrates range from 2–30%.

The width of the transition is a result of slope. Steep slopes produce narrow transitions. Species overlap and vertical stratifcation are confined to lower portions of the transition zone. Steep slopes also support more extensive upland cover, whereas gentle slopes produce long transitions extending species overlap and vertical stratification farther inland. Gentle slopes contain more cover of salt marsh species. Salt marsh species are essentially confined to the lower portion of the transition defined by the capillary fringe of the Bay, while upland species occupy the upper portion. Plants in the lower portion of the transition are low in stature, dense in cover, and luxuriant in growth. Plants in the upper portion of the transition are sparse but larger in stature.

Upland cover values taken by line intercepts (Fig. 5) do not correspond to those taken by quadrats (Table 2), indicating variability in the upland vegetation. Cover values for the dominant salt marsh species are approximately the same for line intercepts as for quadrats, indicating less variability.

Three common salt marsh species are present in line intercepts, and are re-

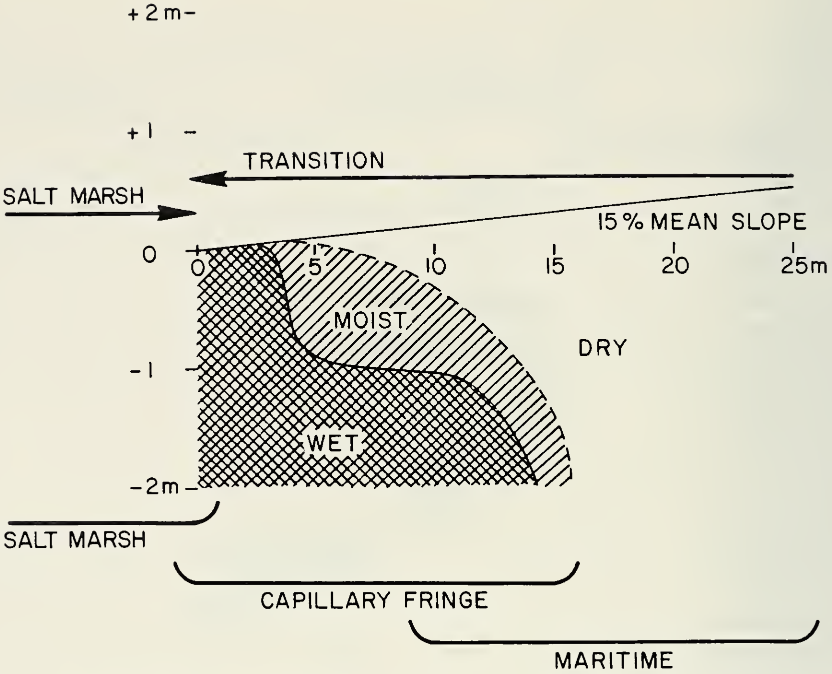

Fig. 6. Average depth to wet, moist and dry sandy loam soil taken by soil cores. The vegetation position of Fig. 5 can be overlaid on the soil moisture characteristics of Fig. 6 so that the transition can be subdivided into the capillary fringe and maritime zones.

stricted to the first 12 m inland, the marsh debris line. Salt marsh species on the lowest sandy loam slopes extend a maximum of 30 m above the debris line. This maximum range is seldom attained.

Transition soils.—Depth to wet or moist soil is proportional to the slope. Depth to moisture increased with the horizontal and vertical distance from the Bay (Fig. 6). The lower portion of the transition, occupied by salt marsh type species, is an area in which roots of these plants receive moisture from the Bay, at least during high tide.

A wetted soil surface is a visual expression of the capillary fringe zone around the Bay. The inland distance from the Bay for the capillary fringe is about 4.75 m. At that distance, the soil moisture suddenly drops to a depth of .75 m where it then extends horizontally at that depth for 6 m. Beyond 10 m from the debris line, the soil moisture suddenly drops off below the rooting depth of most upland species.

Exceptions to the above soil moisture regime are promoted by formations of salt pans. A salt pan was formed in one area on a shallow slope (3%) beginning about 5 m inland from the Bay and extending the entire length of the transition at .2 m below the soil surface. The salt pan induces the extension of salt marsh vegetation into the transition area normally occupied by upland species.

The extension of salt marsh vegetation inland appears to be a result of the soil particle-size distribution and water holding capacity. Sandy loam soil near the Bay had a water holding capacity of 33.4%, but at an elevation above the Bay, it was higher (40.8%). Dune and volcanic substrates have lower water holding capacities with 32.4 and 24.1%, respectively. The higher the water holding capacity, the more well developed and the farther inland the capillary fringe extends. Also, the higher the water holding capacity, the richer and more abundant is the upland vegetation. However, with lower water holding capacity, the upland vegetation is more frequently mixed with salt marsh vegetation.

Discussion

The vegetation of Bahia de San Quintin is of interest because of its almost pristine state and its unique position within a fog-desert. Local upwellings of relatively cool waters off the Bay produce frequent fog, reduce rain along the immediate coastline, and produce enriched waters. Strong and persistent onshore winds remove water, soils, sediments, and salts (Brongerama and Sanders, 1948; Dawson, 1951; Barnard, 1961; Phleger and Ewing, 1962). As a result, the bayside vegetation is sparse and has a large number of lichens (Rundel et al., 1972). Field observations suggest that the prevailing rapidly moving fogs contribute moisture to the transitional and upland plants and soils in the form of condensation and fog drip, but that reproduction in these uplands is only observed after the infrequent winter rains. Except for annual species, seed germination and new plant establishment in the littoral zone is probably confined to the unusual wet periods produced by tropical hurricane rains, since many salt marsh plants need abundant fresh water for successful sexual reproduction (Barbour, 1970; Barbour and Davis, 1970).

The vegetation of salt marshes characteristically has few species with large numbers of individuals per species, illustrating the principle that extreme environments tend to produce simple systems. In Bahia de San Quintin, the salt marshes are dominated by the same few families and genera that dominate salt marshes worldwide.

Of the 17 salt marsh species found in Bahia de San Quintin, five represent tropical floristic elements that occur as far north as Santa Barbara, California. *Monanthochloe littoralis* and *Batis maritima* are the most important tropical elements. The remaining 12 species are widespread with ranges extending to San Francisco Bay, and some occur as far north as Alaska. When Pacific Coast marshes are compared (Macdonald and Barbour, 1974; Barbour et al., 1975; Macdonald, 1977), those of Bahia de San Quintin and Southern California contain more species than the more northern marshes.

Marsh gradients and patterns.—The zonal patterns apparent in the littoral environment are closely tied to elevational gradients. Where the gradients are gentle, the zones are expansive and diffuse as in the large littoral marshes, and where the elevation changes are sharp, the zones are narrow and distinct as in some of the shoreline marshes. Small changes in elevation can result in large changes in exposure or inundation, salinity, pH, temperature, and the vegetation (Stevenson and Emery, 1958). Numerous studies have demonstrated that littoral vegetational responses are largely a result of the inundation-exposure regime working in concert with physical gradients (Purer, 1942; Doty, 1946; Reed, 1947; Bourdeau and Adams, 1956; Chapman, 1960; Adams, 1963; Vogl, 1966; Zedler, 1977).

These frequency distributions (Fig. 7) illustrate that most of the common

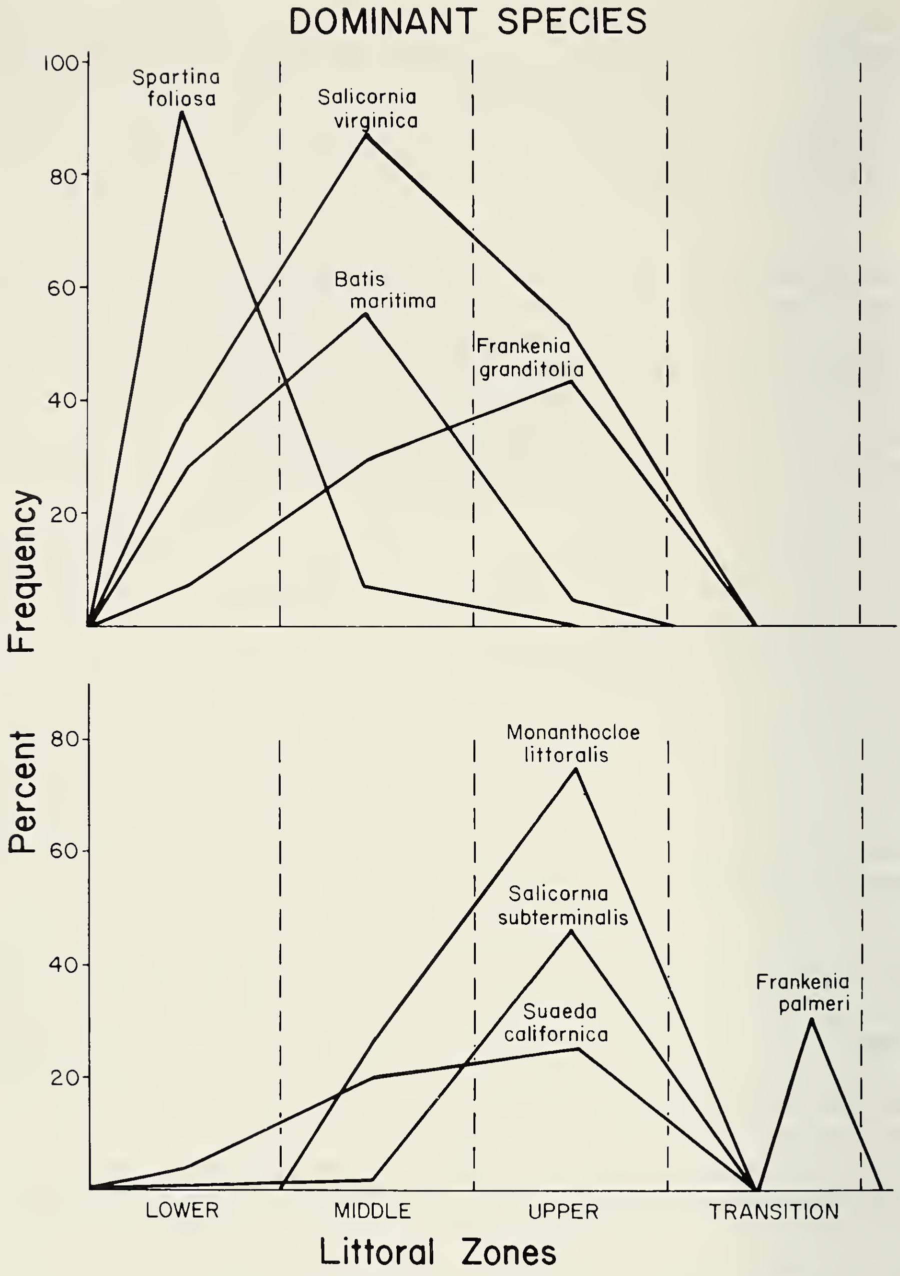

Fig. 7. Average percent frequencies of the dominant species plotted by zones.

species are not restricted to one zone. *Salicornia virginica*, has the broadest amplitude as in Newport Bay, California (Vogl, 1966). In some places *Salicornia virginica* even thrives on open mudflats below the *Spartina* belt; it also grows vigorously in some of the highest and driest parts of the upper littoral zone.

Batis maritima is also a widespread species, dominating all low, wet, and poorly drained areas, regardless of zone. *Frankenia grandifolia* is present in all three zones but favors higher and drier sites. *Spartina* and *Monanthochloe* represent low and high extremes within the emergent vegetation. *Frankenia palmeri* is restricted to the transition or maritime zone.

Apparently, the vegetational composition of the salt marsh is not a cohesive entity explained simply by zonation, but is a complex of individual species responding to environmental gradients. Relatively simple elevational gradients are altered by rain runoff, sediment deposition, tidal action, wave action, storms, erosion, and changing water levels. The resulting micro-topographic differences create variable vegetational patterns as each species selects favorable sites.

Vegetational patterns dictated by various environmental gradients are complicated by the vegetative reproduction common to almost all salt marsh species. Huge clones sometimes give the appearance of zones. Individuals often spread vegetatively into less favorable sites.

Transition zone.—Dominant upland species found in the upland-marsh ecotone are succulent halophytes, and all species appear to be salt tolerant (Boyce, 1954). It appears that the salt marsh species present in the lower transition zone are controlled by the same factors that affect them in the salt marsh proper, namely salt concentrations, soil aeration, and saltwater inundation (Chapman, 1960; Vogl, 1966). Inundation in the transition zone is, however, reduced to the capillary fringe activity of saltwater, and salt concentrations are largely products of evaporation, capillary action, salt spray, and fog drip. Hence, distribution of species at Bahia de San Quintin in transitional areas is not random and species are considered to be regulated by these environmental factors.

The presence of capillary extensions of tidal waters appears to be a critical factor controlling the distribution of species in the ecotones. Near-surface capillary moisture promotes the growth of salt marsh species, particularly *Salicornia subterminalis* and *Monanthochloe,* or perhaps excludes the growth of upland species, thereby allowing the salt marsh species to extend above the debris line and salt marsh proper. Steep slopes reduce the sub-irrigation properties of the tidal waters and permit the growth of upland species which are usually widely spaced *Frankenia palmeri* and *Atriplex julacea.* Slightly higher transitional areas support *Lycium brevipes* with lichen covered branches. The capillary action appears to extend slightly higher in the finer silty ash and sandy loam soils than in the sand and lava substrates.

Investigation of this upland marsh ecotone indicates that the sub-irrigation and capillary action of tidal waters is a significant factor regulating species distributions. Therefore, the transition should be divided into a capillary fringe zone and a maritime zone.

The transition appears to be the focal point of animal activity for both the terrestrial and salt marsh fauna of Bahia de San Quintin. Numerous animal trails cross the transition. During high tides and severe storms, the capillary fringe may provide critical cover-habitat for salt marsh birds. Also, some upland animal species apparently feed in the marsh. Preliminary observation suggests that the transition is an important area for animal use, but this area has not been studied in any Pacific West Coast salt marsh.

Role of Zostera.—*Zostera marina* occurs in deeper water beyond the emergent species. *Zostera* beds in the Bay have been described and mapped by Dawson (1962). Contrary to the usual way that *Zostera* grows on the Pacific Coast, San Quintin *Zostera* beds are exceptionally dense and grow in unusually shallow waters that expose plants and mud during lowest tides.

A factor thought to be responsible for the biotic initiation of salt marshes is the establishment of *Zostera marina* beds in the open water of enclosed bays, estuaries, and lagoons. Beds of *Zostera* retard the erosional tidal flux and result in a continual and ever increasing accretion of sediments. This accumulation of sediments usually resists storm excavation because of the extensive perennial *Zostera* roots and initiates the successional development of an open body of water that may culminate in terrestrial vegetation.

Zostera also contributes to the enrichment of coastal waters by the annual productivity of above ground plant parts that die back each winter and form detritus (Redfield, 1965). Often, during violent storms or die-back periods, huge windrows of dead *Zostera* are carried landward onto the emergent vegetation, particularly in the *Spartina* belt. The windrows mat down the vegetation and eventually kill the underlying plants causing bare spots in the emergent vegetation. These openings are eventually revegetated, usually by *Batis* and *Salicornia virginica*. These gap phase perturbations and their resulting revegetation are probably responsible for the slightly larger number of species in the lower littoral zone of Bahia de San Quintin compared to Newport Bay where *Zostera* is uncommon (Vogl, 1966). In some locations, e.g., the downwind Punta Azufre marshes, *Zostera* debris piles completely kill off the bayside emergent vegetation, thus exposing extensive mudflat edges to erosional forces of tides and waves.

Occasionally dried *Zostera* leaves resist decay and become incorporated into mud and silt deposits, enhancing their ability to withstand erosion. The annual increments of decomposed *Zostera* products must also contribute to the enrichment and siltation of the emergent salt marsh vegetation. Windrows of *Zostera* litter persist year-round at the upper debris line, and were noted to serve as protective cover for insects, marine invertebrates, small mammals, and birds. Previous salt marsh studies have been conducted in locations where *Zostera* beds were absent or severely disturbed, and therefore, have overlooked the role that *Zostera* plays in the ontogeny of Pacific Coast salt marshes. The role of *Zostera* needs further study to determine these relationships.

Acknowledgment

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Gametogenesis and Embryonic Development in the Calcareous Sponges *Clathrina coriacea* and *C. blanca* from Santa Catalina Island, California

Marion Fischel Johnson

Abstract.—Gametogenesis and embryonic development of *Clathrina coriacea* and *C. blanca,* two closely related calcareous sponges from Santa Catalina Island, California, are described. Oogenesis is asynchronous in both species. Spermatogenesis was not observed. Cleavage is total and equal, resulting in the formation of a blastula larva. The larva of *C. coriacea* contains one large posterior granular cell, whereas two posterior granular cells are present in the larva of *C. blanca.* Migration of the larval blastomeres into the blastocoel begins while the larva is in the tube of the parent sponge.

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The life histories of *Clathrina coriacea* (Montagu) and *C. blanca* (Miklucho-Maclay), two closely related calcareous sponges from Santa Catalina Island, California, were studied to clarify their systematic affinity (Johnson, 1976). Minchin (1900), Topsent (1936) and Borojević (1967), among others, treated *C. coriacea* and *C. blanca* as separate species. Burton (1963), on the other hand, believed that the two species names were synonymous.

Lévi (1956) utilized differences in embryological development and breeding period to separate two morphologically identical sponges of the genus *Halisarca* into *H. dujardini* and *H. metschnikovi.* This paper reports the findings of a comparative study of gametogenesis and embryonic development in *C. coriacea* and *C. blanca.*

Methods

Clathrina coriacea and *C. blanca* were studied at Santa Catalina Island from April 1973 through October 1975. The sponges were collected at weekly intervals during the reproductive period in order to obtain detailed information on gametogenesis and embryonic development. Most of the specimens were obtained from a submarine grotto and the Santa Catalina Marine Biological Laboratory pier in Big Fishermans Cove.

Collection of the sponges involved carefully removing them from the attachment surface with forceps and placing them in labelled plastic bags. The specimens were immediately transferred to sea water Bouin's Fixative for preservation of the sponge and decalcification of the spicules. The spicules were dissolved to facilitate observation of the reproductive structures and histological procedures. After decalcification was complete (24 to 48 hours) the sponges were transferred to 70% ethanol. They were then observed under a dissecting microscope for the presence of oocytes. Observations of the location of the oocytes within each sponge also were recorded.

A small piece of each sponge, or the whole sponge when it was less than 5 mm in size, was used for histological study. The sponges were dehydrated, stained temporarily with a weak solution of Fast Green in 70% ethanol, embedded in Paraplast (Sherwood Medical Industries) and sectioned at 8 μm. Every fifth or tenth section, depending on the size of the embedded piece, was mounted on a glass slide with a minimum of 30 sections from each sponge. Minute specimens were sectioned serially. The slides were stained with Ehrlich's Hematoxylin and counterstained with Eosin.

Results

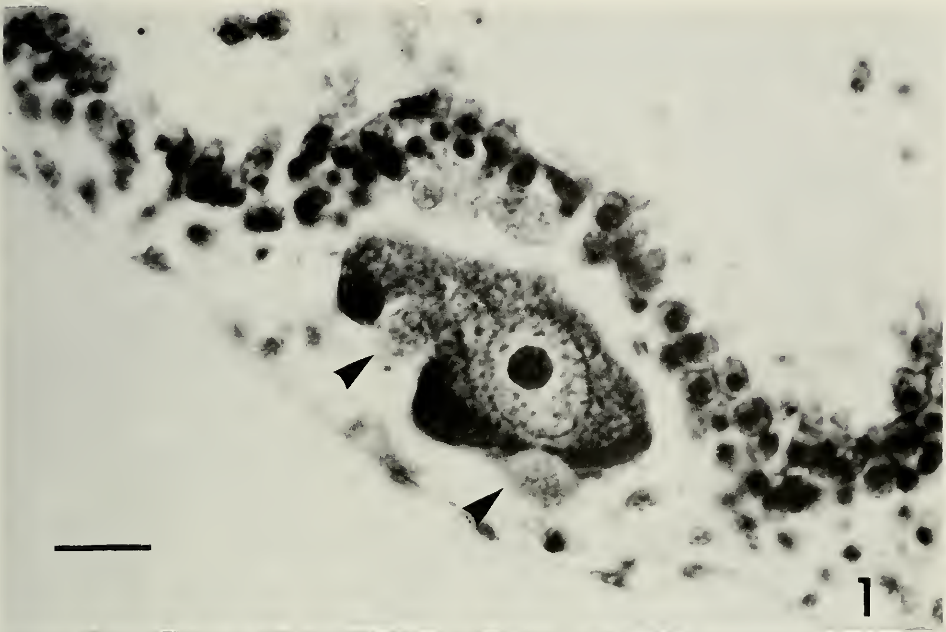
Reproductive Season.—Maturing oocytes were observed in *C. blanca* between April and June in 1973 and 1974, and between April and August in 1975. In *C. coriacea* reproductive elements were seen from July to September in 1973, from July to August in 1974 (specimens were not collected during September and October), and from July through October in 1975 (Johnson, 1978).

Oogenesis.—The process of oocyte development is similar in *C. coriacea* and *C. blanca.* The young oocyte can be distinguished from other nucleolate cells by its strongly basophilic staining cytoplasm, large nucleus and nucleolus surrounded by a deeply staining nuclear membrane. As the oocyte grows it begins to push the surrounding layer of choanocytes into the tube of the parent sponge. Oocytes larger than 30 μm apparently phagocytize the surrounding eosinophilic amebocytes (Fig. 1). These amebocytes are common in specimens with developing oocytes, but rare in nonreproducing sponges. The length of the eosinophilic cells varies from 7 to 10 μm in *C. coriacea* and *C. blanca.* Although there is no distinction in the dimensions of the eosinophilic amebocytes between the two species, noticeable differences exist in the eosinophilic granules. In *C. coriacea* the eosinophilic amebocytes are filled with numerous highly refractile eosinophilic staining granules. In *C. blanca,* on the other hand, the granules are smaller, less refractile and less abundant. Continued growth of the oocyte results in a cell highly granular in appearance (Fig. 2). The maximum length recorded for a mature oocyte of *C. coriacea* was 90 μm. Oocytes 100 μm in length were seen in *C. blanca.*

There is no apparent synchronization of oogenesis within the breeding population of the two species. Some of the specimens collected at the same time contain no oocytes, some have large oocytes and others contain embryos or larvae. Occasionally small and large oocytes, oocytes and embryos or larvae occur in the same sponge. The different stages of development are generally found in different regions of the sponge.

Spermatogenesis.—All of the specimens collected during the reproductive season were examined for stages of spermatogenesis. No sperm or spermatic cysts were seen in the two species.

Fertilization.—The process of sperm transport to the oocyte was not observed with certainty in *C. coriacea* or *C. blanca.* Occasionally a small deeply staining ovoid structure enclosed within a vesicle was seen in a choanocyte near the oocyte. It resembled Tuzet's figure of a spermatozoan in the choanocyte (1947:plate 1, fig. 17). Some cells between the choanocyte layer and the oocyte appeared to contain two nuclei. According to Tuzet (1947:plate 1, fig. 13), one of the "nuclei" is actually a spermatic vesicle in the cytoplasm of a carrier cell. On



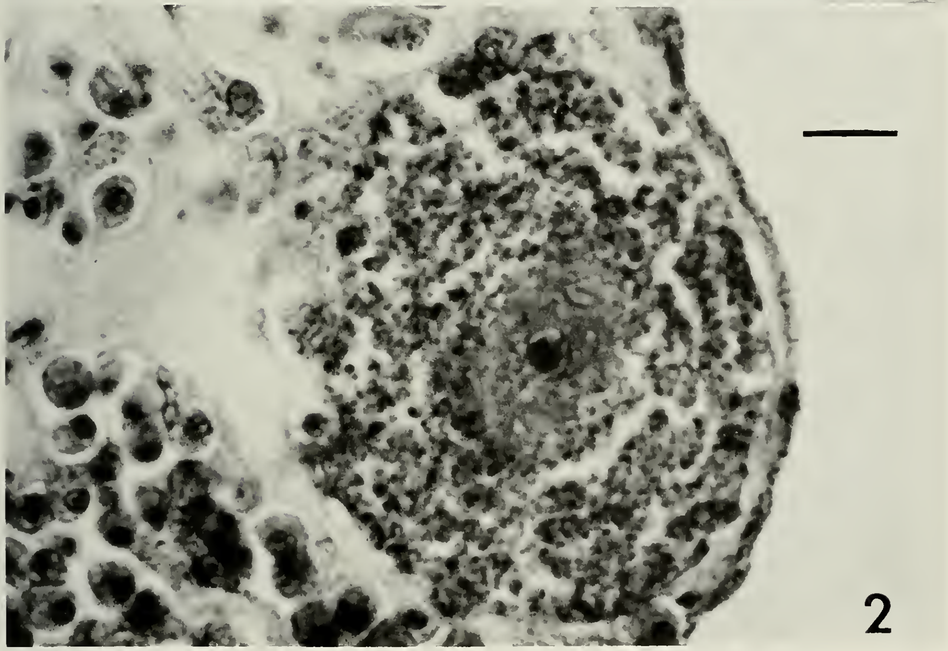
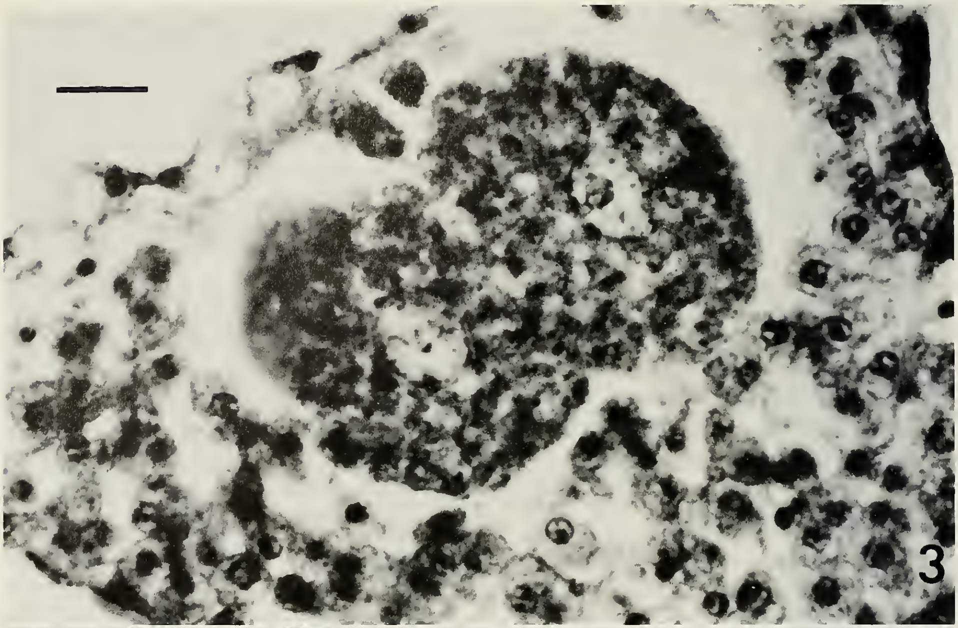


Fig. 1. Oocyte of *Clathrina blanca* phagocytizing eosinophilic amebocytes (arrows). Scale, 10 μm.

Fig. 2. Large granular oocyte of *Clathrina coriacea*. Scale, 10 μm.

rare occasions an oocyte contained two deeply staining masses within a vesicle. These structures resembled Tuzet's figure of the spermatozoan within its vesicle at the periphery of the oocyte (1947:plate 1, fig. 19). Fertilization was not seen in either species.



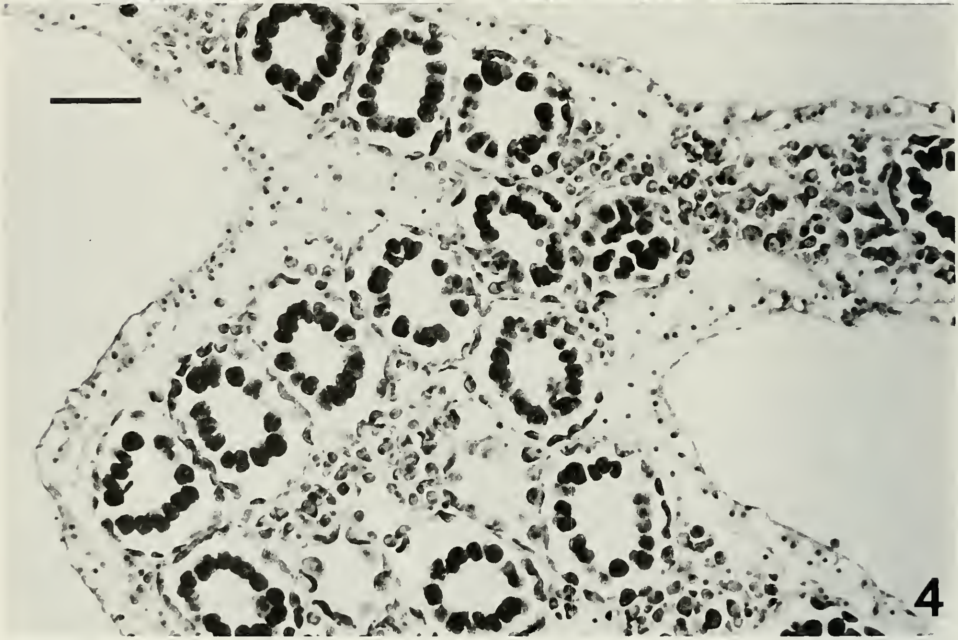


Fig. 3. Two cell stage of cleavage of *Clathrina blanca*; note the nucleus and large nucleolus. Scale, 10 μm.

Fig. 4. Young embryos of *Clathrina coriacea*; note the flattened, elongated cells surrounding each embryo and the unorganized appearance of the parent tissue. Scale, 50 μm.

Embryonic Development.—Cleavage in *C. coriacea* and *C. blanca* is total and equal. The two cell stage, illustrated in Fig. 3, shows the granular cytoplasm, and the nucleus and nucleolus. In the four cell and eight cell stages further equal divisions occur. After the eight cell stage a blastula is formed. The young blastula embryo is composed of cells, approximately 12 μm in dimension, surrounding a large blastocoel (Fig. 4). Each embryo is enclosed within the parent tissue by flattened elongate cells. The sponge tissue in which the embryos develop loses its normal appearance and bears little resemblance to that found in specimens without reproductive elements (Fig. 4). The later stages of cleavage take place in the tubes of the parent sponge and result in the formation of a blastula larva. The blastula larva contains two types of cells, the abundant blastomeres and the rare posterior granular cells. The blastomeres are narrow columnar flagellated cells containing deeply staining elongate nuclei located at the periphery of the larva. The posterior granular cell is a large nucleolated cell. The larva of *C. coriacea* contains one large posterior granular cell (Fig. 5), whereas two posterior granular cells are present in the larva of *C. blanca* (Fig. 6). These cells are not seen in all the larvae in a sponge section as it depends on how the larva is sectioned.

While the larvae are still in the tube of the parent sponge some of the blastomeres begin to migrate into the large blastocoel, losing their flagella and columnar shape and becoming spherical (Fig. 6). The obliteration of the blastocoel progresses at different rates in individual larvae. The blastocoel of some larvae remains relatively free of cells, whereas others are partially or completely filled with cells (Fig. 7). At the completion of larval development the tubes of the parent sponge are solidly packed with larvae moving towards the oscula to be expelled. Measurements of the larvae in the two species reveal much variation in their dimensions. Larvae range from 60 to 150 μm in length in *C. coriacea*, and from 70 to 160 μm in *C. blanca*.

Discussion

Oocytes of *C. coriacea* and *C. blanca* from Santa Catalina Island larger than 30 μm in length appear to phagocytize the eosinophilic amebocytes that aggregate around them. Similar observations were made by Tuzet (1947) in her study of *Leucosolenia coriacea* (=*C. coriacea*). Sarà (1955ac) reported that the oocyte of *C. coriacea* forma *blanca* (=*C. blanca*) first phagocytized choanocytes and then later eosinophilic cells, whereas the oocyte of *C. coriacea* forma *coriacea* (=*C. coriacea*) engulfed only choanocytes. These differences between the two species were not observed in the California specimens. There appears to be no difference in the intensity of phagocytosis between *C. coriacea* and *C. blanca* from Santa Catalina Island. Sarà (1955a), on the other hand, observed that phagocytosis was greater in *C. blanca* than in *C. coriacea*. The eosinophilic amebocytes are rare in nonreproducing individuals from Santa Catalina Island and common in specimens with developing oocytes. Sarà (1955b), however, reported that the eosinophilic amebocytes decreased in specimens with developing oocytes.

The eosinophilic amebocytes differ between the two sponges from Santa Catalina Island. In *C. coriacea* the granules within these amebocytes are larger, more numerous and more refractile than in *C. blanca*. Variations in the eosinophilic amebocytes among species of calcareous sponges also were reported by Minchin (1898), Duboscq and Tuzet (1936) and Borojević (1969). Minchin (1898), in fact, believed that he could distinguish between species of *Clathrina* solely on the basis of the granular (eosinophilic) amebocytes.

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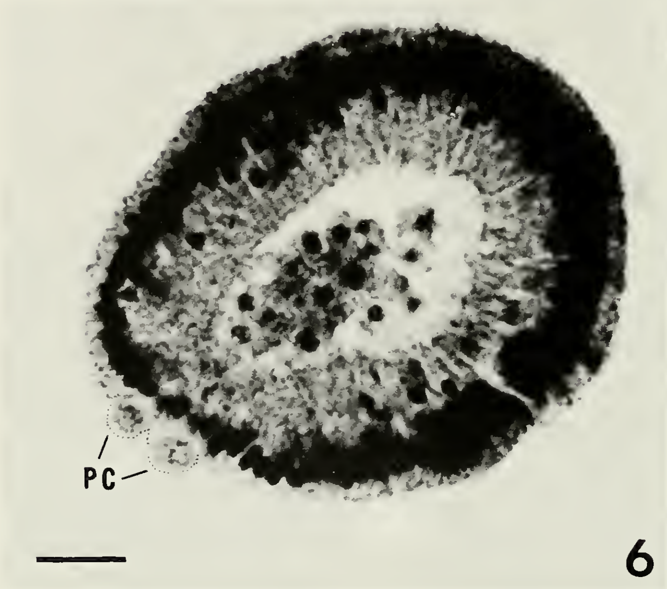

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Fig. 5. Single large posterior granular cell (PC) in larva of *Clathrina coriacea*. Scale, 10 μm.

Fig. 6. Two large posterior granular cells (PC) in larva of *Clathrina blanca*. Scale, 10 μm.

Fig. 7. Larvae of *Clathrina blanca*; note the varying stages of migration of the blastomeres into the blastocoel (B). Scale, 50 μm.

The oocyte in *C. coriacea* and *C. blanca* becomes very granular as it reaches sexual maturity. Similar observations were made by Tuzet (1947) for *C. coriacea*.

Oogenesis is asynchronous in the breeding population of the two California sponges. Some specimens contain developing oocytes, embryos or larvae, whereas other individuals have no reproductive elements. Duboscq and Tuzet (1937) reported that oogenesis also was asynchronous in the calcareous sponge *Grantia compressa.*

Spermatogenesis was not observed in *C. coriacea* or *C. blanca* from Santa Catalina Island. The lack of evidence of stages of spermatogenesis in calcareous sponges has puzzled sponge specialists since the latter part of the nineteenth century. Although Haeckel (1871) described spermatozoa in calcareous sponges, Dendy (1914) wrote that no one else had been able to repeat Haekel's observations. Poléjaeff (1882) collected rare male specimens of *Sycon raphanus* which he said were so completely filled with spermatic cysts that their whole development could be traced in a single section. Görich (1903ab, 1904) reported the presence of spermatic cysts in the upper third of *Sycandra raphanus* (=*Sycon raphanus*) and described the early stages of development. Dendy (1914) described what he thought were spermatic cysts and some stages of spermatogenesis in *Grantia compressa.* Gatenby (1920, 1927) looked at many breeding specimens of *Grantia compressa* and saw only a single stage of spermatogenesis. He concluded that spermatogenesis must take place sporadically and very rapidly. Vacelet (1964) was unable to find stages of spermatogenesis in *Petrobiona massiliana.* Tuzet (1973) reported that spermatogenesis was not known in calcareous sponges. In the demosponges, on the other hand, spermatogenesis has been seen in many species (Tuzet, 1930; Lévi, 1956; Tuzet and Pavans de Ceccatty, 1958; Tuzet and Paris, 1964; Tuzet *et al.,* 1970, among others).

Fertilization was not observed with certainty in *C. coriacea* or *C. blanca* from Santa Catalina Island. Sarà (1955a) and Borojević (1969) also had little success in following the process of fertilization. Borojević (1969) reported that he never saw any figures of fertilization in the numerous specimens of the Calcarea Calcinea he studied, whereas they were easily discernible in the Calcarea Calcaronea. Tuzet (1947), however, described the process of fertilization of *C. coriacea* in great detail, but she did not observe the actual fusion of the male and female pronuclei.

Cleavage in *C. coriacea* and *C. blanca* is total and equal, and a blastocoel forms after the eight cell stage. Similar observations were made by Tuzet (1948) for *C. coriacea* and by Borojević (1969) for other calcinean Calcarea. In the developing blastula larva of *C. coriacea* and *C. blanca* two cell types become apparent, the narrow columnar flagellated cell and the large granular cell. Tuzet (1948) reported that the granular cell determined the posterior region of the larva. Borojević (1969) considered the posterior granular cell to be a blastomere whose division had been retarded. The blastula larva of *C. coriacea* from Santa Catalina Island contains one posterior granular cell, whereas *C. blanca* has two posterior granular cells. These observations agree with Minchin (1900) who reported that *C. coriacea* contains one, *C. blanca* has two, and *C. contorta* and *Ascandra falcata* have four posterior granular cells, whereas *C. cerebrum* and *C. reticulum* do not contain posterior granular cells. In the two California sponges some of the larval blastomeres migrate into the large blastocoel while still within the tubes of the parent sponge. This process also was observed in *Leucosolenia coriacea* (=*C. coriacea*) by Minchin (1896) and Tuzet (1948).

The relationship between the blastula larva of calcareous sponges and other larval types of sponges was discussed by Tuzet (1948, 1973) and Borojević (1969).

Unlike the amphiblastula larva, the blastula larva is formed directly by multiplication of the blastomeres. There is no stage of blastomeres with internal flagella, no inversion of the surfaces, and no formation of the typical "cellules en croix." Borojević (1969, 1970) also found no similarity between the blastula larva and the parenchymella larva of many demosponges. In the parenchymella larva no blastocoel is formed and cellular differentiation occurs very early in the development. The parenchymella larva possesses at its liberation from the parent sponge the principal cell types of the adult sponge, whereas in the blastula larva the larval cells remain totipotent (Tuzet, 1948; Borojević, 1969, 1970).

Conclusion

The differences in the eosinophilic amebocytes, the number of posterior granular cells in the larvae, and the dimensions of the oocytes and larvae, in addition to the differences in the reproductive period between *C. coriacea* and *C. blanca,* reaffirm that the two sponges are separate species.

Acknowledgments

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Research Notes

Observations of a Gray Whale Birth

Observations of births of gray whales (*Eschrichtius robustus*) have been made by Balcomb (1974), Leatherwood and Beach (1975) and Storro-Patterson and Kipping (1977). We report a fourth observation of a gray whale birth; this from Estero de la Soledad in the Bahía Magdalena complex, Baja California Sur, Mexico (Fig. 1). We learned from Storro-Patterson that both his (1977) and Balcomb's (1974) observations were also made in this area; Storro-Patterson's at a location near the cannery at Puerto Adolfo López Matéos, and Balcomb's nearby to the north (per. comm.). Leatherwood's observations were made in the open sea off Mission Bay, San Diego.

On Sunday 19 February 1978 at approximately 1755 hours we approached the arm of the lagoon leading to the fishing village of Matancitas when the senior author noticed a solitary gray whale maintaining a stationary position with its tail flukes held vertically and motionless above the surface. Approximately 2 m of caudal peduncle and the flukes were exposed, holding for one to two minutes (Fig. 2a). The flukes then were lowered closer to the surface, held a few moments, and descended until the posterior margins were awash (Fig. 2b). After another minute the flukes were again raised vertically exposing a meter of caudal peduncle and flukes. The flukes then rotated slowly as the whale moved a few degrees on the vertical.

The flukes were again lowered, this time horizontal to the surface, and we caught our first view of the calf's emerging snout. From a distance of 50 to 100 m the only visible portions of the whales were the mother's flukes barely splashing at the water's surface and the calf's snout. At this point the calf's snout sank momentarily from view, but reappeared almost immediately.

The female's flukes next were positioned nearly vertical just above the surface as the calf was again submerged. This fluke movement was slow, unlike either the thrashing described by Balcomb (and shown in his photographs) or the lurching and violent tail spasms described by Leatherwood and Beach. Within a minute the flukes were again lowered horizontal to the surface as the calf reappeared. At this time we discerned its wrinkled nostril area. As the extrusion of the calf reached this point which, with the shoulders, forms the greatest girth, the calf appeared to be positioned with its left latero-dorsal aspect facing posteriorly. Balcom's photographs (1974) show the calf being presented with its dorsal aspect facing anteriorly. At this point in our observation the birth seemed essentially completed. The calf appeared to wobble in its near vertical position as though adding its own movements. The pectoral fins, or flippers, had not yet cleared the genital orifice as the couple again sank beneath the surface with the mother's flukes only slightly visible.

Within 30 seconds the calf surfaced independent of its mother. Due to poor water clarity and failing light we were unable to determine what, if any, assistance

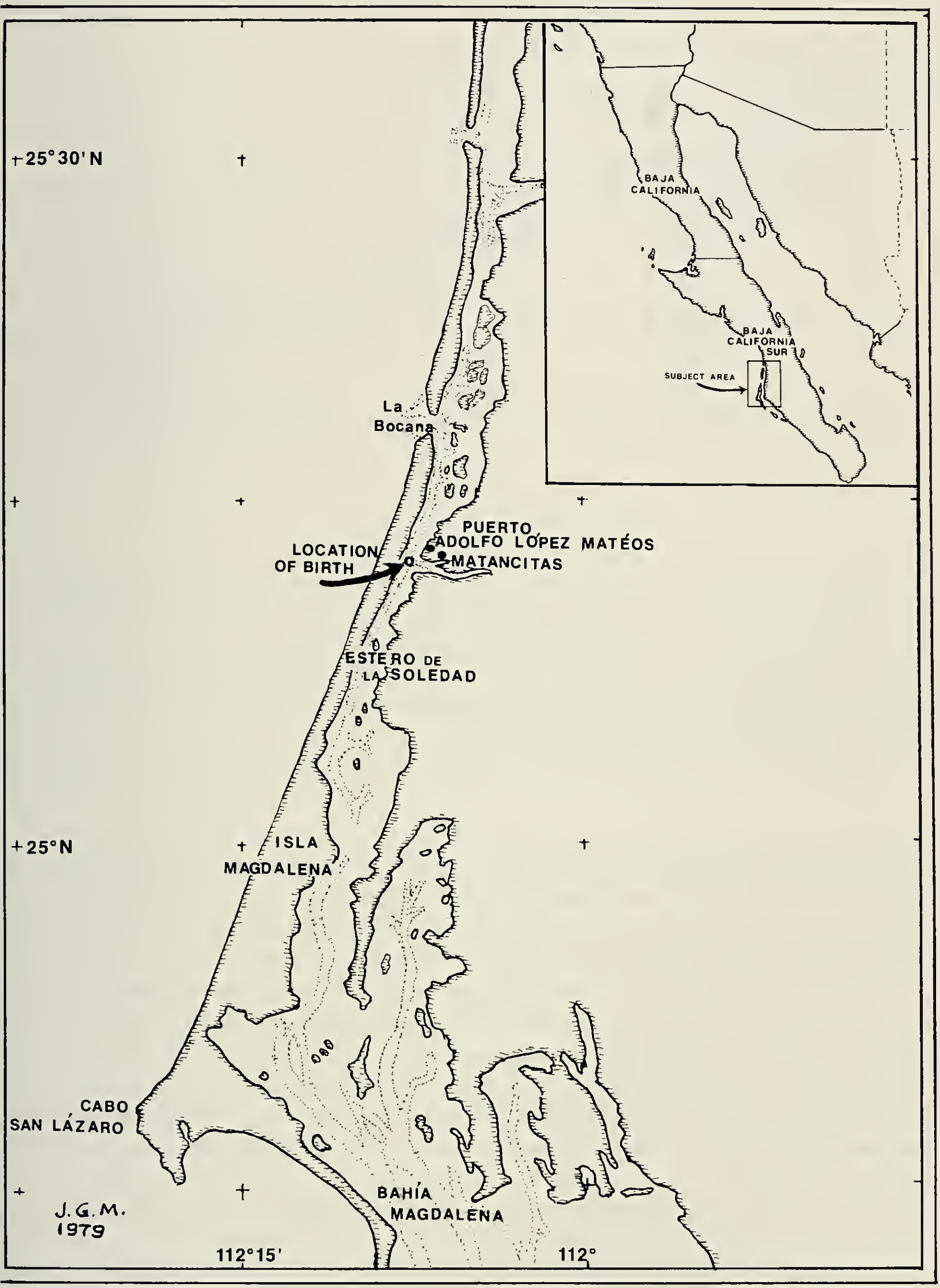

Fig. 1. Locale of birth observations. Configurations of channels determined from Earth Resources Technology Satellite photography.

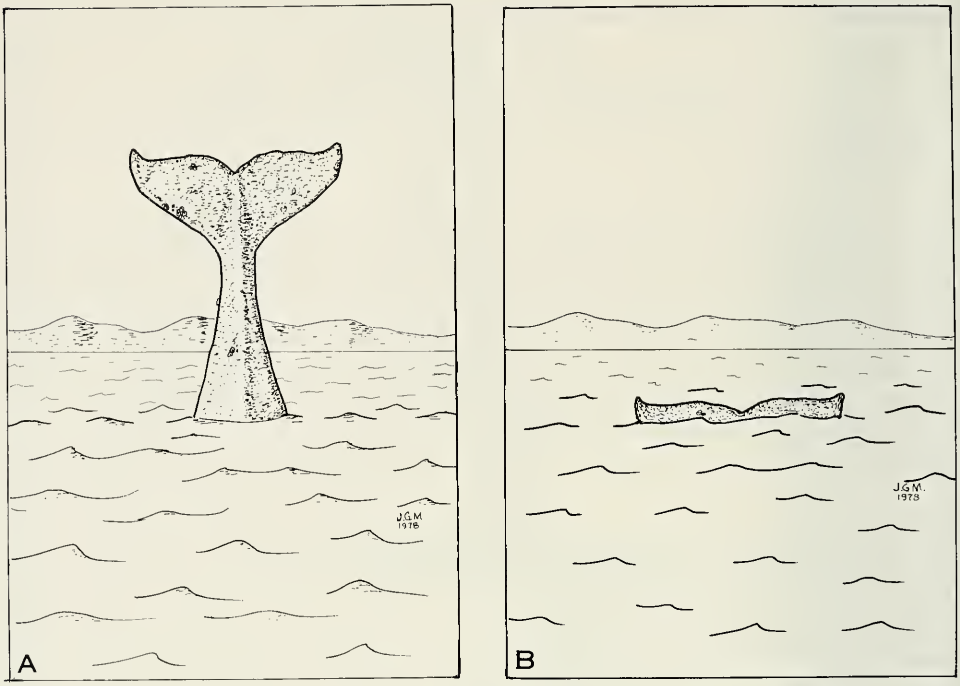

Fig. 2. a. Elevated position of mother's tail flukes at early stage of parturition. b. Subsequent positioning before first appearance of emerging calf.

the female might have rendered, e.g., by way of nudging the newborn to the surface to breathe. The calf did not give any appearance of being held above the water's surface as shown clearly in a Storro-Patterson photograph (1977). It was not for another 30 seconds that the female appeared at the surface and blew.

The whole episode, from our first sighting of the elevated tail flukes until the female's first blow, lasted less than 10 minutes (1755 to 1804). We did not see the female blow until after the birth was completed.

At no time during the birth did we see any portion of the female's body anterior to the genital aperture. This suggests that she kept her head positioned below the surface with her back arched in order to keep the head of the emerging calf above the water (Fig. 3).

The whale reported by Storro-Patterson and Kipping (1977) executed a slow 360° roll at the surface with the calf's rostrum protruding from the vagina as the female's ventral surface became visible. They noted that the newborn calf displayed a lack of coordination in both its early swimming efforts and in initial lunging behavior associated with breathing. We also observed lunging behavior but paid less attention to it since we had observed it before in older calves usually during windy conditions as they encountered some difficulty in clearing the surface of the water with their nostrils.

Poor viewing conditions precluded our observing the calf's use of its tail flukes. As we moved within 25 m the calf appeared a light grayish-white in contrast to

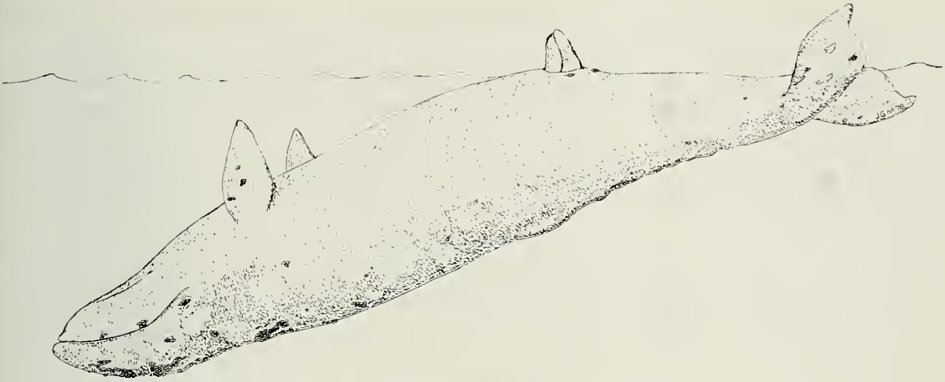

Fig. 3. Position during final stages of birth with calf maintained above surface of water.

the nearly black female. The calf swam quite well as the pair moved purposefully away from us. An unsuccessful search was made for any placental material. No attempt was made to follow the pair which had slowed and was milling around.

The female exhibited a high tolerance to our continued noisy presence. In what must have been trying circumstances for her, not once did she display any hint of aggressive recognition of our presence. Two other females with calves passed within 50 m during this female's parturition with no indication or inclination to ''assist'' with the birth.

Gilmore (1961) noted the likelihood of the tail-first underwater delivery but told us of a verbal report of a cephalic birth at Laguna San Ignacio in very shallow water during the week preceding Easter, 1976 (per. comm.)

While the birth of the whale reported by Leatherwood apparently took place below the surface and out of sight, the remaining three reports in the literature of the gray whale are of cephalic births at the surface.

The possibility remains that all reported cephalic births including Lindsay (1978) are abnormal births; that gray whales, and perhaps by extension, baleen whales, normally deliver their young by breech, or tail-first presentation, just below the surface. This is the case with *Tursiops* and other genera of smaller odontocetes whose births have been observed in various marine aquaria, a majority of which has been of tail-first births.

Additional support for tail-first births has been obtained from the whaling industry.

Slijper (1962) cites records of female baleen whales of several species taken during pregnancy, particularly advanced pregnancy, in which the great majority of fetuses was found with the caudal section oriented toward the cervix.

Additionally, Rice and Wolman (1971) report that all of 55 near-term fetuses of gray whales taken during the course of their study were found to be oriented for caudal presentation, tending to confirm the caudal birth as the normal delivery method.

For the present, it can be stated that births of gray whales, in spite of their annual abundance in relatively restricted locations and time periods, are rarely observed.

An additional point, possibly relating to the hazardous conditions of the birth process of a mammal in an entirely marine environment, came to our attention. A Sr. Modesto, a fisherman resident at Matancitas, reported to us that three dead calves had been encountered in Estero de la Soledad during the season of 1977 and none up to the date of our observations in 1978.

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Range Extension and Notes on the Habitat of the Isopod *Munna halei* Menzies

The small asellote isopod *Munna halei* Menzies, 1952, was described from Tomales Point, Marin County, California, from under stones and in kelp (*Macrocystis*) holdfasts in the lowest intertidal zone (Menzies, 1952). It remained unknown elsewhere until Iverson (1974) reported it at El Capitan Beach, San Luis Obispo County, California, from among the spines of the purple sea urchin *Strongylocentrotus purpuratus* (Stimpson) from mid-intertidal rocks.

Munna halei has now been discovered at Cape Arago, near Coos Bay, Oregon. The isopods were living among the spines of the sea urchin *S. purpuratus* which inhabited a relatively open, wave swept, rocky section of the coast. The isopods were collected from four of five study areas around Cape Arago: the South Cove of Cape Arago, the Middle Cove of Cape Arago, Squaw Island, and the rocky intertidal zone to the west of Squaw Island. They were not found at Sunset Bay near Cape Arago, but this may be due to the small sample size of urchins taken from that area.

Sea urchins both in urchin holes and "free-living" were collected from all five areas, placed in individual plastic bags without water and immediately transported to the laboratory where the plastic bags were placed in a seawater drip table in order to maintain them at the proper temperature. Within a twelve hour period the urchins were removed from their bags and individually submerged in a bowl of seawater where they were examined under a dissecting microscope for isopods. The number of isopods that had been dislodged from the urchin and had subsequently fallen into the bag was recorded. The number of isopods that remained on the urchin and their positions were also recorded.

A total of 50 sea urchins was collected and 147 isopods were recovered from 25 of the urchins. The number of *M. halei* per urchin ranged from zero to 18 with a mean of 2.94 per urchin (standard deviation 4.70). At the Middle Cove of Cape Arago, where the majority of samples were collected (27 urchins), the mean number of *M. halei* per urchin was 3.77 (standard deviation 5.51). *M. halei* showed no preference for sea urchins occurring in holes; 74 were found on urchins in holes and 72 were found on urchins not in holes. There was no correlation between the size of the urchin and the number of isopods present on it.

The isopods were observed usually clinging to the spines of the sea urchins rather than crawling upon the test of the urchin (96% on spines, 4% on the test). There appeared to be no oral-aboral distinction in their position on the urchins, with 51% occurring on the oral side of the urchins and 49% on the aboral side.

M. halei exhibited several interesting behavioral traits with regard to its microhabitat. Typically a *M. halei* clung to an urchin spine by wrapping its pereopods around the spine, with no region of the spine appearing to be frequented more than any other. In moving, an isopod, while holding on with its posterior pairs of pereopods, would lean off the spine it was on and grab another spine with its anterior pereopods, pulling itself over and onto the second spine. Occasionally *M. halei* was observed crawling off a spine and along the test surface a short distance before climbing another spine.

The isopods were usually able to move without appearing to disturb the urchin. On occasion, however, the isopods set off a "spine reaction," indicating a local disturbance to the sea urchin. The sea urchin spines would fold down at the point of the disturbance in an apparent attempt to protect the surface. While the spines were folded down the *M. halei* normally was trapped between spines or under a "pile" of spines. If the isopod was unable to squeeze through the moving spines it remained still until the spines became erect and the isopod would crawl away.

On several occasions the sea urchin's pedicellaria were actually observed clutching an isopod's legs. The pedicellaria would hold tightly to the leg and occasionally tug on it as the isopod clung precariously to a nearby spine. The pedicellaria would eventually release its hold and the isopod would crawl away without any apparent harm to the appendage. Usually, however, the pedicellaria in the vicinity of an isopod would not react to the isopod's presence.

On one occasion a single *M. halei* was observed perched approximately halfway up a spine, waving its antennae in the water, and then wiping the antennae across the mouth parts in a possible feeding motion.

In this study two other invertebrates were found to occur regularly in association with *S. purpuratus.* 97 specimens of an unidentified flatworm (Platyhelminthes, Turbellaria) were observed, as were 107 specimens of an undescribed species of the purple amphipod, *Pontogeneia* sp. This same amphipod had previously been collected from *S. purpuratus* at Cape Blanco, Oregon (Barnard, 1954), as *Pontogeneia inermis.* Other invertebrate epizoics of purple sea urchins have occasionally been noted in the literature. The shrimp *Betaeus macginitieae* Hart, 1964, occurs in pairs underneath both *S. purpuratus* and *S. franciscanus* from Monterey Bay, California, south to Santa Catalina Island (Hart, 1964). *Flabelligera commensalis* Moore, 1909, a polychaete worm, occurs among the spines of purple sea urchins (Moore, 1909; Light, 1978). Johnson and Snook (1927: 291) reported that the isopod *Colidotea rostrata* (Benedict, 1898), "lives among the spines of sea urchins, and its coloring resembles that of the sea urchin." MacGinitie and MacGinitie (1949:265) specifically indicate that *Colidotea* occurs with *S. purpuratus.*

It is of interest to speculate that there may be a protective advantage for *M. halei* to live in association with *S. purpuratus.* If a potential isopod predator, such as a small fish, were to attempt to feed on a *M. halei* clinging to an urchin spine, almost invariably a "spine reaction" would be set off, and the isopod would immediately be covered under moving spines out of the predator's reach. Some indirect evidence for this was provided by laboratory attempts to remove *M. halei* from the urchin spines by using forceps, a procedure that repeatedly set off a spine reaction making the isopods inaccessible. The protective array of erect spines on the sea urchin may be a further deterrent to the predators of *M. halei.* The urchins may also provide a low energy microhabitat for the isopods, protecting them from the strong wave action of their environment.

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Species of Demersal Zooplankton Inhabiting a Kelp Forest Ecosystem off Santa Catalina Island, California

Demersal zooplankton are those animals that migrate at various times between the benthic and pelagic environments. Previous studies have concentrated on coral reef habitats (e.g. Emery, 1968; Porter, 1974; Alldredge and King, 1977; Porter and Porter, 1977; Porter et al., 1977; Hobson and Chess, 1979; Ohlhorst and Hutchinson, 1979). Inverted funnel traps were used by Thomas and Jelley (1972) to study demersal zooplankton in an estuarine ecosystem. King and Alldredge (1978) reported on the emergence patterns of demersal zooplankton from a subtidal sand-flat. Diel changes in zooplankton composition over an intertidal eelgrass flat were monitored by Robertson and Howard (1978).

Demersal zooplankton studies are of considerable interest to kelp forest ecology because these organisms may have substantial impact on food availability, feeding strategies, and behavior patterns of other community members, especially the ecologically and economically important kelp forest fishes. The only published study of kelp forest zooplankton is that of Hobson and Chess (1976), based on integrated plankton net collections. In contrast, emergence traps provide discrete samples of demersal zooplankton populations inhabiting specific substrates. The following study provides data from emergence traps on the species composition of demersal zooplankton inhabiting six substrates in a kelp forest ecosystem off Santa Catalina Island, California.

The study site was located on Harbor Reefs, approximately 1 km northwest of the Catalina Marine Science Center, Santa Catalina Island, California (Fig. 1).

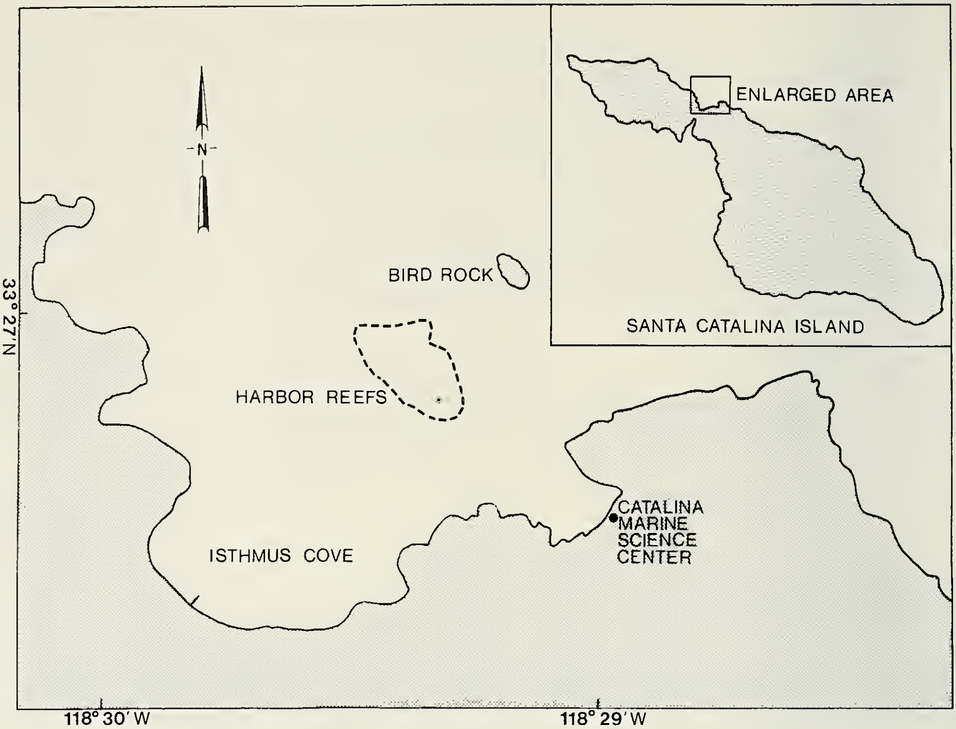

Fig. 1. Map of the study site at Harbor Reefs, Santa Catalina Island, California.

Each station was selected as representative of the various substrates within the kelp forest. Station 1 was composed of algal turf and *Cystoseira* sp. at a depth of 3 m. For the purposes of this study, algal turf is defined as those species of algae, primarily members of the Rhodophycophyta, that do not form a canopy but instead produce a thick mat that covers the bottom to a height of 10 cm or less. The habitat at Station 2 consisted of sand and pebbles in water of 3 m depth. Station 3 had similar sand and pebble substrate but was in 5 m of water and the southern sea palm, *Eisenia arborea,* was present. The depth at Station 4 was 6 m and the substrate was composed of algal turf located under a canopy of the giant kelp, *Macrocystis pyrifera*. Station 5 consisted of *M. pyrifera* holdfasts at a depth of 9 m. The primary stipe was cut and removed from the holdfast just before the traps were set in position. The region around the holdfasts was composed of large rocks, sand, and pebbles. Station 6 was located outside the kelp canopy at a depth of 11 m in a bed of *Dictyopteris undulata* and *Sargassum muticum* on a sand and pebble substrate.

Cone-shaped emergence traps designed by King and Alldredge (1978) were used to capture demersal zooplankton emerging from each substrate (Fig. 2). Samples of demersal zooplankton were collected with 2 emergence traps per substrate type. Emergence traps were set by SCUBA divers at 1930 h on 5 July 1978 and samples were collected after a 24-h new-moon period. Samples were preserved in a solution of 5% formaldehyde in sea water and returned to the

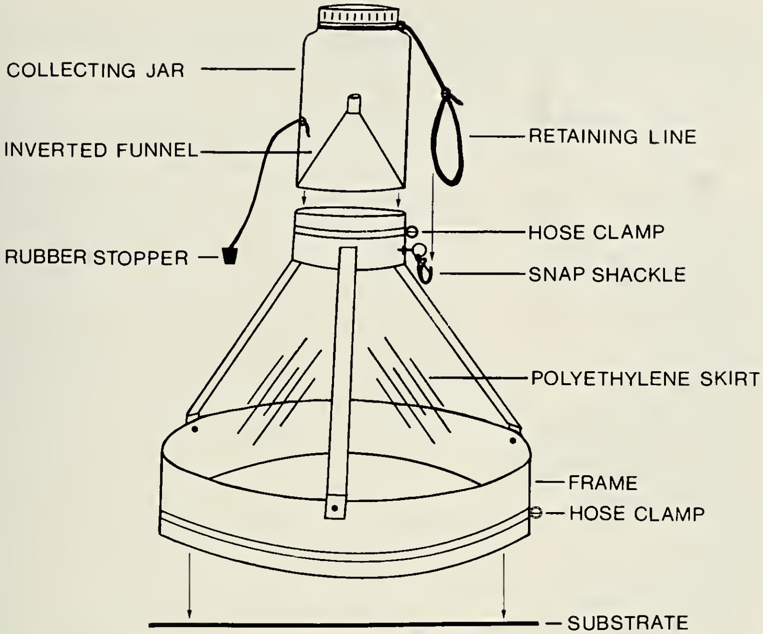

Fig. 2. 0.25 m^2 emergence trap for collecting demersal zooplankton (modified from the basic design provided by Dr. Alice L. Alldredge).

laboratory for analyses. All specimens within each sample were sorted, identified, and counted using dissecting microscopes.

This study provides the first demonstration of the existence of demersal zooplankton in a kelp forest ecosystem and the first list of species caught in emergence traps (Table 1). The number of species per substrate is as follows: 59—algal turf and *Cystoseira*; 79—sand and pebbles; 79—*Eisenia* on sand and pebbles; 61—algal turf under *Macrocystis* canopy; 78—*Macrocystis* holdfasts; and 58—*Dictyopteris* and *Sargassum* on sand. A total of 134 species were collected from the six substrates, 114 of which were crustaceans. Thirty six species of gammaridean amphipods were captured, many more than in any other taxon. The gammaridean and caprellid amphipods, most of the harpacticoid copepods, the ostracods, isopods, caridean shrimp, mysids, cumaceans, tanaids, nebaliaceans, polychaetes, cephalopods, and fish are all generally considered to be true demersal zooplankton (see references cited above). The gastropod mollusc *Tricolia pulloides* probably entered the traps by crawling rather than by swimming. The remaining groups of organisms collected in the traps are presently considered as possible contaminants because they are usually regarded as being planktonic all day and night (Hobson and Chess, 1979). The emergence traps are being modified to determine whether these organisms are actually contaminants or true demersal forms.

The quantitative data generated from this study were highly variable. A more comprehensive quantitative sampling program with additional replicate samples collected over short time intervals is in progress to determine the abundance, biomass, and diurnal migratory patterns of kelp forest demersal zooplankton.

Table 1. Species collected from the six kelp forest substrates. + = presence. Station 1 = algal turf and *Cystoseira* substrate, 2 = sand and pebbles, 3 = *Eisenia* on sand and pebbles, 4 = algal turf under *Macrocystis* canopy, 5 = *Macrocystis* holdfasts, 6 = *Dictyopteris* and *Sargassum* on sand and pebbles.

	Station Number					
Taxon	1	2	3	4	5	6
POLYCHAETA						
Alciopidae, species A						+
Autolytus sp.	+				+	
Diopatra ornata						+
Eunoe sp.		+				
Exogone sp.		+				
Lumbrineris sp.			+		+	
Odontosyllis sp.		+	+	+	+	+
Platynereis bicanaliculata	+	+		+	+	+
Schistomeringos longicornus						+
Syllidae, species A			+	+	+	
MOLLUSCA						
Gastropoda						
Gastropoda, Larva	+	+	+	+	+	+
Tricolia pulloides			+	+	+	+
Cephalopoda	+	+				
CRUSTACEA						
Cladocera						
Penilia avirostris					+	
Ostracoda						
Cycloleberis sp.			+			
Cxlindroleberididae, species A	+	+	+	+	+	+
Cylindroleberididae, species B		+	+		+	
Cylindroleberididae, species C			+	+	+	
Cypridae, species A	+	+				
Neonesidea phlegeri				+		
Rutiderma, species A	+	+	+	+		
Rutiderma, species B			+			
Rutiderma, species C						+
Sarsiella sp.			+			
Vargula tsujii	+	+	+	+	+	+
Copepoda						
Calanoida						
Acartia tonsa		+		+	+	+
Candacia bipinnata			+			
Candacia sp., juvenile					+	
Clausocalanus furcatus	+	+	+	+	+	+
Clausocalanus sp.	+	+	+	+	+	+
Copepodite	+	+	+		+	
Paracalanus parvus	+	+	+	+	+	
Cyclopoida						
Corycaeus amazonicus		+	+	+	+	+
Corycaeus anglicus				+		
Farranula curta					+	
Oithona similis					+	
Oncaea sp.	+	+	+	+	+	+

Table 1. Continued.

Taxon	Station Number					
	1	2	3	4	5	6
Harpacticoida						
Altheutha langi	+	+	+	+	+	+
Diosaccus spinatus	+	+	+	+	+	+
Ectinosomatidae, species A	+	+	+	+	+	+
Euterpina acutifrons					+	+
Laophonte sp.		+				+
Microsetella rosea						+
Paraltheutha sp.		+			+	
Porcellidium spp.	+	+	+	+	+	+
Tisbe spp.	+	+	+	+	+	+
Monstrilloida		+	+	+	+	+
Cirripedia						
Cypris Larva	+	+	+	+	+	+
Nebaliacea						
Nebalia sp.			+		+	
Mysidacea						
Acanthomysis sculpta		+	+	+	+	
Erythroponii, species A	+	+	+	+	+	
Siriella pacifica		+	+	+		+
Cumacea						
Cumella sp.	+	+	+	+	+	+
Tanaidacea						
Leptochelia sp.		+	+	+	+	+
Pancolus californiensis	+			+		
Isopoda						
Antias sp.	+	+				
Bathura luna		+				
Cirolana harfordi		+				
Cirolana parva	+	+	+	+	+	+
Cryptoniscus Larva		+		+		
Eurydice caudata		+	+	+	+	
Gnathia sp.	+	+	+	+	+	+
Idotea resecata			+			
Idotea sp., juvenile	+		+			
Paracerceis cordata	+		+		+	+
Paranthura elegans				+		
Sphaeromatidae, species A	+	+	+	+	+	
Sphaeromatidae, species B		+	+		+	
Amphipoda						
Gammaridea						
Ampelisca lobata	+	+	+	+	+	+
Ampithoe plea	+	+	+			+
Ampithoe pollex		+				
Ampithoe simulans	+	+	+		+	+
Amphithoe sp., juvenile		+	+		+	+
Aoroides columbiae		+	+		+	
Batea transversa	+	+	+	+	+	+
Ceradocus sp.					+	

Table 1. Continued.

Taxon	Station Number					
	1	2	3	4	5	6
Chevalia aviculae		+		+	+	
Erichthonius brasiliensis	+	+	+	+	+	+
Gammaridae, species A	+	+	+		+	+
Gammaridae, species B		+				
Gammaridae, juvenile			+	+	+	+
Gammaropsis thompsoni	+	+	+	+		
Gitanopsis vilordes	+	+	+	+	+	+
Heterophlias seclusus		+	+		+	+
Hyale frequens	+	+	+	+	+	+
Lysianassa dissimilis					+	
Lysianassa macromerus			+			
Lysianassidae, juvenile						+
Maera similie		+	+	+	+	
Microjassa litotes					+	
Paraphoxus obtusidens	+	+	+			
Paraphoxus oculatus		+	+			
Paraphoxus spinosus		+	+			
Parapleustes oculatus	+	+	+	+	+	+
Parapleustes pugettensis					+	
Photis californica	+	+	+	+	+	+
Photis sp.					+	
Pleustes platypa	+	+	+			+
Podocerus cristatus	+	+	+		+	+
Polycheria osborni				+		
Pontogeneia intermedia		+	+	+	+	
Pontogeneia quinsana	+	+	+	+	+	+
Pontogeneia rostrata	+		+			
Stenothoe sp.				+		
Hyperiidea						
Hyperella sp.			+			
Parathemisto sp.	+				+	
Unidentified	+					
Caprellidea						
Caprella angusta		+	+			
Caprella californica		+	+	+	+	+
Caprella mendax			+			
Caprella verrucosa		+				+
Caprella sp.	+	+	+	+		+
Mayerella banksia						+
Tritella laevis					+	
Unidentified	+	+				
Euphausiacea						
Euphausia recurva						
Calyptopis Larva				+	+	+
Natantia						
Alpheus bellimanus		+	+	+	+	+
Alpheus clamator	+		+	+		
Alpheus sp.	+				+	
Betaeus sp.	+		+		+	+
Caridea Zoea Larva	+	+	+		+	

Table 1. Continued.

Taxon	Station Number					
	1	2	3	4	5	6
Heptacarpus stimpsoni	+		+	+	+	+
Hippolyte clarki	+	+	+	+	+	+
Lysmata californica	+	+	+	+	+	+
Brachyura						
Megalopa Larva	+	+		+	+	+
Nauplii Larva		+				
BRYOZOA						
Cyphonautes Larva	+		+		+	
LARVACEA						
Oikopleura sp.			+		+	
PISCES						
Chromis punctipinnis				+		
Gobiesox rhessodon						+
Lythrypnus dalli	+			+		
Oxyjulus californica		+				
Paraclinus integripinnis		+				

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Discovery of the Male of the Katydid *Idiostatus viridis* Rentz, with Descriptions and Biological Notes (Orthoptera: Tettigoniidae: Decticinae)

Charles L. Hogue

Abstract.—Discovery of the male of the katydid *Idiostatus viridis* Rentz, with descriptions and biological notes (Orthoptera: Tettigoniidae: Decticinae) by Charles L. Hogue, *Bull. Southern California Acad. Sci.*, 79(1):1–5, 1980. The male of *Idiostatus viridis,* hitherto unknown only for this species in the genus, has been discovered. Two specimens from the type locality are now available and serve as the basis for description. Color photographs of the live female also permit redescription of this sex. Some biological notes are made on the basis of the author's collecting experiences.

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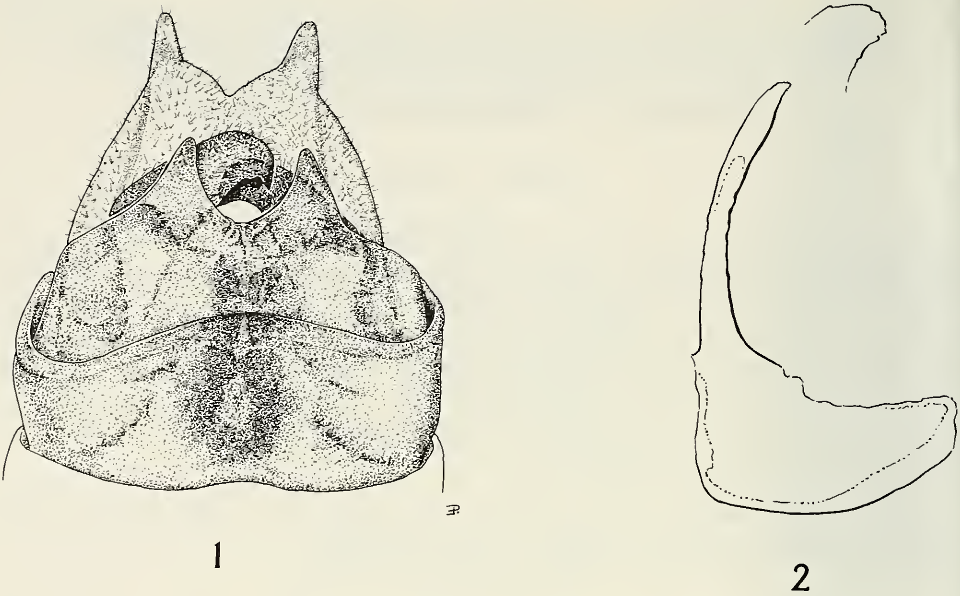
At the time of Rentz' (1973:134) original description of *Idiostatus viridis* only females were available, the one species in the genus for which this deficiency persisted. Thanks to the perseverance of my collecting companions David Turner and James Hogue, two males were discovered at the type locality in September 1979. Also a few additional female specimens and color photographs of living material are now available that permit complete descriptions of both sexes. Some fragmentary notes can also be made on the species' biology, although host plants, microhabitat and other details still elude us.

Idiostatus viridis Rentz
Figures 1–2

Idiostatus viridis Rentz, 1973:130–4. Holotype female, California, San Bernardino County, San Bernardino Mountains, Camp O'Ongo, near Running Springs, Elev. 6200 feet, Natural History Museum of Los Angeles County.

Description of the male.—The following is based upon the plesioallotype and color photographs of same; unfortunately, the second individual was badly damaged by yellow jackets (*Vespula pensylvanica*) before it was found, including complete removal of the genitalia, and is not adequate for descriptive purposes. The format and terminology follow that of Rentz' (1973) generic revision.

Size medium for genus, form slender. HEAD with fastigium of vertex low, distinct, broad, sides of latter slightly concave, margin broadly rounded, without distinct knob. Third segment of antennal flagellum distinctly longer than second. Eye situated high, distinctly dorso-ventrally elongate. PRONOTUM smooth, deplanate, no structural evidence of median carina. Anterior margins slightly produced laterad, concave in dorsomedial area; posterior margin truncate, barely concave medially. Posterior and ventral margins of lateral lobe straight; submarginal portion of posterior sector with conspicuous oval swelling defined dorsally



Figs. 1, 2. *Idiostatus viridis*, male. 1. Terminalia, dorsal aspect. 2. Right titillator.

by transverse sulcus. A shallow, U-shaped median sulcus on disc. TEGMEN broad, protruding beyond apex of pronotum for a distance of about one-half the mid-dorsal pronotal length. APPENDAGES. Hind femur projecting beyond apex of abdomen for a distance of about one-half the femur length. Fore tibia unarmed on anterodorsal margin, posterodorsal margin with four widely-spaced spines. Dorsal margins of hind tibia with two subapical spurs, distinctly more erect and longer than adjoining spines. Ventral margins with two apical uncinate spurs, slightly larger than dorsal pair opposite. Femora without teeth. Plantula of hind tarsus distinct, as in female. All legs hispid. Mid-dorsal carina of abdomen evanescent. TERMINALIA (Figs. 1–2). Tergite ten modified, U-shaped medially with distinct lateral projections without soft mesal area. Cercus extending for one-quarter or less their length beyond apex of tergal projection. Cercus uncinate, single internal hook apical. Titillator (Fig. 2) with well-developed triangular base; arm elongate, longer than base, without teeth, apex of latter only slightly broader than shaft. Subgenital plate with distinct V-shaped, moderately deep median incision; styles elongate, length about equal to side of median incision. COLORATION (photograph of living specimen). General color and pattern similar to that of female, basic green somewhat lighter. Vertex of head pale brown, remaining portions of head capsule pale green with violaceous intrusions. Antennal scape purplish, flagellum medium-brown. Eye deep reddish brown, eye ring black. Disc of pronotum light reddish brown, yellowish marginally and dark along median carinal line. Ventral margin of lateral lobe creamish yellow ventral to black submarginal sulcus. Remainder of pronotum green, no stripes on humeral angle. Labium, maxillae (including palps), ventral portions of pleural sclerites, coxae, trochanters and ventrolateral portions of abdomen all purplish-light brown. A broad, white spiracular band separates this color from green dorsopleural area of abdomen. Dorsum of abdomen with two distinct, parallel creamish-yellow lines continuing from beneath tegmina to abdominal apex, the submedian dorsal areas between these lines pale reddish brown adjoining a broad median dorsal line. Leg segments all green, except for yellowish articular areas; all tarsi medium brown, segment three on all tarsi of legs black basally. Tegmen translucent yellow anteriorly, the rest brown except for distinctly dark-brown median vein; no dark subapical spot. Apices of all spines and inner tooth of cercus dark. MEASUREMENTS (in mm). Length: Body, 21.0; pronotum, 5.6 × 4.5; left tegmen, 4.0; fore femur, 5.7; fore tibia, 7.0; middle femur, 6.4; middle tibia, 7.6; hind femur, 17.5; hind tibia, 17.5; titillator (apex of arm to base extreme), 1.60.

Partial redescription of female.—Rentz' description of the female coloration was based on dry specimens and admittedly incomplete. The following utilizes a series of color transparencies that I made of specimens from the type series while in a live state and which require modification as reflected by live material as follows: COLORATION. Head dorsally same green as rest of body (not brownish). Hind femora entirely green, except for yellow at extreme apex (no yellowish cast). Longitudinal yellow stripes dorsally are intermittently reddish brown on the anterior third of each tergite, the yellow following posteriorly pale. Ovipositor green basad (not totally reddish brown).

An error is corrected in describing one appendage structure (Rentz 1973:131): the clause reading, ". . . apex of dorsal margin of hind femur with two slender apical spurs . . ." (p. 131, lines 33–4), should read, "apex of dorsal margin of hind *tibia* with two slender apical spurs . . . ."

Material.—To the two females known to Rentz from the type locality, I can add the following four specimens:

CALIFORNIA: San Bernardino County, San Bernardino Mountains, Camp O'Ongo, near Running Springs, 20–25 August 1978, C. & J. Hogue No. 254 (2 females:LACM); 23 August 1979, C. Hogue et al. (designated here PLESIOALLOTYPE male and one additional fragmentary male in alcohol, LACM).

Identification.—The male of *viridis* will run to *aberrans* in Rentz' key, page 36, couplet 22. The following modifications, if inserted into the key at that point, will allow correct identification of the species:

22. Dorsal projections of abdominal tergite ten acute. Cercus attenuate. Tegmen light straw brown; overall coloration greenish with two yellow, longitudinal stripes dorsally. Mountains of southern, central and northern California 22a

Dorsal projections of abdominal tergite ten obtuse, rounded. Cercus with apex rounded, varying geographically. Tegmen reddish brown; overall coloration greyish or brownish. Owens Valley and adjacent areas of eastern California .... *inyo* Rehn & Hebard

22a. Apex of cercus bifurcate, outer tooth present. Styles of subgenital plate short, knob-like, hardly distinguishable from plate itself; indistinct median incision. Mountains of central and northern California .... *aberrans* Rentz

Apex of cercus simple, outer tooth absent. Styles of subgenital plate elongate, length about equal to side of median incision; median incision moderately deep. San Bernardino and San Jacinto Mountains .... *viridis* Rentz

No changes in the key to females are necessary.

Biological notes.—I have spent a week during the late summer (20 August to as late as 12 September) at the type locality every year since 1966. During this period I have been able to find only six specimens of *viridis,* four females and two males, and this in spite of intensive searching by myself and my companions on vegetation and around the general area. Such a score in collecting success indicates that the species is indeed rare or occupying a niche largely out of reach to the ordinary searcher.

All of the specimens have been found on the ground directly beside or on the concrete and wood porches of mountain cabins. All but the one battered male last taken were discovered during the night, between approximately 2000 and 2400 hours, PDST, when they were presumably normally active and attracted to lights which are customarily kept burning inside and outside the structures. The second male was found after sunrise in the morning after it had suffered severe attacks from yellow jackets.

I and my collecting associates named above have made intensive efforts to find specimens on vegetation near the cabins but so far have been completely unsuccessful. I have hypothesized that the green ground color pattern, broken only by thin longitudinal yellow stripes, is cryptic to match the general appearance of a bundle of pine needles and therefore have searched most ardently among the branches of *Pinus jeffreyi* and *coulteri* at the locality, but to no avail. At least some trophic compatibility with *Pinus* is indicated by the complete acceptance of the plant as food in captivity. The male plesiotype was kept alive for six days and fed unhesitatingly on the needles and needle scales of *Pinus jeffreyi.* The specimen produced normal-appearing fecal pellets, which further implies that the plant was suitable food. *Idiostatus aberrans,* the species most closely related to *viridis,* has been found on fir (*Abies*) in nature (Rentz 1973:128).

The apparent rarity of *viridis* may otherwise possibly be due to an activity season that peaks earlier or later than the time of year when our collecting was done. A similar situation has been suggested by Rentz with the closely similar *I. aberrans.* Therefore, collectors are urged to watch for this poorly known species in the Yellow Pine Forest belt (5000–8000 feet elevation) of southern California's Transverse Range mountain system from early August to late September.

We are familiar with the stridulatory sounds of the katydids of the type locality, which include those of *Neduba gurneyi* Rentz and Birchim and *Platylyra californica* Scudder, but have not been able to identify any sonification associated with *Idiostatus viridis,* nor for *I. aequalis* Scudder and *Neduba morsei* Caudell which also occur in the area.

Taxonomy.—The characteristics of the male that are now available show clearly that Rentz' original placement of *viridis* next to *aberrans* was correct. The genitalia of the two species are very similar and only show the specific differences cited in the key supplement given above. The distribution pattern of the members of the Aberrans Group suggests that they are geographically disjunct sister species whose origins are probably associated with orogenic events in California's mid-Cenozoic history.

Acknowledgments

The help of David Turner and James Hogue in finding *viridis* deserves my special thanks. I also appreciate the contributions of both Dr. David Rentz who kindly reviewed this paper and offered comments and Eugenia Paul who rendered the figure of the male terminalia.

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Postfire Seedling Reproduction of *Adenostoma fasciculatum* H. and A.

George F. Howe and Linn E. Carothers

Abstract.—Postfire seedling reproduction of *Adenostoma fasciculatum* H. and A. by George F. Howe and Linn E. Carothers, *Bull. Southern California Acad. Sci.*, 79(1):5–13, 1980. Seedlings and crown sprouted plants of *Adenostoma fasciculatum* H. and A. were studied at various times after fires in the chaparral near the Newhall-Castaic area in California. In contrast to certain reports in which it was stated that chamise seedlings seldom contribute to mature chaparral cover, eighty-six percent of all chamise plants were seedlings, fourteen percent crown sprouts. Mean seedling height was significantly shorter than the crown sprout height six years after fire but not at eight or nine years postfire.

Another area which burned twice in four years had two types of crown sprouted plants but no seedlings following the second fire.

Differences in numbers of taxa in certain genera are discussed in relation to reproductive strategies following fire.

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Introduction

Certain species of chaparral shrubs such as *Arctostaphylos glauca* and *Ceanothus greggii* may be classified as "obligate seeders" because they are non-sprouting and must reproduce after fire by seedlings alone—Keeley and Zedler (1978). *Arctostaphylos glandulosa* and *Ceanothus leucodermis* may be called "sprouters" as they are able to regenerate after fire by sprouts from the burl of old plants, as well as by seedlings. *Adenostoma fasciculatum* H. and A. (hereafter referred to as "chamise" or simply *Adenostoma*) is a sprouter also.

Wells (1969) noted that chapparral genera which have the ability to regenerate by both crown sprouting and seedlings, such as *Adenostoma,* contain relatively few taxa. Conversely, he reported that genera in which certain species are unable to reproduce by crown sprouting (such as *Ceanothus* and *Arctostaphylos*) possess many taxa. He concluded that the tempo of evolution in *Arctostaphylos* and *Ceanothus* was quickened by ". . . abandonment of the conservative, crown-sprouting mode of reproduction in favor of a non-sprouting, obligately-seeding response to recurrent fire that results in a greater frequency and intensity of selection."

Keeley (1977) and Keeley and Zedler (1978) have developed a different model in which they ascribe adaptive significance to the obligate seeding mode as well as the sprouting habit among chaparral species—suggesting that under certain circumstances, one mode of reproduction or another is favored.

In their studies of regrowth after fire in the chaparral of the San Jacinto Mountain region, Vogl and Schorr (1972) reported that seedling mortality in chamise was high and they concluded that chamise seedlings seldom contribute to the mature chaparral cover. Wells (1969) has asserted that "When maximum population density is attained, the crown-sprouters tend to regenerate only vegetatively." But in other studies by Hanes and Jones (1967), Hanes (1971) and Christensen and Muller (1975) generous numbers of chamise seedlings were found after chaparral fires in various regions.

It was our purpose to locate and study areas in which seedling survival of *Adenostoma* after fire was high. As the project developed, we also attempted to assess the measure of fit our data might have with Wells' model on the one hand or that of Keeley and Zedler on the other.

Methods

Regrowing populations of chaparral shrubs were observed at three different fire sites over a period of several years following each burn. These fires occurred on north or south facing slopes of ridges that run east and west.

Dates of various fires are either from personal observation or the records of the Newhall Station, Los Angeles County Fire Department. The growing season corresponds to the rainy season which extends from approximately November to the following May. Plants observed in Spring 1978, for example, would have experienced nine growing seasons following a fire in Autumn 1969.

One 10 × 10 m quadrat was established in the regrowing chaparral at each of the three postfire localities. Since it had been asserted in some of the literature that seedlings seldom if ever contribute to regrowth, quadrats were located in places where seedling survival was obvious. While such a choice of sites for quadrats produces an internal bias towards seedling reproduction, it was our intent to study reproduction under just such conditions and in just such localities. In actuality, the bias toward seedling reproduction was minimal in two of the three localities because seedlings were prevalent throughout those two entire slopes.

It was possible to distinguish seedlings of chamise from old sprouted specimens because the seedlings are usually narrower and have no charred stem or burl at ground level. A crown sprouted plant, however, has at least one burned stump visible amid the new, leaf-covered branches.

All living chamise plants in each quadrat were scored as seedlings or crown sprouts and a count was made of dead chamise stumps that failed to sprout after fire. The height of each plant from the top of the tallest branch to ground level was recorded for each living individual.

Site descriptions.—On 28 August 1973, a fire occurred east of Wildwood Canyon Road, Newhall, CA. This area has a north-south running ridge with several east-west running branch ridges. Approximately six growing seasons after the fire, 15 February 1979, a quadrat was established on the south facing slope near the crest of an east-west running lateral ridge at an elevation of 440 m.

On 2 June 1969, a fire burned a mixed stand of vegetation composed largely of chamise and *Ceanothus crassifolius* Torr. (Hoary-leaved *Ceanothus*) covering several east-west running ridges north of Oak Orchard Lane, Newhall, CA. The study quadrat was established on the north facing slope of one ridge at an altitude of 410 m.

A large area of chaparral burned in Autumn of 1970 on a gentle south facing slope in the vicinity of Lake Hughes Road, Castaic, CA. at an elevation of 595 m. Most of this same Castaic region was burned once again in Autumn 1974. But one large south facing slope area did not burn a second time. On 26 April 1978 (8 growing seasons after fire) a 10 × 10 m quadrat was established in the midst of this section that burned in Autumn 1970 but not in 1974.

At the Castaic site, a second quadrat was established on a steep east facing slope (about 400 m south and down the ridge from the previously mentioned quadrat) at an elevation of 549 m. This east facing slope was burned during both the Autumn 1970 and Autumn 1974 fires and will be called the "Castaic double-fire" quadrat.

Statistical procedures.—Means and standard deviations of height data from each quadrat were calculated. The Mann-Whitney U-test was used to evaluate the null hypothesis that any two samples came from the same population. The Mann-Whitney sample statistic was tested against two-tailed critical values of Student's T for a 5% level of significance at infinite degrees of freedom. The nonparametric Mann-Whitney test was used instead of a Student's T-test because of failure to meet assumptions of normality—see Sokal and Rohlf 1969.

Results

An analysis of seedling survival and regrowth on five circular quadrats within the Wildwood Canyon Road fire zone has been reported elsewhere (Howe 1976). Data for chamise regrowth on the Wildwood Canyon Road 10 × 10 m quadrat and data for subsequent quadrats of the present study are reported in Table 1. It will be noted that reproduction was largely by seedlings on the south facing slopes of the Wildwood Canyon Road fire. However, on nearby north facing slopes, chamise reproduction was by means of crown sprouts, no seedlings were evident six growing seasons after the fire.

On the Oak-Orchard Lane quadrat, chamise reproduction by seedlings and sprouts was vigorous nine years after fire with seedlings far outnumbering sprouted plants. In the same stand, *Ceanothus* had been largely destroyed by the fire—*Ceanothus* seedlings being few in number. At this Oak-Orchard Lane fire area

Table 1. Chamise seedling and crown sprout reproduction after 6, 8, or 9 years since the last fire on quadrats from three areas near Newhall, CA.

Location and time after fire	Elevation meters	Slope aspect	Total chamise on 10 × 10 m quadrat	Number chamise seedlings per quadrat and % of total	Mean height seedlings and standard deviation	Number chamise crown sprouts per quadrat and % of total	Mean height crown sprouts cm and standard deviation	Number dead chamise per quadrat
Wildwood Canyon Road 6 years	440	south facing	115	74, 64%	33 ± 19	41, 36%	82 ± 22	34
Castaic single fire 8 years	595	south facing	131	123, 94%	91 ± 27	8, 6%	108 ± 17	10
Oak Orchard Lane 9 years	410	north facing	127	123, 97%	93 ± 30	4, 3%	111 ± 46	5
Total of all 3 quadrats	—	—	373	320, 86%	—	53, 14%	—	49

the quadrat chosen was representative of the whole burn since crown sprouted plants were in low percentages over this entire north facing slope. They were present in slightly greater numbers in the more mesic environment at the bottom of the ravine, however.

Four years after the fire at the Castaic site, seedlings outnumbered crown sprouts approximately 3 to 1 as reported by Howe (1976). Data for 26 April 1978, eight growing seasons after the fire at Castaic, are reported in Table 1. Here, as at the other two localities, seedlings far outnumbered the resprouted plants.

Observations of the Castaic double-fire quadrat revealed that two distinct types of chamise plants existed four years after the second fire: (1) type-1 crown sprouted plants that were relatively small, having grown as postfire seedlings after the 1970 burn and then crown sprouting after the 1974 fire and (2) type-2 crown sprouted plants which gave evidence of having sprouted twice—once after the 1970 fire and again after the 1974 burn. This was apparent from the fact that the type-2 plants had both large and small burned stumps present. There were no postfire seedlings of the 1974 burn. On the double-fire quadrat 37 chamise plants (82%) were type-1 while 8 (18%) were type-2. There were 7 dead crowns on the quadrat on 26 April 1978. Statistical comparisons involving type-1 and type-2 crown sprouts are presented in Table 3.

Height comparisons.—After six growing seasons following fire, the mean height of chamise seedlings at the Wildwood Canyon Road quadrat (Table 2) was significantly shorter than the mean height of chamise crown sprouts on that same quadrat ($P < 0.001$). These same six-year chamise seedlings of Wildwood Canyon Road were significantly shorter in mean height than the eight-year seedlings of Castaic ($P < 0.001$) and the nine-year seedlings of Oak Orchard Lane ($P <$

Table 2. Mann-Whitney U-test values for various chamise quadrat comparisons with the level of significance and sample size in parenthesis. N.S. indicates not significant at the 5% level.

Location and time after last fire	Type of plants	Wildwood Canyon Road 6 years		Castaic 8 years	Oak Orchard Lane 9 years	
		Seedlings (n = 72)	Crown (n = 41)	Crown (n = 8)	Seedlings (n = 123)	Crown (n = 4)
Wildwood Canyon Road 6 years	Seedlings (n = 72)	—	2817 ($P < 0.001$)	—	—	—
Wildwood Canyon Road 6 years	Crown sprouts (n = 41)	—	—	259 ($0.01 < P < 0.02$)	—	114 (N.S.)
Castaic 8 years	Seedlings (n = 123)	8410 ($P < 0.001$)	—	686 (N.S.)	7570 (N.S.)	—
Oak Orchard Lane 9 years	Seedlings (n = 123)	8457 ($P < 0.001$)	—	—	—	310 (N.S.)

0.001). The mean height of chamise crown sprouts at Oak Orchard Lane (9 years), on the other hand, was not significantly different than the mean height of crown sprouts at Wildwood Canyon Road (6 years).

Comparing the mean height of seedlings with that of crown sprouts from the same quadrat eight or nine years after five (Castaic and Oak Orchard Lane respectively) there were no significant differences—see Table 2.

Where two fires had occurred within four years of each other (Castaic double-fire quadrat) no significant difference existed between the mean height of the type-1 and type-2 sprouters (Table 3). These type-1 and type-2 Castaic double-fire plants likewise showed no significant mean height differences when compared to the six-year crown sprouted plants of the Wildwood Canyon Road quadrat.

Discussion

Seedling survival.—Since the data of this study arise from selected quadrats where seedling survival was obvious, sweeping conclusions may not be legitimately drawn regarding the overall reproductive tendencies of *Adenostoma* throughout its entire range. However, the results are characteristic of postfire regrowth in this particular region of Southern California and they demonstrate that seedling reproduction of chamise is not unknown and certainly not unimportant after fires in the chaparral.

Seedlings were of greater importance than crown sprouts in the postfire reproduction of chamise on all three quadrats selected for study in the Newhall-Castaic CA. area (see Table 1). Six years after the Wildwood Canyon Road fire, seedling reproduction was more vigorous than crown sprouting on the south facing slope but not on the north facing slope of that same ridge.

This north facing slope where sprouters predominated doubtlessly differs in irradiation, available moisture, and certain other factors from the south facing

Table 3. Mann-Whitney U-test values for various chamise quadrat comparisons with the level of significance and sample size in parenthesis. N.S. indicates not significant at the 5% level.

Location and time after last fire	Type of plants	Castaic double fire, 8 years, 4 years Type-1 crown sprout (n = 37)	Castaic double fire, 8 years, 4 years Type-2 crown sprout (n = 8)
Castaic double fire: 8 years, 4 years	Type-1 Crown sprouts (n = 37)	—	199 (N.S.)
Wildwood Canyon Road 6 years	Crown sprouts (n = 41)	779 (N.S.)	200 (N.S.)

ridge where seedlings were most abundant. Our data here conform to a suggestion by Hanes (1971) that sprouters may be at a disadvantage on xeric sites when compared to seedlings. In other areas sprouters may have the advantage, depending on available moisture and drought stress after fire. Certain other factors such as intensity of the fire also have a bearing on which types of reproduction will be most advantageous.

Vogl and Shorr (1972) concluded ". . . that *Arctostaphylos* and *Adenostoma* seedlings seldom contribute to mature chaparral cover." They indicated that perhaps selective herbivore activity explained the demise of seedlings. Likewise, Wells (1969) asserted that when a taxon can reproduce by both crown sprouting and seedlings after fire, crown sprouted plants will consistently be more important than seedlings in the establishment of the new population.

Horton and Kraebel, however (1955) reported that chamise seedlings were still surviving and had reached an average height of 31.9 inches 25 years after fire in chaparral near San Bernardino. In citing an earlier 1944 paper by Sampson, Wells indicated that ". . . chamise possesses an equally superb capacity for reproduction by crown-sprouting or by seed . . . ."

Hanes and Jones (1967) found prolific germination of *Adenostoma* seeds producing seedlings after fire in the San Gabriel Mountains. In a comprehensive study, Hanes (1971) reported that at altitudes between 1000 and 2000 feet, 27% of the chamise plants regrowing after fire were known to be seedlings. This figure might have actually been higher as some of the 22% which he reported as "undetermined" in origin (seedling or sprouter) may also have been seedlings. Concerning *Adenostoma* he wrote that "It sprouts vigorously and also germinates from dormant seeds, and composes about one-third of the plant cover during the first decade after fire . . . ." He found that altitude has a bearing on which type of reproduction of chamise predominates—"Chamise, for instance, has a higher proportion of seedlings at 1,000–2,000 ft (ca. 300–600 m) than at 2,000–4,000 ft (ca. 600–1,200 m)."

In undertaking a major study of factors which affect germination of seedlings in *Adenostoma* chaparral, Christensen and Miller (1975) found that seeds of chamise germinated at least to some extent in all four conditions they studied—undisturbed shrub cover, artificial clearings, the first year following fire, and in the second year following fire. They found that the foliar leachate from chamise was inhibitory to the germination of certain herbs and not others. They reported no data on the effect such foliar leachate might have on the germination of *Adenostoma* seeds themselves. Yet they indicated that seedling growth was widespread after fire.

While seedling survival may be low under certain circumstances (Vogl and Shorr 1972; Wells 1969) the results of the present study are in clear agreement with Horton and Kraebel (1955), Hanes and Jones (1967), Hanes (1971) and Christensen and Muller (1975) in that chamise seedlings survived vigorously and contributed in large measure to the postfire stands of *Adenostoma* on the quadrats studied.

Differences in height between seedlings and crown sprouted plants existed at the six-year stage but had vanished after eight or nine years of growth after fire. Such data fit with the observation that crown sprouted plants are larger than corresponding seedlings during the first few years after fire. This difference may be attributable to several factors. Crown sprouts form on burned plants in just a few weeks and shoots over 12 inches tall may exist before the first rainy season begins. Likewise, crown sprouted plants may have a fully developed root system immediately after the fire whereas seedlings generally do not begin growing until the rains arrive which may be a period of up to six months, depending on the date of a particular burn.

Seedlings on the Castaic and Oak Orchard quadrats had grown eight or nine years respectively to the point where they were just as high as the corresponding crown sprouted individuals. It may be reasoned from such data that although seedlings grow more slowly during the first few years after fire, they ultimately achieve a height which is equal to that of the sprouters.

In the Castaic double-fire, seedlings that had grown for four years after a fire were able to survive a second fire in good numbers, although there was an unusually large number of dead chamise crowns on this quadrat as compared to the number of dead crowns on the single-fire quadrats. Some of the original plants survived the second fire, demonstrating the ability of chamise to sprout twice in four years time.

The fact that there were no seedlings evident four years after the second fire may have been attributable to one or more of the following factors:

(1) low seed production during the first four years of growth after the first fire (1970–1974).
(2) different moisture regime after the second fire (1974) than after the first (1970).
(3) different herbivore densities after the second than after the first fire.

Crown sprouting, speciation, and fire adaptation.—Wells evaluated twenty chaparral genera regarding the number of taxa they contain and the modes of reproduction they manifest after fire. The two genera having the largest number of taxa (*Arctostaphylos* with 75 and *Ceanothus* with 58) each contain whole sections which do not reproduce by crown sprouting. Among the other 18 genera, all of which regenerate after fire by sprouting as well as by seedlings, the number of taxa per genus is much lower, ranging downward from *Quercus* with twelve, to genera like *Pickeringia* (chaparral pea) and four others having only one taxon per genus. Wells attributed the large number of taxa in a genus to the loss of the ability to crown sprout which in turn forced that particular group (*Arctostaphylos* or *Ceanothus*) to reproduce sexually after each fire, thus causing the rate of natural selection and speciation to exceed that found in sprouting genera.

Our data have little fit with Wells' genetic hypothesis since it was quite easy to find whole areas in the Newhall, CA. region in which seedling germination and survival after various fires was vigorous. If *Adenostoma* produces large numbers of seedlings that survive (as in our data and in the results of others) then speciation would be expected to have gone on just as rapidly as among the obligate seeders. Thus Wells' theory does not explain why *Adenostoma* has fewer taxa than either *Arctostaphylos* or *Ceanothus*.

Keeley (1977) evaluated the hypothesis of Wells as ". . . not overly compelling" because the ". . . nonsprouters do not appear to have any such obvious advantage; sprouting species are very successful." Furthermore, Keeley wrote that ". . . the sprouting species of *Arctostaphylos* and *Ceanothus* also produce many seedlings," as we have also shown in this one locality for *Adenostoma*.

Keeley has proposed instead what he called a "Stochastic Fire Hypothesis" (1977) to explain how both obligate seeders and sprouters may each manifest an adaptive advantage under different circumstances. Since the crown sprouting adaptation is apparently beneficial in chaparral regions, Keeley and Zedler (1978) addressed the question of why certain species of *Ceanothus* (such as *C. greggii*) and *Arctostaphylos* (such as *A. glauca*) have no capacity to sprout—reproducing only by seedlings after fire.

Based on an extensive series of their own experiments and reports of others, they concluded that sprouting reproduction is advantageous where there has been an abnormally short length of time between fires. They reasoned that such a situation ". . . would be only slightly damaging to a sprouting species, and reproduction could be safely deferred or reduced for the first years after fire and all energy dedicated to growth." The data from our double-fire plot support this contention in that no seedlings of *Adenostoma* survived when a second fire followed four years after the first burn. But under such circumstances sprouters of two classes were present—type-1 plants which grew as seedlings after the first fire and sprouted after the second fire and type-2 plants which sprouted after both fires.

In the stochastic fire hypothesis of Keeley and Zedler, on the other hand, the obligate seeders such as *C. greggii* and *Arctostaphylos glauca* have a distinct advantage wherever there has been an especially long fire-free period before the burn. After a long period, they reasoned, the sprouting individuals such as *Adenostoma* will be few in number because of previous thinning in the old stand prior to the fire and death as a result of the intensity of such a fire. Keeley and Zedler (1978) proposed that under such circumstances ". . . the longer the fire-free period, the larger the opening after fire." Since seedlings are well equipped to survive in chaparral openings, the obligate seeder adaptation is of advantage where fires are infrequent.

By the same token, the sprouter species are adapted for survival and spread where fires come in close succession. By means of the stochastic fire hypothesis it is thus possible to envision how both obligate seeders and sprouters can be successful in the same chaparral area.

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A New Frog of the Genus *Eleutherodactylus* (Leptodactylidae) from the Monteverde Forest Preserve, Costa Rica

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Abstract.—A new frog of the genus *Eleutherodactylus* (Leptodactylidae) from the Monteverde Forest Preserve, Costa Rica by Jay M. Savage, *Bull. Southern California Acad. Sci.*, 79(1):13–19, 1980. *Eleutherodactylus cuaquero* from the Monteverde Forest Reserve in the Cordillera de Tilaran, Costa Rica, is described as new. The species appears to be closely allied to *El. andi* of central montane slopes of Costa Rica. Both forms appear to be members of the *fitzingeri* species group. *El. cuaquero* is unique in the family Leptodactylidae in the condition of the jaw muscles with three major slips to the depressor and only an externus adductor (formula: DFSQAT + e).

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In 1964 as part of the fieldwork associated with the discovery of the unusual toad, *Bufo periglenes* (Savage 1967), collections were made of other amphibians in the area around the famous Quaker colony at Monteverde, Provincia de Puntarenas, Costa Rica. Included in these samples were two female *Eleutherodactylus* resembling *El. andi* of the *fitzingeri* group (Savage 1974, 1976) that seemed to represent an undescribed species. Description of this form has been delayed in the hope that a male example might be obtained. After 15 years the hope has not materialized. The forest area around Monteverde has now been established as a preserve to protect *B. periglenes*, where all collecting is strictly prohibited and there appears to be little likelihood that another 15 year wait will produce a male example. For this reason it seems wise to describe the new form at this time as:

Eleutherodactylus cuaquero, new species

Figure 1

Holotype.—LACM 128460, an adult female from 1.75 km east southeast of Monteverde; Provincia Puntarenas, Canton de Puntarenas, Costa Rica; 1520 m; collected by Jay M. Savage and Fred S. Truxal, May 17, 1964. *Paratype*: CRE 7213B, an adult female, with same data as holotype.

Diagnosis.—*El. cuaquero* is a member of the *fitzingeri* group (Savage, 1976) and allied to Central American members (*andi*, *fitzingeri*, *rayo*, and *talamancae*) of this stock having a minimal amount of toe webbing. The other Central American members of the group (*crassidigitus* and *longirostris*) have the web between toes III–IV extending nearly to the distal subarticular tubercle on finger III and to halfway between proximal and penultimate subarticular tubercles on finger IV. From its congeners of this group with minimal webbing (features for *cuaquero* in parentheses) it is immediately distinguished from *El. rayo* of Costa Rica and *El. talamancae* of Atlantic lowland Nicaragua, Costa Rica and Panama which have the posterior thigh surface uniform (posterior thigh surface spotted). In addition *rayo* has a heel calcar (absent) and *talamancae* has a distinct enamel white stripe or series of spots along the upper lip (absent).

The two remaining allied forms with spotted thighs (*El. fitzingeri* and *El. andi*), that might be confused with the new form have toe webbing that usually extends to the proximal subarticular tubercles between toes I–II–III and slightly beyond the proximal subarticular tubercles between toes III–IV (webbing barely extending to level of proximal margin of proximal subarticular tubercle on any toe). The three forms may be further separated by the following features:

andi—finger disks greatly enlarged, III–IV emarginate, equal to or broader than length of inner metatarsal tubercle; posterior thigh surface dark chocolate brown with discrete large bright-yellow (in life) stripes or spots; groin with bright-yellow (in life) large spots or stripes; throat almost solid black to dark brown, undersurfaces of body and limbs heavily marked with dark brown spots or mottling; light areas on posterior undersurfaces bright yellow, almost always suffused with

Fig. 1. Dorsal view of adult female holotype, LACM 128460 of *Eleutherodactylus cuaquero.*

bright salmon red in life; adult males 40–55 mm in standard length, adult females 65–80 mm.

cuaquero—finger disks greatly enlarged, III–IV emarginate, broader than length of inner metatarsal tubercle; posterior thigh surface dark brown, with small bright yellow spots or vertical stripes; groin mottled; throat and hindlimbs heavily marked with dark brown pigment; posterior undersurfaces bright yellow, suffused with bright pink in life; adult females 33–47.5 mm in standard length.

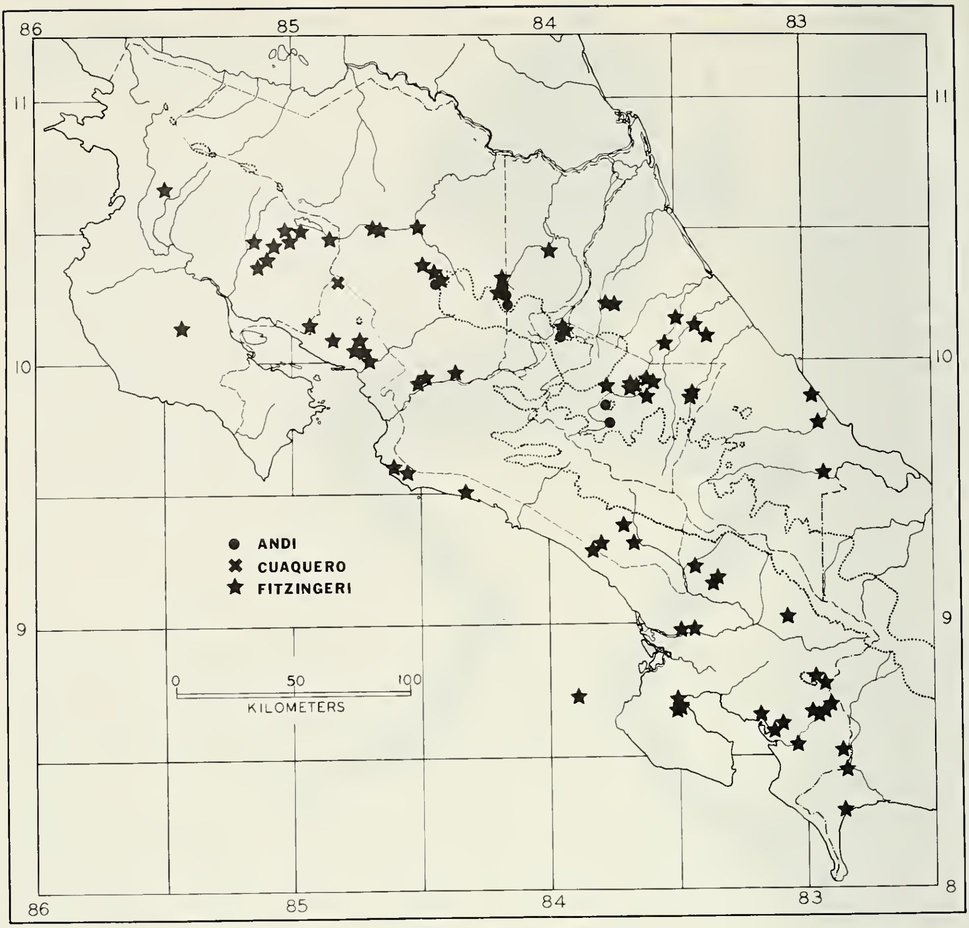

Fig. 2. Distribution of *Eleutherodactylus cuaquero* and allied species of the *fitzingeri* group in Costa Rica. The dotted line indicates the 1500 m contour.

fitzingeri—finger disks moderately enlarged, III–IV barely indented, narrower than length of inner metatarsal tubercle; posterior thigh surface dark black to brown, with numerous small pale yellow spots in life; groin mottled or uniform; throat almost immaculate to heavily mottled with dark brown; undersurfaces white with a yellow cast posteriorly and under thighs, usually immaculate but sometimes weakly mottled with dull gray and rarely strongly mottled with dark brown; adult males to 35 mm in standard length, adult females to 52 mm.

Summary of characteristics.—GENERAL: Head about as wide as long. Nostril closer to tip of snout than to eye. Dorsal outline of snout subovoid to subelliptical; rounded in profile. Canthus sharp; loreal outline obtuse. Choanae ovoid, vomerine teeth located between and behind choanae in two transverse series separated at mid-line. Tympanum internal, indistinct, oval, a little less than ½ height of orbit. Skin of head and upper surfaces essentially smooth with a few scattered pustules. Each upper eyelid with a distinct tubercle. Finger II longer than I.

Finger disks about 2 times as wide as digits on fingers III–IV: rounded and expanded on finger I, palmate on finger II, emarginate on fingers III–IV. No distinct fringes on fingers. Subarticular tubercles flattened, rounded in outline, globular; no supernumerary tubercles; thenar tubercle elongate, palmar large cordate; no accessory palmar tubercles. No calcar, although heel with several tubercles. Toe disks emarginate or notched, about 1.5 times width of digit on toes I–IV. Toe fringes weak. Modal toe webbing formula: I2^{+}–½II2^{+}–3½III3^{+}–4^{+}IV4^{+}–3^{-}V. Subarticular tubercles projecting, ovoid, in outline, obtuse in profile; no supernumerary tubercles; outer plantar tubercle round, ¼ size of inner oval plantar tubercle. An inner tarsal fold. Venter smooth.

COLORATION: Upper surfaces of head and body dark brown, limbs lighter brown. An obscure interocular dark bar bordered anteriorly by an obscure light area; upper lips with three dark bars; a definite supratympanic dark mark running from middle of eye above tympanum and downward toward shoulder. Iris of eye dark brown below, upper half silver, in life. Dorsum nearly uniform with weak dark spots associated with dorsal tubercles. Dorsal surfaces of limbs with dark crossbars. Posterior surface of thigh dark brown with distinct light spots or spots lined up to form vertical stripes. Throat and underside of hindlimbs heavily marked with dark brown pigment; distinct light longitudinal stripe running length of throat. Plantar surface uniform. Groin and flanks without distinctive markings. In life, hindlimbs and groin suffused with pale rose.

MEASUREMENTS: In the following section the measurement for the holotype is given first followed by that for the paratype (CRE 7213B) in parentheses. Standard lengths are in millimeters; other measurements are given as percentages of standard lengths.

Standard length 47.5 (33.0); head length 39.6 (40.9); head width 39.4 (38.2); length of orbit 15.2 (16.7); snout length 18.7 (19.7); loreal length 12.0 (13.0); height of tympanum 6.9 (7.0); hindlimb length 230.7 (227.9); tibia length 75.4 (71.8).

Jaw musculature.—The types have the depressor mandibulae originating as three distinct slips, one each from the dorsal fascia, squamosal and annulus tympanicus. This is the DFSQAT condition according to the system of Starrett (1968). An adductor mandibulae externus superficialis is present (e).

Distribution.—Known only from the lowermost portion of the lower montane rainforest 1.75 km ESE Monteverde in the Cordillera de Tilaran, Costa Rica, 1520 m (Figure 2).

Ecological associates.—Both known examples of *El. cuaquero* were taken early in the evening (7–9 p.m.) on herbaceous vegetation 1–1.5 m high. Ecological associates included the frogs: *Eleutherodactylus angelicus, El. cruentus, El. diastema, El. melanostictus, El. ridens, Hyla rivularis, H. pseudopuma, H. uranochroa, Centrolenella colymbiphyllum* and *C. prosoblepon* and the lizard *Norops tropidolepis*.

Remarks.—The name *cuaquero* is an arbitrary combination of letters that happens to mean Quaker in Spanish. The name is used in allusion to the habitat of this frog, whose type locality is located on part of the property that formed the original land holdings of the Quaker colony at Monteverde. The settlement was established in 1951 on the Pacific slope by 15 families of North American Quakers whose moral and economic beliefs led them to emigrate so that their taxes would not be used for the construction of nuclear armaments. By 1954 the Quakers had established a cooperative cheese factory where the famous Monteverde brand cheeses continue to be made.

The Quakers from the beginning at Monteverde strongly believed in preservation of forest tracts and a watershed preserve. The flora and fauna of the area is especially rich and the discovery of the unique toad, *Bufo periglenes* Savage, 1967, on the continental divide above Monteverde, heightened the Quakers' interest in conservation of the local biota. George Powell, originally an American Peace Corps worker, conceived the idea of establishing a permanent nature preserve in the area in 1971 and led a campaign to raise funds from a variety of sources to make the Monteverde Forest Preserve a reality. The Quaker colony donated 900 hectares of the some 2800 hectares that now comprise a preserve that involves both Atlantic and Pacific slope areas to the north and east of Monteverde proper. The preserve includes 7 major tropical plant formations and ranges in elevation from 1500–1842 m. The preserve is now owned and operated by the nonprofit Tropical Science Center of San Jose and is enjoyed by many visiting nature lovers each year. A visitor's center and a recently completed field station supplement the accommodations at Monteverde, for those interested in observing and/or photographing the rich biota of upland Costa Rica in this essentially undisturbed preserve.

Relationships.—Eleutherodactylus cuaquero clearly belongs, on the basis of external morphology, to the *fitzingeri* group (Savage 1976). Members of this stock have smooth venters, an inner tarsal fold, at least basal toe webbing and enlarged disks on all fingers and toes. Lynch (1976) has advocated inclusion of a number of species usually associated with the *rugulosus* (Savage 1975) and *gollmeri* (Savage 1976) groups into a larger unit including the *fitzingeri* group (*sensu* Savage), on the basis of trivial external features. Savage and DeWeese (1979) pointed out similarities between the *fitzingeri* and *rugulosus* groups in karyology and jaw musculature, but refrained from attempting to undertake a full critique and evaluation of Lynch's schemata.

Up until the present time all members of the *fitzingeri* group whose jaw muscles had been examined had the depressor mandibulae forming a single slip with an origin primarily from the dorsal fascia and a few fibers coming from the squamosal and the adductor mandibulae externus superficialis present (dfsq + e, using the formula of Starrett 1968). *El. cuaquero,* which on the basis of all other features seems very close to *El. andi,* differs not only from other members of the *fitzingeri* group in which the jaw musculature is known, but is unique in the family Leptodactylidae in having a formula of DFSQAT + e. The interpretation of the significance of this feature must await detailed studies of interspecific and intergroup variation in jaw muscle features. Suffice it to say that the muscle character strongly confirms the validity of *El. cuaquero* as a distinctive species.

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Navajo Social Interactions in an Urban Environment: An Investigation of Cognition and Behavior

Shirley J. Fiske[1] and J. C. Weibel[2]

Abstract.—Navajo social interactions in an urban environment: an investigation of cognition and behavior by Shirley J. Fiske and J. C. Weibel, *Bull. Southern California Acad. Sci.,* 79(1):19–37, 1980. This paper explores the relationship between the way people think and what they do, among a recently migrated urban ethnic group. The hypothesis is that people will seek assistance (housing, employment, friends) from other people whom they perceive as most similar to themselves. The paper compares two sets of data in an attempt to examine this relationship. Both cognitive and behavioral data on social interactions were collected from Navajo women in Los Angeles, California. The data indicate that urban Navajo women tend to establish their social assistance networks based on *some* of the underlying dimensions of their cognitive classifications of the urban social world, but that in other respects their behavior diverges from the expected

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pattern of social interaction. The dimension of traditional vs. acculturated, used as a tribal marker in choosing assistance and friends, appears to be the strongest predictor of behavior. Regionalism and anti-white sentiment are not as strongly associated as expected with choice of assistors. The anomalies in these expectations and their implications for understanding the relationship between cognition and behavior are discussed.

Introduction

In the last 30 years anthropology has demonstrated much theoretical and methodological interest in determining the "native's" point of view. This trend has borne many labels, namely, formal analysis, componential analysis, ethnoscience, the "new ethnography," and cognitive anthropology. One common assumption is that the goal of ethnography is to understand what the native will do in any given situation. Thus, as phrased by Goodenough (1964:36), a goal of ethnoscience is a description "of whatever it is one has to know or believe in order to operate in a manner acceptable to its [a society's] members." A more basic premise, then, is that culture is an ideational phenomenon; it is a system of categories and rules for their use.

With the aid of 25 years of hindsight it appears that cognitive anthropology has focused almost entirely on discovering and organizing the ideational aspects of culture. The enduring criticisms of ethnoscience are that it is trivial, too devoted to obscure methodologies, too time consuming, and above all too isolated—it has ignored the relevance of cognitive structure to people's everyday behavior (see Berreman 1966; Burling 1964; Harris 1968).

Recognizing both sides of the issue, Keesing has proposed that the nature of culture is similar to the nature of language: just as linguistic behavior includes both competence *and* performance, so too culture includes an ideational aspect *and* observable behavior (Keesing 1971). The challenge inherent in conceptualization of culture lies in refining the relationship between the two aspects.

In recent years there have been several notable attempts to link cognitive analyses with measures of observable behavior. Johnson (1974) shows that the manner in which people categorize land types and appropriate crops predicts the pattern of planting (i.e., the direction of deviation from a random planting pattern). He concludes that the "cognitive model does appear to summarize or account for the main trends in observed planting behavior" (1974:96). Additionally, Howe and Sherzer have analyzed what they call a "practical" classification of crops—one based on rules of access to the crops. They discuss the relevance of the classification to understanding behaviors of theft, generosity, and economic behavior (Howe and Sherzer 1975). Sanjek (1977) analyzes urban ethnic terms in Accra, Ghana, and compares the classification with actual interactions; Young analyzes Tarascan illness categories and relates the distinctions among them to strategies for prevention (1978).

This paper is a continuance of this hopeful trend. We will outline the cognitive configuration of social groups *and* the actual interactional patterns which Navajo demonstrate. We will examine the degree of fit between the two data sets. Two distinctive data types are used: the first set are cognitive data, gathered using ethnoscientific techniques and analyzed using nonmetric scaling. The second set are behavioral data, gathered from intensive interviews and informant recall of social and assistance resources over a 10 year period in Los Angeles.[3]

Navajo in Los Angeles

Navajo are the most heavily represented tribal group in Los Angeles (Price 1968; U.S. Dept. of Commerce 1970). They are a recently arrived population from a culturally traditional rural area where the characteristic settlement pattern is sparse and widely dispersed. Except for the occasional visit to a bordertown, trading post, or the boarding school experience, the reservation social world is made up almost exclusively of other Navajo.

The incentive for migration to Los Angeles is primarily economic—to find jobs, higher wages, and improved living conditions. Upon arrival in Los Angeles Navajo tend to find residences (or are placed by the Bureau of Indian Affairs) either in the the Central City or Southeast sections of Los Angeles. Both are areas of high Indian concentration in which friends and relatives are well established. Navajo are a highly mobile and geographically dispersed population, exhibiting a general movement away from the Central City area into the Southeast and other more outlying suburban areas of the Los Angeles basin. The neighborhoods in which Indians choose to live were originally Anglo neighborhoods, now becoming increasingly Latino in influence and population.

While Navajo women generally enter the urban area as single individuals, most are now married. The vast majority of Navajo women have married within the tribe (Weibel 1977; Fiske 1975). The majority of Navajo women do not work outside the home but remain at home raising their young families. Those that are wage-earners are employed at unskilled factory, assembly, semi-skilled, and piece-work garment positions with commensurate incomes. Most of the women who do not work have husbands in blue collar positions.

Navajo consistently exhibit strong ties to their cultural tradition. The need to perpetuate certain Navajo crafts and skills, the use of traditional medicine and curing ceremonies and tribal language in the urban environment is still strongly felt by most people. Annual and seasonal trips back to the Navajo reservation are a way of life for a major segment of this population even after spending most of their adult lives in the urban environment. As the ethnographic data indicate, when Navajo migrate to urban areas the strong interactional ties within the tribe tend to be perpetuated (Ablon 1964; Fiske 1977; Hirabayashi 1972; Snyder 1971). Not only do they limit their interactions with Anglos, other ethnic groups, and Indians other than Navajos, but also their use of institutionalized public services is minimal. This social phenomena evokes several separate but related questions—how do Navajo organize and classify their social world? Given a social environment in which alternative assistance sources and friendship choices are

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multiplied, how do the Navajo solve the problems of living in a large cosmopolitan area? Is there any relationship between the social conceptualization and the people Navajo choose to assist them?

Cognitive Structure

Previous research with Navajo indicates that there is a domain of "living things," including "those with five fingers" or "people," and that the classification is used in traditional reservation areas (Perchonock and Werner 1969); but the classification does not include the most recent additions to the domain of people; namely, the tremendous variety of people experienced by Navajo when they reach a large metropolitan area such as Los Angeles. What happens to this new information? How is it integrated into peoples' cognitive organization?

Ethnoscientific techniques of elicitation frames (see Black 1969; Metzger and Williams 1966) and sorting tasks were used to discover the categories and inclusion/exclusion relations among all the terms within the domain. The analysis was carried one step further; lexical items were tested using both paired comparisons and triads tests. The triads and paired comparison tests were administered to the set of terms in Figures 1 and 2 (see Romney and D'Andrade 1964; Berlin, Breedlove, and Raven 1968; Nerlove and Burton 1972). Triads testing requires a respondent to choose the most similar (or dissimilar) terms in a set of three; for example, in the triad of intertribal terms: Navajo, Choctaw, and Cherokee, the two terms Choctaw and Cherokee were judged to be most similar. Triads data can be arranged in similarity matrices which yield quantitative information on how similar terms are to each other.

Paired comparisons require the respondent to verbalize both the similarities and differences between every possible pair of terms; this is a very useful (albeit time consuming) technique for discovering the semantic bases on which the triads judgments are made. Thus, for example, if the two terms Choctaw and Cherokee have a similarity measure of 89/100 by triad testing (that is, 89 times out of 100, these two tribes were judged to be most similar out of the triad of terms), the researcher does not necessarily have any understanding as to *why* they are judged most similar. Paired comparisons provide these data; each term is compared with every other term, such that the respondents generate information and distinctions which are important to them. For instance, Cherokee and Choctaw *share* the attributes of being

> "from the East; both show signs of a lot of education—go to college; both were the first to approve of their kids going to school; a lot of them are teachers; usually work in offices."

The two tribes are different in "their skin shade. Cherokee are light; Choctaw are darker." This kind of information about the content of the terms allows the researcher to interpret the triads data and subsequent scaling plots more completely.

The results of the triads tests were arranged in similarity matrices and analyzed using nonmetric multidimensional scaling to assess structure in the domain. Nonmetric multidimensional scaling indicates by arranging in multidimensional space the configuration which best represents the similarity data generated by the testing procedures (see Shepard 1962; Kruskal 1964; Burton and Romney 1975).

The cognitive data were gathered from three female Navajo respondents in a series of intensive interviews, elicitation, and testing sessions from 1971–1973. The small sample is a limitation to generalization, but there is reason to believe that the respondents and data are representative of the larger Navajo population. The women were purposively selected because their rural-urban experiences and current lifestyles were similar to many of the urban migrants. This is confirmed by comparison with Weibel's 47 respondents in her independent study (1977); the women in both studies are similar in length of time spent in Los Angeles (7.3 years in 1971 vs. 9.7 years in 1975), years of education (11.6 years vs. 11.2 years), and age (29.3 in 1971 vs. 30.2 in 1975). The women were selected from both suburban and downtown population areas and they represent both traditional and less traditional Navajo backgrounds. In addition there was a high degree of agreement among the respondents as to the terms and their structure. The classification is validated by Navajo behavior in the pan-Indian arena (Fiske 1977), and by the nature of the inter-ethnic relations established by Navajo women (Fiske 1978).

The multidimensional scaling results can be seen in Figures 1 and 2 in two separate analyses. As Burton and Nerlove point out, it is important that triads data be tested from the same semantic domain and be on the same level of contrast (1975:248). Hence, two separate testing procedures and analyses were carried out—one from the contrast level of ethnic groups (Fig. 2) and one for the intertribal contrast level under the cover term *bitsį'yishtłizhii* ('Indians') (Fig. 1).

As can be seen in Figure 1, there are two main clusters of people in the domain "five fingered beings"; (a) Indians and Mexicans cluster together at the extreme lower pole of the vertical dimension, (b) 'foreigners,' 'people from overseas,' 'enemies,' and 'white Americans' cluster together at the extreme top of the configuration. Asians and Blacks are in intermediate positions peripheral to either cluster.

In interpreting the Figure 1, the strongest dimension is the vertical one of social distance between Indians and Mexicans, and the constellation of concepts which represent Caucasians. Both Asians and Blacks are intermediate in social distance. Mexicans are unequivocably the most psychologically accessible group to Indians (from the Navajo perspective).

Turning to the second analysis—the intertribal domain—it appears that Navajo women conceptualize other Indians in two major clusters which can be interpreted along two dimensions. Figure 2 illustrates the configuration of the partial domain *bitsį'yishtłizhii*. The cluster on the upper half of the scaling plot, which includes Navajo-Apache and Hopi-Zuni dyads, is considered to be a Southwestern group of tribes; that is, they share a regional and ecological base with Navajo. The clusters on the lower half of the configuration are from very different geographical bases, and at the farthest regional extremity from Navajo are *hak'az dine'e*, 'Eskimo,' who live in a region of snow and cold—very different from the Navajo desert environment. Hence, the two clusters are arranged along a vertical dimension of *regionalism*, ranging from the 'Pima' (*ketł'ahi*) in the extreme Southwest, through Navajo and Oklahoma Indians, and with 'Eskimo' on the polar end of the dimension.

The two clusters also demonstrated a horizontal dimension of traditionalism and acculturation. On the extreme right-hand side of the configuration are *diné*

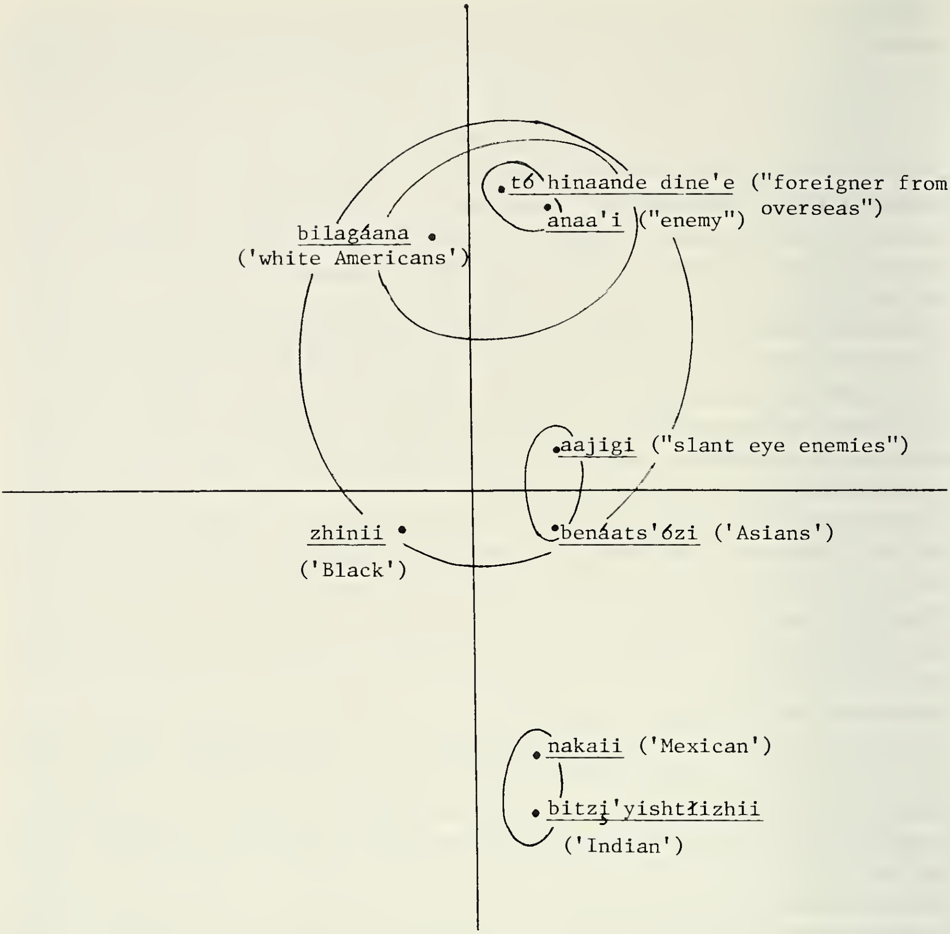

Fig. 1. Multidimensional scaling plot for triads test, ethnic categories. The clusters indicate hierarchical clustering results (see Johnson 1967; D'Andrade 1973).

('Navajo'), who in their own opinion are the most traditional—the most "Indian" of all the tribes. On the extreme left-hand side of the tribal array are the Cherokee, a tribe who the Navajo feel have capitulated their tribal customs to become part of the white world.

As mentioned previously, Navajo perceive themselves to occupy the position of most extreme traditionalism. Clustered closely with them are Apache, Hopi, and Zuni; these core traditional tribes are perceived as retaining their language, traditional housing, clothing, hair styles, and ceremonies. Pima and Paiute are seen as somewhat more acculturated than the core tribes; but they along with California Indians and Eskimo[4] are seen as having lost most of their traditional culture, retaining fewer of their religious ceremonies, and having less dependence

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[4] The Eskimo are perceived as very traditional by most Navajo, but this is not reflected in their position on the scaling plot because of general unfamiliarity with specific traditions.

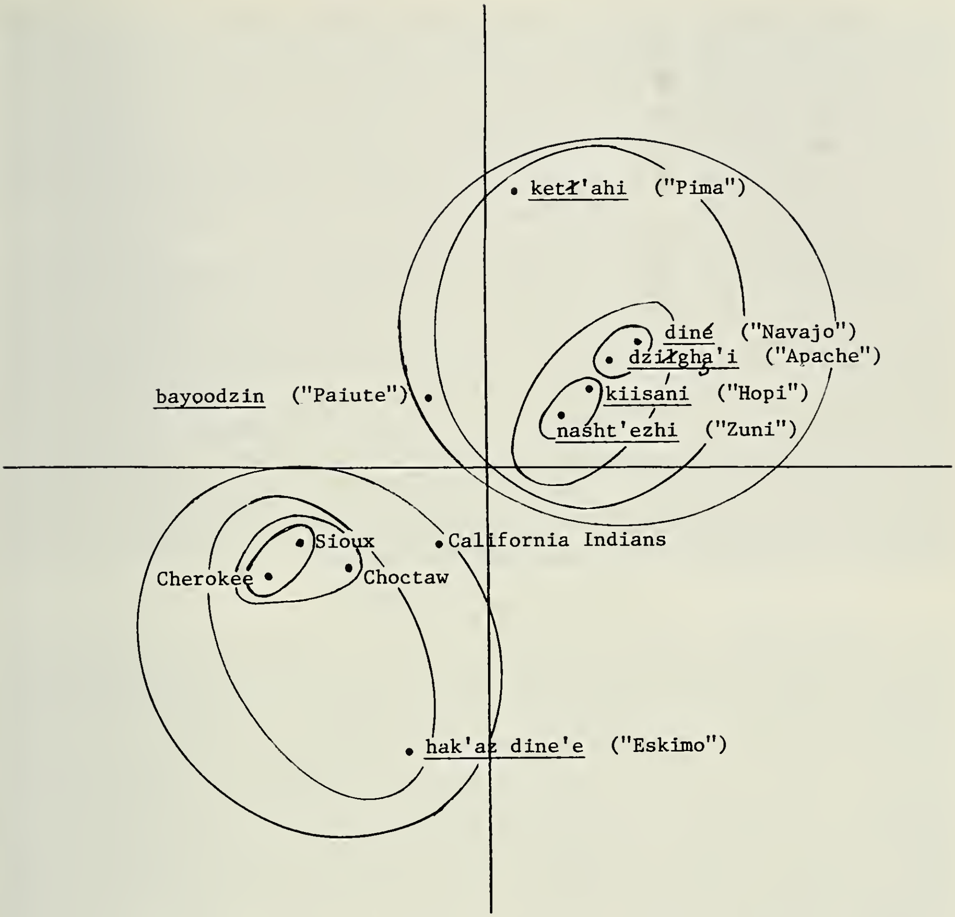

Fig. 2. Multidimensional scaling plot for triads test, intertribal categories.

on traditional subsistence activities (such as growing one's own food, making one's own household utensils).

Moving farther to the left-hand side along the traditional/acculturation dimension, the Choctaw, Cherokee, and Sioux are perceived as least traditional of the major tribes. On the extreme pole of the acculturation dimension, Cherokee are characterized as "eating out of cans, like the whites," having lots of education, not being shy around whites, being more city-oriented and less reservation-oriented, not speaking their language, etc.[5]

To summarize, in interpreting the social-psychological classification of Navajo women, there is a strong affinity for Mexican-Americans, an ambivalence towards Blacks and Asians, and definite social distance from the constellation of concepts for Caucasians. In the intertribal domain the social world is clustered into two

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[5] For a more detailed analysis of Navajo perceptions of the intertribal domain as it relates to participation in pan-Indian organizations and social interaction, see Fiske 1977, and 1975.

main groups: those traditional tribes of the Southwest, with whom the Navajo feel most comfortable and share a traditional orientation; and a second cluster, with whom the Navajo feel they share less in common regionally and who have become more acculturated than the Navajo. We might expect, then, given these cognitive organizations of the social universe, that Navajo women would prefer to interact with members of those social categories with whom they share the most identifying traits—Mexican-Americans among major ethnic groups, and Navajo and Southwestern Indians among Indians.

Research has shown that as perception of similarity between items increase (i.e., the more traits, dimensions, etc. which are shared in common between items), then those items will receive similar behavioral responses (Romney and D'Andrade 1964; D'Andrade 1974). In other words, if Navajo judge themselves to be most similar with Apache, Hopi, and Zuni, and least similar to Oklahoma Indians, then one would expect that they will behave toward these Southwestern Tribes as they would toward members of their own tribe—initiate social relations, friendships, seek assistance, and so on. One would not expect these kinds of behaviors to be directed toward people for whom there was little demonstrated judgment of similarity, namely the Oklahoma Indians.

Social Interactional Patterns

In an independent study conducted in 1975 and 1976, Weibel worked with Navajo, Choctaw, and Cherokee, Creek, Seminole, and Chickasaw informants[6] who had migrated to Los Angeles since 1950. Starting with a list of clients from a major Los Angeles Indian health service agency and by initiating a system of personal referrals, Weibel was able to interview intensively 47 Navajo and 37 Oklahoman Indians who, at the time of the interview, were predominantly young mothers with pre-school and school age children still in the home. The women were 30.2 years old on the average, had 11.2 years of schooling, and were living in neighborhoods with approximately the same socioeconomic status. These areas are predominantly low income, older working class white or Mexican-American neighborhoods. For purposes of analysis here, we will utilize only the Navajo patterns of interaction.

The interview consisted of both open-ended and semi-structured questions which elicited personal history of pre-Los Angeles life, the migratory process, and the problem-solving strategies they employed in the re-establishment of their lives in the urban environment. The respondents were asked to recall real life situations in which they had sought out information and assistance in the urban setting for such necessities as housing, employment, medical services, and general social services. To account for the influence of time in the city on their behavior, the respondents were asked to recall both their *initial* and their *most recent* assistance seeking situations.

Opportunely, one of three measures of assistance patterns is ethnicity. The vari-

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[6] Choctaw, Cherokee, Creek, Seminole, and Chickasaw Indians are the tribes who make up the so-called "Five Civilized Tribes." Historically agriculturalists indigenous to the southeastern sector of the United States, their ancestors were "removed" as a matter of federal policy to Oklahoma in 1830. In the interest of time, space, and enlightened anthropology we chose not to use the term "Five Civilized Tribes"; subsequently, this sub-cultural group will be referred to as the Oklahoma Indians.

able was coded in such a way that the descriptive categories are comparable to the ethnic categories of Figures 1 and 2. These sets of data, then, lend themselves to a comparison of cognitive perceptions and actual social interaction in the urban milieu. We suggest that the cognitive categories and perceptions of social distance as identified by Fiske's work (1975, 1977) are operative and influence the selection, out of a wide array of possible ethnic categories, of those people whom one cognizes as most similar.

Given the previous discussion about the cognitive classification, we hypothesize that Navajo interact with other Navajo significantly more often than they do with other Indian groups; that they prefer to interact with Southwestern Indians over other tribes; and that they interact least with the most acculturated and regionally different Indians (Oklahomans). Further, they interact more with other Indians and Mexican-Americans than they do with Anglos. Three behavioral areas are examined—locating housing, finding a job, and choosing friends. The first two are situations of involuntary action, where the ethnicity of assister may be a coincidental rather than purposive choice; the friendship network, however, is a matter of voluntary choice and personal preference. These two types of behavior patterns are chosen in hopes of discerning a difference between them.

Finding a Place to Live

One of the first problem-solving situations with which a person deals in the migration process is the location of a permanent place of residence. Two questions were asked to elicit this information: "How did you go about finding the first place you lived in Los Angeles?" and "How did you go about locating the house you presently live in?"

As can be seen in Table 1, in the initial search for housing, the assistance given by the Bureau of Indian Affairs (BIA) field office in Los Angeles was considerable; 50% of the Navajo's initial residence assisters were BIA counselors. If the individual had migrated to Los Angeles on her own, the most salient housing assister was another tribesperson or kin (44% of the assisters). Only three Navajo sought out housing assistance initially from anyone other than the BIA or another Navajo; the other assisters included a Mexican-American in-law, a Caucasian family for whom the participant had worked as a domestic, and the tribal newspaper *The Navajo Times*.

Importantly, in the initial housing search no Navajo interacted purposively with an Oklahoma Indian, who are conceptualized as being least like Navajo, even though there are proportionately more Oklahoma Indians than Navajo in the Los Angeles area. These two tribal groups constitute the two most heavily represented tribal groups in Los Angeles (Price 1972). One reason for this tribal exclusivity is that the bulk of the "same tribe" assisters were kin. This pattern of kin as the initial gatekeeper is a cross-cultural phenomenon of rural-to-urban migration (Aldous 1962; Gulick 1965; Farsoun 1970; Gans 1962; Hauser 1965; Snyder 1971).

Table 1 compares the initial search for housing with the strategy for finding the present residence. If the city exerts a sophisticating influence on interactional behaviors this early pattern of ethnic exclusivity should be modified in the later housing search.

In fact, in their most recent move, Navajos were even more exclusive in their choice of residence assisters (see Table 1). Fifty-seven percent of the Navajo

Table 1. Social interactions by cognitive categories.

		Tribal affiliation/ethnicity											
Behavior		Navajo	South-western[1]	Sioux	Okla-homa[2]	Other Indian	Total Indian	Mexi-can	Asian	Black	Anglo	BIA	Second-ary sources[3]	N
Housing assistance	initial	44% (21)					44% (21)	2% (1)			2% (1)	50% (24)	2% (1)	47
	last	57% (27)		4% (2)	2% (1)	2%* (1)	66% (31)	4% (2)			8.5% (4)	4% (2)	17% (8)	47
Employment assistance	initial	32.5% (14)	4.6% (1)			4.6%** (2)	42% (18)		2% (1)		7% (3)	23% (10)	26% (11)	43
	last	38% (6)	6% (1)			13%*** (2)	56% (9)	6% (1)			13% (2)		25% (4)	16
Choice of friends		64% (115)	3.4% (6)	2.8% (5)	2.8% (5)	1.1%**** (2)	74.1% (133)	11% (20)	2.8% (5)	1.1% (2)	11% (19)			179

* Winnebago.

** Tribes unknown (not Navajo).

*** Indian Center, Winnebago.

**** Umatilla, Chippewa.

[1] Apache, Hopi, Zuni, Pima, Papago, Paiute (Cluster #1).

[2] Cherokee, Choctaw, Creek, Chickasaw, Seminole.

[3] Secondary sources include newspaper, classified ads, vocational school counselors.

sample interacted with only other Navajos. Dependence on the BIA was greatly reduced (two interactions). Two women used the help of Sioux and Mexican-American friends or neighbors. One used the help of a Winnebago and Cherokee friend from an all-Indian church. Interestingly, four Navajos chose assisters who were Caucasian, and eight answered ads in the classified section of a newspaper or employed the services of a real estate agent in locating their present housing. This distribution suggests some sophistication in use of urban institutions on the part of the Navajo sample, but indicates a continuing preference on the part of the Navajo sample for intra-tribal assistance in problem-solving situations.

The fact that the BIA was the most salient assister in the initial search for housing raises an interesting question in that Fiske's (1975) study elicited no equivalent cognitive social category. Where does this salient assister fit in a hierarchy of cognitive categories? If pressed, the women could remember that the BIA counselor was usually white. Occasionally an Indian would surface at the BIA field office; but that was not often the case, and we feel that the actual ethnicity of the BIA counselor is not an important variable since the participants who used the BIA relocation services exercised no personal selection in the ethnicity of their BIA counselor. The individual was simply assigned to the next available counselor when they arrived to be processed.

We suggest that the BIA is a buffer or marginal social category (Snyder 1971). When an Indian decided to move to the city, the migrant had the further choice of either going it alone (perhaps with the assistance of friends or kin already settled in the target urban center) or making the transition with the sponsorship of a BIA relocation program. That 50% of the Navajo sample chose to avail themselves of BIA assistance programs in making the shift from reservation or rural life to an urban-industrial lifestyle is indicative of the BIA's mediating influence and salience in the lives of the relocated Indian families. The BIA is a social category which serves initially as a bridge between two social interactional milieux (the reservation and the city); its salience decreases over time, presumably because ties with the Relocation Program are severed after housing is located and employment secured.

One further characteristic of these interactional patterns should be noted. Thirty-seven percent of the Navajos' last house hunting strategies consisted of self reports something like this: "Well after a while I got to know where the cheap housing was and where they would take kids, so I just went to that place and walked up and down the streets looking for 'For Rent' signs until I found a place." This self-reliance or "walk and search" strategy frequently recurred as an effective problem-solving technique of Navajo families. It suggests that these families have successfully developed a cognitive map of their urban environment and rather than initiate extratribal interactions have elected to problem-solve independently. When this behavior occurred, therefore, it was coded as an exclusively Navajo interactional pattern.

To summarize, even after an average of eight years in the city, the intra-tribal assistance pattern is the modal preference for Navajo women. Interaction with other tribes in the housing search is remarkably low. There were no cases of interaction with other Southwestern tribes, and after eight years, the Navajo women sought help from only one Sioux and one Oklahoman Indian. Among the other ethnic groups, Navajo sought help from Mexicans at a low but consistent rate.

The proportion of Navajo who contact Caucasians for help in locating housing increased somewhat over time, as did the percent of Navajo who used secondary sources to find housing. The discrepancies from expected behavior will be discussed more fully below.

Finding a Job

Locating steady employment in the urban work market pulls the individual into more heterogeneous social situations. If the traditional interactional patterns persist over time, they would suggest a strong cultural bias in the inclination to seek out one specific type of assister over the vast array of assistance possibilities in the urban environment.

The data indicate that essentially the same interactional patterns occur in the employment seeking situations as occurred in the search for housing. A third of the Navajo preferred the help of a Navajo friend, kinsman, or the self-reliant "walk and search" strategy in locating their first job in the city. Initially, 23 percent used the BIA vocational services and another 26 percent were assisted in their initial job search by the employment offices of the vocational schools in which they had been placed by the BIA vocational training program. Indians, other than Navajos, constituted only 9% of the interactions. There were no interactions with Oklahoma and Sioux Indians. Only three women were assisted by Anglo friends and one college student found work because of a suggestion by a Filipino classmate.

The general pattern of these assistance-seeking behaviors tends to persist over time. In the last employment search, once again, there is a very small proportion of interactions with Southwestern Indians; however, there are no cases of seeking assistance from either Sioux or Oklahoman Indians over the ten-year period. There is a continued reliance on a small number of Caucasians, and one quarter of the population use secondary sources to find employment.

One problem in comparing initial and last job search strategies is that 63% of the Navajo women who ever worked in the city were no longer working at the time of the interview. Of those who are still working, the modal strategy is to handle the job hunt independently or ask for the assistance of a Navajo friend.

One trend which appears to be borne out by both types of assistance-seeking behavior is that Navajo groups apparently interact in exclusion of other Indians. 83% of all the interactions among Indians were either "self-help" or the enlistment of help from one's own tribal members. This exclusivity is underscored by the relative availability of contacts with other Indian tribes, and particularly with Oklahoman Indians, who are also present in the neighborhoods in similar proportions. We suggest that the decision to seek the assistance of members from one ethnic group rather than another is a selective process that may reflect the cognitive salience of relative ethnic affinity.

Socio-Affective Ties

As has been suggested, assistance patterns in the urban environment are not always a statement of personal preference. The circumstances around the initial migration process and the vicissitudes of the job market in the urban-industrial complex place certain constraints upon the individual's selection of an effective assister. Alternatively, who one chooses to associate with during one's non-work-

Table 2. Tribal affiliation of five closest Indian friends by tribe of respondent.

Tribe of respondent		Tribal affiliation of friends Navajo	South-western	Sioux	Oklahoma	Other*	
Navajo	O	115	6	5	5	2	n = 133
	E	(65.96)	(5.95)	(4.33)	(43.79)	(12.98)	
Oklahoman	O	7	5	3	76	22	n = 113
	E	(56.04)	(5.05)	(3.67)	(37.21)	(11.02)	
Total		122	11	8	81	24	246

$\chi^2 = 174.53$.
df = 4.
$P = .001$.

* The category "other" includes one Chippewa and one Umatilla friend among the Navajo. The Oklahomans listed two friends from each of the following tribes: Arapaho, Winnebago, Athabascan, Mission, and one friend from each of the following tribes: Shoshone, Lummi, Menominee, Arikara, Cheyenne, Pomo, Sac and Fox, Kiowa, Caddo, Shawnee, and Natchez. Oklahomans could not identify the tribe of one closest friend but knew that one was from Oklahoma originally and one was from some place other than Oklahoma.

ing, non-problem solving time is an exercise of relatively greater personal choice and control. If the social cognitive categories are translated into observable behaviors, we would expect to observe more intra-tribal and intra-regional ties, and relatively fewer purely social interactions between the Navajo women and members of tribal groups outside the Southwest and ethnic groups other than Indian.

The women were asked to identify, by tribal affiliation or ethnicity, their five closest friends. The distribution of closest friends across the salient cognitive ethnic categories is summarized in Table 2. Navajo overwhelmingly (74%) seek out and maintain close friendship ties with other Indians rather than other ethnic groups. In addition, 64% of the Navajo's Indian friends are other Navajo. Contrary to our expectations, there seems to be relatively little difference in the frequency with which Navajo choose friends from among Southwestern, Sioux, and Oklahoma Indians.

Is this pattern of Navajo friendships different from other tribal groups? How can we suggest that these cognitive configurations correspond with behavior which is specific to Navajo? Using data collected by Weibel (1977) on Oklahoman Indian women, we are able to compare Navajo and Oklahoman patterns of friendship in Table 2 and Table 3 below.

The results show an interesting pattern. The discrepancy between the observed frequency and the statistically expected frequency of interactions suggests that Navajos do, indeed seek out other Navajos in the ethnically heterogeneous social milieu. They cultivate those friendships on a significantly higher level than chance alone would lead one to expect. In particular, there is virtual exclusion between Navajo-Oklahoma social networks. These data indicate that Navajo choice of friends is based on a quite different set of assumptions from those of the Oklahomans. Given the Navajo perception of Oklahoman Indians as irrevocably assimilated into Caucasian society, the behavior is quite understandable.

Table 3. Ethnicity of five closest friends by tribe of respondent.

Tribe of respondent		Ethnicity of friends					
		Indian	Mexican	Asian	Black	Caucasian	
Navajo	O	133 (74%)	20 (11%)	5 (.03%)	2 (.01%)	19 (11%)	n = 179
	E	129.13	15.22	2.62	2.10	29.92	
Oklahoman	O	133 (70%)	9 (6%)	0 (0%)	2 (.01%)	38 (23%)	n = 162
	E	116.87	(13.78)	2.38	1.90	(27.08)	
Total		246	29	5	4	57	341

$\chi^2 = 18.44$.
df = 4.
$P = .01$.

Table 3 reveals Navajo ethnic preferences for friends in light of comparable data for Oklahomans. The preference of both groups for Indian friends is clear. Additionally it appears that Navajos have more Mexican friends than do Oklahoman Indians. Friendships with Caucasians occur at higher levels among Oklahoman Indians, and are lower than expected for Navajo. These data again suggest that Navajo may be operating with a different "cognitive screen" which tends to favor Mexican relative to Caucasian contacts. Given the fact that Navajo and Oklahomans live in Los Angeles in the same areas, the fact that Navajo have twice as many Mexican-American friendship ties as do Oklahomans in a predominantly Caucasian social milieu, suggests a relative ease with which Navajo initiate and maintain close social ties with Mexican-Americans and their relative reluctance to interact socially with Caucasians.

Discussion

Our original hypothesis was based on a cognitive analysis of the domain of "five fingered beings," including the major ethnic groups and pan-tribal array. We hypothesized that Navajo women would seek assistance and social ties from Navajo, Southwestern Indian, Sioux, and Oklahoma Indians in decreasing order of frequency, corresponding to the social dimensions perceived among Indians (Fig. 1). Secondly, based on the analysis of the configuration of major ethnic groups (Fig. 2), we hypothesized that Navajo would interact most frequently with Caucasians (Asians and Blacks in intermediate positions).

The behavioral data bear out some but not all of our expectations. Considering the pan-tribal data first, it appears that the polar extremes of the traditionalism dimension are supported: there is clear preference for Navajo assistance and friends, and Oklahoman Indians are excluded. An important confirmation of this tendency is the increase rather than decrease of the proportion of Navajo-Navajo contacts *over time* in the city and the mutual exclusion between Navajo and Oklahoma networks shown in Table 2. The interpretation of the interactional trends with other tribes is less clear. We had expected a much greater proportion of Southwestern Indians to be included in the Navajo assistance and friendship networks. In general, there is a relative flatness to the distribution of pan-Indian interactions that was unexpected. The finely tuned gradient of ethnic preference which characterizes the cognitive analysis does not appear in the behavioral data.

Several factors must be taken into consideration in interpreting the results. Foremost is the fact that there are numerically fewer Southwest Indians than there are Oklahoma Indians in the Los Angeles area (Price 1972: 431). Aggregating Price's data on tribal representation in Los Angeles, the Indians from eastern Oklahoma constitute 21.1 percent, Navajo 13.7 percent, Sioux 11.7 percent, and Southwestern Indians other than Navajo 13.7 percent of the Los Angeles Indian population. Given the preponderance of Oklahoma Indians, the near abstention from Oklahoma contacts indicates the strength of the traditionalism dimension in the cognitive analysis. Navajos tend to stay away from Oklahoma Indians even though it would be relatively easy numerically to seek help or initiate friendship with them. Navajos see Oklahoma Indians as acculturated, nontraditional, and not like Navajo; and they infrequently seek assistance or friendship with them. The relatively low interactions with Southwestern Indians and other Indians in general may be a function of sample size, relative numbers of tribal representatives in Los Angeles, and geographical dispersion.

Turning to the analysis of the major ethnic groups, we hypothesized that Navajo would interact most frequently with Mexican-Americans, and least frequently with Caucasians. We did find a tendency on the part of Navajo to seek out and maintain close ties with Mexican-Americans more often than other ethnic groups beside Caucasians. The proportion of interactions is low but consistently greater than with other ethnic groups beside Caucasian. In the case of friendship ties, Navajo women had more Mexican-American friends than other Indians combined.

Given the extreme social distance between Anglos and Navajos, as expressed by the Navajo dimension of enemy/stranger which orders the ethnic group configuration, the frequency with which Navajos indicated close social ties with Caucasians was an unexpected finding. Several factors may have influenced this apparent anomaly. It must be remembered that Navajo live in neighborhoods which are, on the average, 75% Caucasian and 22% Mexican-American (U.S. Census 1970).

The relatively frequent interaction with Caucasians may reflect the natural probability of Navajo-Anglo interactions in a predominantly urban environment. Additionally, over half of the Caucasian friends mentioned by Navajos are members of Christian churches in which Navajo women are active members. These fellowships provide the bulk of their social-interactional structure and mitigate or override the cognitive dimensions. While Navajo interactions with Anglos may appear high in absolute number, the Oklahoman interactional patterns shown in Table 3 suggest that, relative to other tribes, Navajo may initiate fewer friendships with Caucasians.

In summary, the polar extremes on the traditionalism dimension of the cognitive analysis are supported—the Navajo prefer other Navajo and avoid the less traditional Oklahoman Indians. The regionalism dimension of Southwestern preference is not clearly supported by behavioral data. Preference for Indians above all other ethnic groups is clearly supported. There appears to be a preference for Mexican assistance and social ties, but again it is not an overwhelming choice.

The dimension of enemy/stranger which orders the ethnic groups appears to be diluted by the pragmatics of urban living, and more Navajo-Caucasian interactions are reported than expected.

Cognition and Behavior—Situational Determinants

The field of ethnoscience and cognitive anthropology has consistently been criticized as producing formally correct but inapplicable analyses of linguistic phenomena. A hopeful trend in recent years has been the growing interest in understanding the relationship between people's classificatory systems and how these systems influence real world behavior. Johnson (1974) compares Brazilian sharecroppers' cognitive categories of land types with their actual choice of land for planting crops. He found that beliefs about land types did predict the deviation of choice away from random selection; but in addition he offered the caveat that "no simple cognitive paradigm can predict behavioral outcomes absolutely" (1974b:93). Howe and Sherzer (1975) consistently elicit considerable variation among respondents as to their classification of rules of access to crops among the San Blas Cuna.

In an article which analyzes ethnic cognitive domains in urban Ghana, Sanjek (1977) finds close correspondence between the "implicit underlying structure of the domain" and the frequency of interaction with those categories of people (1977:611). The author found that

> There is considerable correspondence between the two sets of data. While *precise prediction* of cognitive salience from behavioral data is not possible, a more general prediction of the first five, second five, and subsequent ten most frequently encountered southern Ghanaian ethnic identities can be made. The opposite prediction from cognitive salience to behavior is also possible. (Sanjek 1977:612) (authors' emphasis)

Johnson and Bond (1974) compare the expectations for appropriate exchange with actual behavior using food sharing in tribal and peasant groups as examples. The authors conclude that behavior may contrast with cognitive expectations, and that the presentation of only the normative descriptions of a community may portray a one-sided view which "obscures certain practical aspects of social life in each community" (Johnson and Bond 1974:56).

The growing number of studies in the area of cognition and behavior indicate that the relationship is complex, and at times only very general correlates are found empirically between the two. In Sanjek's investigation of ethnic terms in the Adabraka section of Accra, Johnson's analysis of planting rules and practices, and Young's (1978) study of disease categories and illness prevention strategies, there is a support for the argument that cognition and behavior correspond to a considerable degree. Johnson and Bond's work comparing ideal and real interpersonal exchange structures among the Boa Ventura and Muyombe, on the other hand, indicate very little correspondence between cognition and behavior. The findings reported here suggest that very *general* predicted correspondences between categories and behavior are realized among Navajo women in Los Angeles, but there is some deviation from the expected pattern. The data suggest that to assume a close linear correspondence between cognitive dimensions and behavior may be an overstatement.

In understanding the relationship between cognitive dimensions and behavior, other researchers have suggested the importance of such situational variables as historical and economic forces (Howe and Sherzer 1975:443; Young 1978:94). The data in this study suggest more specifically that the *demographic profile* of the immediate urban environment and the nature of the *bureaucratic-institutional* milieu may affect the use of cognitive dimensions. Both of these factors appear to influence the relationship between the cognitive dimensions of Navajo and the actual behavioral outcomes. These factors are considered to be situational variables because they are demographically specific to Los Angeles, to American social service delivery and public life, and to the historical relationship between the U.S. and Indians; also, they are not *informant-based* variability such as the twelve dimensions discussed by Sanjek 1977:618, or as found in Howe and Herzer 1975.

Some of the demographic factors have been discussed previously. An overwhelming proportion of the population with whom Navajo must interact in Los Angeles are Caucasian, and the Indian population is geographically dispersed throughout the metropolitan area. In addition, Navajos realize that Anglos have greater access to economic rewards than other population groups. Thus, when Sanjek (1977:612) found that rank order salience of ethnic terms among Adabrakan residents corresponded with the frequency of interaction among those groups, one must consider that the demographic distribution among the tribes in Accra was more evenly divided than is the proportion of Navajo, Caucasian, Mexican-American, and other ethnic groups in Los Angeles. The residents of Adabraka had a better opportunity based on chance alone to interact with preferred groups than do Navajo in Los Angeles who are usually without transportation and limited to contacts within the immediate Anglo community. Therefore, while the cognitive classification of Anglos is extremely distant, demographic factors and realities of economic stratification increase the chances that Navajo will interact with Caucasians—a practical choice not necessarily based on one's cognitive dimension.

Finally, in order to understand the interaction between cognition and behavior, it is important to understand the bureaucratic-institutional milieu of the population. Sanjek notes the importance of educational and national cultural policy on the ethnic categories in Ghana (1977:617); Howe and Sherzer emphasize the Cuna classification is "neither static nor timeless . . . it reflects both the situation in which the Cuna now find themselves and the dominant social and economic changes they have undergone in the last century, and we cannot fully understand the classification without taking these processes into account . . ." (1975:443). This is especially true for administered populations such as American Indians. The BIA is a salient category because of the historical and current relationship between Indians and the federal institution; and particularly because of the BIA's policy to encourage migration and assist the migrant in locating employment and housing. Cognitive categories and behavior are not in a static relationship, but are influenced by situational variables. It is these factors which need to be determined in future studies; what are the situational determinants in the relationship between how people think and how they behave? The findings here suggest that there is a complex relationship between cognition and behavior.

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Range Extensions of Four Species of Crangonid Shrimps in the Eastern Pacific Ocean (Decapoda: Crangonidae)

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Members of the family Crangonidae, often called sand shrimp or blacktailed shrimp, are common inhabitants of sandy, muddy, or mixed bottoms. Recent identification of specimens at the Allan Hancock Foundation has provided a good series of shrimp of this family. New records of four species have been found outside their recorded ranges. *Sclerocrangon alata* is reported for the first time from California. The range of *Neocrangon zacae* is extended south from Baja California to Colombia. *Crangon munitellus* has been found in Baja California. *Crangon lomae* is reported for the first time since the description of the species in 1921.

Sclerocrangon alata Rathbun, 1902

Sclerocrangon alata Rathbun 1902:891–892.—Rathbun 1904:134–135, fig. 72, pl. III, fig. 2.

Previous records.—Bering Sea to Puget Sound, Washington, 11–168 m. Type locality: Admiralty Inlet, Puget Sound, Washington, 74 m, *Albatross* station 2865 (Rathbun 1902).

Material.—Pacific Grove, California, depth not recorded, 20 August 1937, Burch station 3710, 1 specimen. Friday Harbor, Washington, at surface, 27 August 1949, John L. Mohr, 1 specimen.

Remarks.—There is one previous record of a specimen of the genus *Sclerocrangon* in "California." Ross and Owen (1835) recorded a specimen of *Sclerocrangon boreas* (Phipps). I have been unable to locate the original material on which this record was based. Holmes (1900) and Rathbun (1904) mentioned *S. boreas* from California on the basis of this one record.

S. boreas is a circumpolar species, known from Arctic Siberia, Alaska south to the Strait of Georgia, the Canadian and Alaskan Arctic, eastern Canada south to Cape Cod, Greenland, Iceland, and northern Europe (Rathbun 1919). *S. alata* was not recognized as a species distinct from *S. boreas* until 1902. It seems likely that the shrimp taken by Ross and Owen was *S. alata* rather than *S. boreas*.

Members of the genus *Sclerocrangon* are broad, heavy shrimps distinguished by the presence of second pereiopods, dactyls of the fourth and fifth pereiopods not broad and flattened, and the absence of an arthrobranch from the third maxillipeds (Holthuis 1955). *S. alata* has a carapace nearly as long as wide. The blade of its antennal scale does not exceed the spine. Unlike *S. boreas, S. alata* tends to be small, about 26–38 mm in total length (Rathbun 1904).

The species of *Sclerocrangon* are most common in Arctic or boreal waters. *S. alata* may be a rare visitor to Monterey Bay rather than a resident species.

Crangon lomae (Schmitt, 1921)

Crago lomae Schmitt 1921:100–101, pl. 12, figs. 3 and 4.

Previous records.—Type locality: off Point Loma, California, 929–999 m, *Albatross* station 4334. Off Point Loma, California, 1159–1182 m, *Albatross* station 4353 (Schmitt 1921).

Material.—California: 7.3 miles, 46° true from Point Bennett, San Miguel Island (33°56′N, 120°33′W to 33°56′N, 120°31′W), 830–1126 m, rock dredge, 29 April 1976, *Velero IV* station 24889, one male, total length 31.8 mm.

Remarks.—*C. lomae* is one of the deepest species of its family in California, exceeded in depth range only by *Pontophilus occidentalis* Faxon.

Crangon munitellus Walker, 1898

Crangon munitellus Walker 1898:275, pl. 16, fig. 1.—Holmes 1900:176.

C. munitella.—Rathbun 1904:132.—Carlton and Kuris 1975:404.—Word and Charwat 1976:81–82.

C. munitella.—Schmitt 1921:101–102, fig. 70.

Previous records.—Type locality: Puget Sound, Washington (Walker 1898).—San Francisco Bay to Santa Catalina Island, California, 6.5–74 m (Schmitt 1921).

Material.—BAJA CALIFORNIA, MEXICO: 3.75 miles NNW of Punta Eugenia (27°54′45″N, 115°06′0″W to 27°54′20″N, 115°06′35″W), 37 m, 5 March 1949, *Velero IV* station 1702, 3 specimens. Between Melpomene Cove and Inner Guadalupe Island (28°52′N, 118°19′W), 9–28 m, 18 December 1949, *Velero IV* station 1914, 4 specimens. Melpomene Cove, Guadalupe Island (28°55′23″N, 118°18′38″W to 28°51′0″N, 118°17′30″W), 92–94 m, 19 December 1949, *Velero IV* station 1920, 2 specimens. 1.25 miles from Sandstone Point, Guadalupe Island (28°54′08″N, 118°15′36″W to 28°53′57″N, 118°15′41″W), 46–55 m, 20 December 1949, *Velero IV* station 1924, 2 specimens. 2 miles, 142° true to Thurloe Head (27°35′45″N, 114°49′15″W), 37 m, 7 December 1967, *Velero IV* station 11842, 1 ovigerous female. CALIFORNIA, U.S.A.: 62 specimens from 29 other stations: Santa Rosa, Santa Cruz, Anacapa, Santa Catalina, and San Clemente Islands; Port Hueneme, Redondo Beach, Point Vicente, White's Point to Portuguese Bend, Newport Inlet, and Corona del Mar, 0–185 m, 1926–1962.

Remarks.—The records suggest that *C. munitellus* prefers shallow sublittoral bottoms of clean sand or sand mixed with rock and shell. Kuris and Carlton (1977) related the squat body forms of *C. handi* and *Lissocrangon stylirostris* to habitat specialization, in which their shape allows rapid escape response over short distances. *C. munitellus*, a short, broad shrimp, may have adapted in a similar fashion to its environment.

Neocrangon zacae (Chace, 1937)

Crago zacae Chace, 1937:136–138, fig. 9.

Crangon zacae.—Word and Charwat 1976:93–94.

Neocrangon zacae.—Kuris and Carlton 1977:554.

Previous records.—Type locality: east of Cedros Island, Mexico (28°13′N, 115°07′W), 81 m, mud bottom, 27 March 1936, *Zaca* station 125 (Chace, 1937). Monterey Bay to Dana Point, California (Chace 1937; Word and Charwat 1976).

Material.—North of Gorgona Island, Colombia (3°01′25″N, 78°10′W), 18–37 m, mud and rock bottom, 24 February 1938, *Velero III* station 851-38, 1 damaged specimen. Sulphur Bay, Clarion Island, Mexico (18°20′45″N, 114°44′15″W), 9.2 m, among coralline algae, 16 March 1939, *Velero III* station 915-39, 1 male and 1 ovigerous female.

Remarks.—N. zacae is distinguished from the closely related *N. communis* (Rathbun) by the lack of carinae on its fifth abdominal segment, the dactyl of the first pereiopod closing more longitudinally than horizontally, and the smaller size of the adults in the former species. These differences may be difficult to detect in damaged or poorly preserved specimens. Chace (1937) suggested that *N. zacae* might be a southern subspecies of *N. communis.*

In the collections of the Allan Hancock Foundation, there are about 700 specimens identified as *N. zacae* from 105 stations in southern California and Baja California, Mexico. These were taken in 1938–1977 at depths from the shore to 572 m. At 75 of the 105 stations, the specimens were collected at depths of 185 m or less. *N. communis* was taken at 34 stations at 21–230 m. One hundred eighty-eight specimens were collected in 1917–1976. At 23 stations, the species was taken at 92–277 m. The records suggest that *N. communis* prefers somewhat greater depths than *N. zacae,* although both occur over a wide range of depths in southern California.

N. zacae is the only member of the family Crangonidae recorded so far from the continental shelf of the Panamic zoogeographic province, the region of coast from northern Peru to southern Baja California. *Pontophilus occidentalis* occurs in bathyal depths in the region.

Acknowledgments

I thank Fenner A. Chace, Jr. of the National Museum of Natural History for examining the specimens of *Neocrangon zacae*. The specimen of *Crangon lomae* was collected during the Southern California Baseline Studies and Analysis, sponsored by the U.S. Bureau of Land Management contracts 08550-CT5-52 and AA550-CT6-40.

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INSTRUCTIONS FOR AUTHORS

he BULLETIN is published three times each year (April, August, and November) and includes articles in English any field of science with an emphasis on the southern California area. Manuscripts submitted for publication iould contain results of original research, embrace sound principles of scientific investigation, and present data a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide r contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, hieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous ference of pronouns, and logically placed modifiers.

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Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452–458.

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A Synopsis of the Larvae of Costa Rican Frogs and Toads

Jay M. Savage

Abstract.—A synopsis of the larvae of Costa Rican frogs and toads by Jay M. Savage, *Bull. Southern California Acad. Sci.*, 79(2):45–54, 1980. Of 87 species of Costa Rican frogs and toads with free living larvae, 61 tadpoles are known in sufficient detail to be distinguished. Of the remaining 16 forms, all but two will probably share distinctive combinations of generic features that will allow them to be recognized as previously undescribed tadpoles of an appropriate genus when discovered. A synoptic key to Costa Rican tadpoles that will distinguish larvae from the time the operculum closes through the time of front limb eruption is presented. It is supplemented by a guide to published accounts and illustrations of all described tadpoles of Costa Rican forms.

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The characteristics of the aquatic free-living larvae (tadpoles) of frogs and toads have long been known to be distinctive for a spectrum of taxonomic categories ranging from suborders to species (Starrett 1973). Generally the larvae show a series of special adaptations for a particular kind of ecologic role superimposed upon a basic morphology that is consistent for a number of related frog families. Because of this mixture of plastic and conservative features, respectively, in well-studied areas (e.g., the United States, Altig 1970; or Southern Africa, Wager 1965) or taxonomic groups (e.g., the mesoamerican Hylidae, Duellman 1970) most tadpoles may be distinguished at the specific level. As pointed out by Altig and Brandon (1971) an essential precursor to any detailed study of the ecology and behavior of the immature forms in any area must be the ability to identify and associate them with adult species populations. In reality, attempts to fully understand the evolution and ecology of the species require this same ability.

As part of my long-term studies of the herpetofauna of Costa Rica (Savage 1976), I have accumulated specimens and data for a synopsis of the larvae of the Anura of the republic. The present paper is a summary of the available knowledge presented in a simple and convenient format.

Costa Rica has a known amphibian fauna of 150 species, 3 caecilians, 27 salamanders and 120 frogs and toads. Unlike the situation in areas east of central Panama (caecilians) and north of the Isthmus of Tehuantepec (for salamanders) no free-living larvae of caecilians or salamanders or known or are likely to be discovered in Costa Rica. All species of the genera of caecilians represented in Costa Rica retain the developing eggs in the oviduct and give birth to living young (M. H. Wake 1977). All species of the genera of salamanders known from Central and South America have land-laid encapsulated eggs that undergo direct development (D. B. Wake and J. F. Lynch 1976).

Of the 120 known species of frogs and toads that occur in Costa Rica, 33 belong to the leptodactylid genus *Eleutherodactylus.* Insofar as known (J. D. Lynch 1976) all members of this genus lay terrestrial encapsulated eggs that undergo direct development into small frogs. Free-living tadpoles of 87 species of anurans in the families Rhinophrynidae (1), Microhylidae (3), Leptodactylidae (6), Bufonidae (14), Hylidae (39), Dendrobatidae (7), Centrolenidae (13) and Ranidae (4) occur in Costa Rica. Available data make it possible to include 62 of these species in the synoptic key presented below.

The eggs of most of these species are deposited in aquatic situations. Exceptions include: 1) two species of *Leptodactylus, fragilis* and *poecilochilus,* that lay their eggs in a foam-filled burrow (Heyer 1969); 2) the tree-frog *Hyla ebraccata* that lays its eggs on the leaves of broad-leafed herbaceous plants emergent from ponds (Duellman 1967); 3) all members of the family Centrolenidae (Starrett 1960), the hylid genera *Agalychnis* and *Phyllomedusa* and *Hyla lancasteri* (Duellman 1970) lay eggs on vegetation, usually leaf-surfaces, a considerable distance above a stream or other body of water; and 4) all members of the family Dendrobatidae lay their eggs in moist terrestrial sites and transport the hatched tadpoles on the adult's back to water (Savage 1968).

Larval Structure and Terminology

The characteristics of anuran larvae that may be used in taxonomic description have been detailed by Orton (1952), Altig (1970), Duellman (1970) and Starrett (1973). Distinctions among preserved tadpoles generally can only be made in developmental stages 25 (operculum closure) through 40 (immediately before front leg eruption) using the Gosner (1960) system. The synopsis that follows is based on tadpoles of these stages and the characterizations provided by the cited authors. Points of minor departure or preference include:

1. denticle is used instead of tooth since larval Anura have no true teeth but only a series of non-homologous keratinized structures;

2. the jaws, beaks, labia and denticle rows are referred to as upper and lower because of their association with the upper and lower jaw structures common to all vertebrates; Altig (1970) uses anterior and posterior, respectively, since most tadpoles have a ventrally located mouth;

3. a complete oral disk refers to an unindented disk;

4. description of mouth position and size and body form follows the terminology of Duellman (1970).

Identification of Costa Rican Tadpoles

The tadpoles of 61 Costa Rican species have been described and/or illustrated in considerable detail. Reasonably accurate predictions as to the basic features of several other species can also be made as follows:

1. Microhylidae; the features of the only other four species of the genus *Gastrophryne* are known; *Glossostoma* tadpoles will probably agree in general with *Gastrophryne* and *Hypopachus* when discovered;

2. Bufonidae; tadpoles of all known members of the genus *Atelopus* have the peculiar enlarged ventral disk found in *varius* (Starrett 1967; Duellman and Lynch 1969); all known Central American *Bufo* agree in having 2/3 denticle rows, an indented oral disk and oral papillae incomplete across both upper and lower labia; it seems likely the unknowns from Costa Rica will share these features;

3. Centrolenidae; it is anticipated that other Costa Rican tadpoles of the genus *Centrolenella* will agree with known species in having 2/3 denticle rows, the oral disk complete, a median anus, the spiracle posterior in position and the denticle row just above the mouth restricted to two short segments.

The guide to identification of the tadpoles is organized into two parts. First is a synoptic key based upon available specimens and published data. It is designed to lead to an identification when well-preserved material conspecific with described tadpoles is available. In most cases it is anticipated that material of as yet undescribed tadpoles of known species will be correctly identified at the generic level. Tadpoles of the genera *Agalychnis, Atelopus, Bufo, Centrolenella* and *Phyllobates* fall into this category.

The second portion of the guide consists of an index to published illustrations of the tadpoles. In cases where species are very similar or where material may be of a form whose tadpole has not been described reference to the illustration should be the final authority.

The following species of Costa Rican frogs do not have their tadpoles described or illustrated and remain cryptic. In cases where material does not conform to the synopsis and/or cited illustrations the possibility that one has discovered a previously missing immature stage must be given serious consideration.

Agalychnis calcarifer
Atelopus chiriquiensis
Atelopus senex
Bufo coccifer
Bufo coniferus
Bufo fastidiosus
Bufo haematiticus
Bufo luetkenii
Bufo melanochloris
Centrolenella albomaculata
Centrolenella chirripoi
Centrolenella colymbiphyllum
Centrolenella euknemos
Centrolenella ilex
Centrolenella pulverata
Centrolenella talamancae
Centrolenella valerioi
Centrolenella vireovittata
Crepidophryne epioticus
Dendrobates granuliferus
Glossostoma aterrimum
Gastrophryne pictiventris
Hyla lythrodes
Hyla miliaria
Hyla xanthosticta
Phyllobates lugubris

A SYNOPSIS OF COSTA RICAN TADPOLES

I. NO DENTICLES

A. NO BEAKS

1. Two Ventral Spiracles
   barbels present
   Rhinophrynus
2. One Ventral Spiracle
   no barbels
   i) oral flaps without scallops or papillae; spiracle opens immediately ventral to anus
   Gastrophryne
   ii) oral flaps with scallops or papillae; spiracle opens near anus
   Hypopachus variolosus

B. BEAKS PRESENT
and
One Sinistral Spiracle

1. Tail terminating in a thin filament
   - a) one row of papillae under mouth; median anus
     - *Hyla ebraccata*
   - b) no papillae; dextral anus
     - *Hyla microcephala*—no postorbital dark stripe
     - *Hyla phlebodes*—a distinct postorbital dark stripe
2. Tail not forming a thin terminal filament
   - a) no oral papillae
     - *Colostethus nubicola*
   - b) oral papillae complete around mouth
     - *Hyla picadoi*

II. DENTICLES AND BEAKS PRESENT

A. AN ENLARGED VENTRAL DISK

Atelopus varius

B. NO ENLARGED VENTRAL DISK

Denticle Rows: 0/1 1/1 1/2

1. Anus dextral; denticle rows complete; labial papillae rows complete
   - *Hyla zeteki*
2. Anus median; denticle rows very short; no labial papillae above mouth
   - *Dendrobates pumilio*

2/2

1. Oral disk bordered by large papillae
   - *Anotheca spinosa*
2. Oral disk bordered by minute papillae
   - *Hyla rufioculis*
   - *Hyla uranochroa*

2/4

1. No preorbital stripe
   - *Hyla rosenbergi*
2. A dark preorbital stripe
   - *Hyla rufitela*

2/3

1. Oral disk indented laterally

- a) oral papillae incomplete on upper and lower labia
  - i) body black or brown above and below
    - *Bufo marinus*—2 rows of papillae
    - *Bufo periglenes*—1 row of papillae for most of disk
  - ii) body dark above, light below
    - *Bufo holdridgei*—6–7 large papillae
    - *Bufo valliceps*—numerous small papilla
- b) oral papillae complete across lower labium
  - i) 1 row of papillae below mouth
    - uniform body and tail
      - *Physalaemus pustulosus*
    - tail spotted
      - *Rana "pipiens"*
  - ii) 2 rows of papillae below mouth
    - uniform dark body and tail
      - *Phyllobates vittatus*
    - body black, tail spotted
      - *Colostethus talamancae*

2. Oral disk complete
    a) median anus

- i) spiracle about halfway between eye and posterior margin of body; denticle row just above mouth complete or barely interrupted medially
    - x) tail with dark spots and blotches a distinct light spot posterior to oral disk; mouth anteroventral
        - *Leptodactylus fragilis*—body uniform
        - *Leptodactylus poecilochilus*—body with dark flecks
        - no distinct light spot posterior to oral disk: mouth terminal
            - *Leptodactylus pentadactylus*
    - xx) tail without dark spots and blotches, uniformly dark or with a few light spots
        - *Leptodactylus bolivianus*—all rows of denticles complete; papillae extending well onto upper lip
        - *Leptodactylus melanonotus*—denticle row above mouth usually with a median gap; papillae essentially restricted to sides of oral disk
        - *Dendrobates auratus*—denticle row above mouth complete; oral papillae incomplete across upper labium
- ii) spiracle much closer to posterior margin of body than to eye; denticle row just above mouth restricted to two short segments near corners of mouth
    - y) lowermost denticle row much shorter than other two lower rows
        - *Centrolenella prosoblepon*
    - yy) lowermost denticle row equal to or only slightly shorter than other two lower rows
        - *Centrolenella granulosa*—lower beak with large blunt serrations
        - *Centrolenella spinosa*—lower beak with large sharp serrations
        - *Centrolenella fleischmanni*—lower beak with small fine serrations
        - *Centrolenella valerioi*—lower beak with small fine serrations

b) dextral anus
    i) oral papillae complete across upper labium

- z) no more than 3 rows of papillae below mouth
- zz) 4–7 rows of papillae below mouth

- *) body depressed, wider than deep; 2–3 rows of papillae above mouth; body and tail with dark spots
    - *Hyla debilis*—mouth large, as wide as body
    - *Hyla lancasteri*—mouth small, about ⅔ width of body
- **) body ovoid, depth equal to width; 1 row of papillae above mouth; body uniform tan, tail tan with flecks and dashes of darker pigment that tends to form cross-bars on dorsal surface of tail musculature
    - *Smilisca sordida*
- *) body and tail spotted with dark
    - *Hyla tica*—tail fin not extending onto body
    - *Hyla rivularis*—tail fin extending onto body
- **) body black with golden lichenous markings, tail tan with clear fins
    - *Hyla pictipes*

- ii) oral papillae incomplete across upper labium
    - x) oral papillae incomplete across lower labium; short lowermost denticle row mounted on a vertically moveable extension
        - *Hyla boulengeri*
    - xx) oral papillae complete across lower labium

- y) spiracle ventrolateral
    - *) tail fin extending onto body
        - *Phyllomedusa lemur*
    - **) tail fin not extending onto body
        - body slightly deeper than wide
            - *Agalychnis saltator*
            - *Agalychnis callidryas*
            - *Agalychnis spurrelli*
        - body deep, at least 15% deeper than wide
- yy) spiracle lateral
    - *) body ovoid, depth and width approximately equal
        - tail fin not extending onto body; mouth ventral
            - *Hyla pseudopuma*—mouth small
            - *Hyla angustilineata*—mouth small
            - *Smilisca sila*—mouth medium
        - tail fin extending onto body; mouth

Agalychnis annae

anteroventral
  body dark brown or black
    Smilisca baudinii—body not tuberculate
    Hyla fimbrimembra—body tuberculate
  body pale brown to tan
    Hyla loquax
    Smilisca phaeota
    Smilisca puma

**) body deep, much deeper than wide; tail fin extending onto body; mouth anteroventral, small
  Hyla elaeochroa
  Hyla staufferi

Denticle Rows: 2/5
  oral disk complete; dextral anus
    Hyla legleri

3/4–6
  oral disk complete; median anus
    Phrynohyas venulosa

3/5–4
  oral disk indented; dextral anus
    Rana palmipes
    Rana vibicaria

Denticle Rows: 6/4
  oral disk complete: dextral anus
    Rana warschewitschii

6/9
  oral disk complete; dextral anus
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Ecology of a Coastal Salt Marsh after Long-Term Absence of Tidal Fluctuation

H. Peter Eilers

Abstract.—Ecology of a coastal salt marsh after long-term absence of tidal fluctuation by H. Peter Eilers, *Bull. Southern California Acad. Sci.*, 79(2):55–64, 1980. Tidal access to Bolsa Bay, California, was removed in 1899 then partially returned in late 1978. Investigation in 1977–1978 revealed that salt marsh vegetation had adjusted to lowered water levels and subsidence by establishment of zonal patterns at anomalously low elevations. Net production in macrophytes decreased with elevation (4380 to 164 g m^{-2} yr^{-1}), soil nitrogen (NH_3) remained high at all levels, and soil salinity was seasonally variable (7 to 54 ppt). Low redox potentials indicated persistent anaerobiosis. With the recent removal of tide gates and return of tidal fluctuation, much of the pre-existing marsh has been drowned.

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Introduction

In the fall of 1978, limited tidal fluctuation was restored after nearly 80 years to a 52 ha section of Bolsa Bay, California. Because tidal marsh in southern California has been declining in area since the establishment of the State (USDI 1972), this reclamation project is an important reversal of a long-standing trend. The research presented here was designed to consider the effects of such long-term tidal removal on the ecology of a salt marsh, especially macrophyte production, substrata characteristics and the relation of plants to potential tide levels.

Bolsa Bay

Bolsa Bay or Bolsa Chica Bay (the spanish "little purse") occupies the seaward end of an alluvial-filled valley originally excavated at lower sea level in the Bolsa Chica-Huntington Mesa of western Orange County (Fig. 1). The present bay comprises two subdivisions. Outer Bolsa, directly to the west of Bolsa Chica Mesa, is tidally controlled through a narrow channel leading to adjacent Sunset Bay. A closure dam containing culverts with flap valves to prevent incursion of flood tides and extending from the southern edge of the mesa to the beach separates Outer from Inner Bolsa.

The history of human use and modifications of Bolsa Bay are considered in detail by Talbert (1952), Dillingham (1971), Speth et al. (1976), and EDAW (1978). First mentioned in the late 1790's as within Rancho Bolsa Chica, Mexican title was established in 1840 and reconfirmed in the treaty of Guadalupe-Hidalgo 1948. The earliest detailed survey of Bolsa Bay, published in 1874 (Fig. 2), reveals an undisturbed wetland system of over 800 ha supplied with some terrestrial drainage

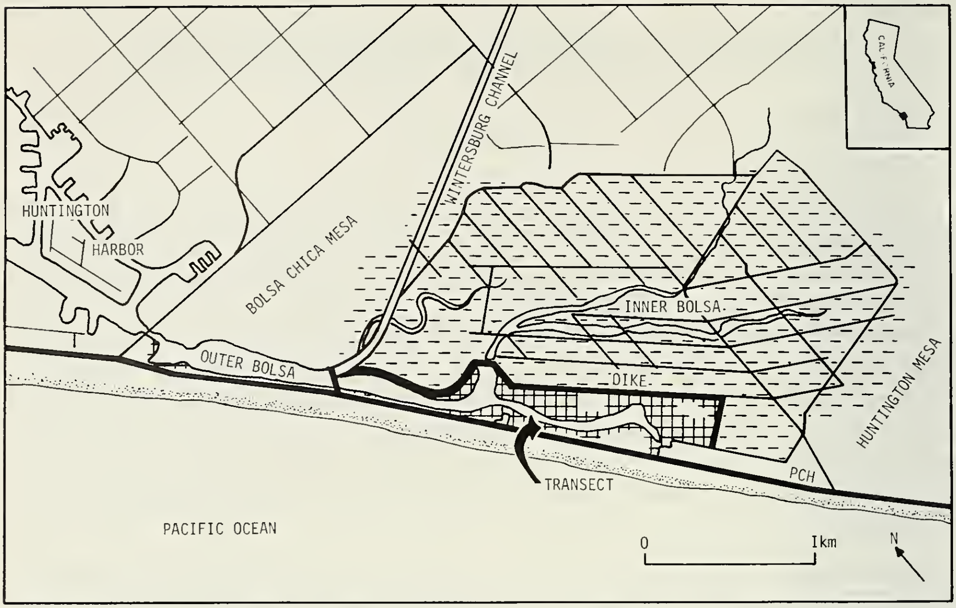

Fig. 1. Bolsa Bay, California. Dashed lines represent remnants of degraded marsh, old diked ponds, and filled areas. Roads interconnect oil well sites in Inner Bolsa. Square pattern denotes salt marsh. Dike is the landward boundary of Bolsa Chica Ecological Reserve and PCH is Pacific Coast Highway (State Highway 1). Note position of sampling transect.

through the Freeman River and open directly to the Pacific Ocean. Alteration of the natural system began in 1899 with ownership of 211 ha granted to the Bolsa Chica Gun Club by the State of California. Dam emplacement in that year restricted tidal fluctuation to Outer Bolsa and presumably enhanced waterfowl hunting. Loss of the tidal prism led to rapid siltation and permanent closure of the bay mouth within six months necessitating a new channel between Outer Bolsa and the present site of Huntington Harbor in adjacent Sunset Bay (Moffatt and Nichol 1971). Later the hunting club constructed a series of diked ponds in the more elevated marsh. Oil was discovered in 1926 with leases to the Signal Oil Company granted by the duck club decendants in 1940. Oil and gas exploitation followed extensive diking and well pad construction in 1943, and extraction continues to the present. Signal Oil became sole landowner of Outer and Inner Bolsa in 1970 and initiated plans to convert the bay to a marina when soil resources are exhausted in about 15 years.

Against this backdrop, however, existed pressure from local residents and the State of California to restore the wetlands and public access to them. In addition, study of tidally controlled wetlands suggested the importance of marshes to estuarine and coastal food chains (Teal 1962). Through a complex agreement between the Signal Oil Company and the State of California in 1973, Signal retained title to all but 140 ha of wetland. An additional 90 ha will revert to the State in 1987 if a new ocean channel is established. Following this agreement, the State of California through the Department of Fish and Game initiated the Bolsa Chica Ecological Reserve and began planning for the restoration of tidal fluctuation to Inner Bolsa and the construction of ocean access.

Fig. 2. Bolsa Bay, 1874. Note ocean inlet.

Methods

To understand the effect of long-term absence of tidal fluctuation on the salt marsh system at Bolsa Bay, study was initiated in October 1977 and continued through March 1979. Concurrent investigations of other less altered southern California salt marshes (Sweetwater River, Los Penasquitos Lagoon, and Upper Newport Bay) were underway by me to provide comparative data (Eilers 1980).

Vegetation

A transect of five 2.0 × 2.5 m macroplots (BB-1 to BB-5) was located within the salt marsh perpendicular to the elevation gradient along the main channel in Inner Bolsa (Fig. 1). At intervals of six to eight weeks for a period of 13 months (October 1977 through October 1978), a 20 × 50 cm quadrat frame was located within each macroplot (at a different position each session) and all above-ground vascular plant material in the frame was harvested, placed in plastic bags, then refrigerated within two hours to minimize fermentation losses (Milner and Hughes 1968). In the laboratory each sample was divided into component species. Species fractions were further divided into living and dead material. Subfractions were then dried to constant weight in a gravity convection oven at 85°C and weighed to the nearest 0.1 g.

Annual net production estimates for macroplots were calculated by the method of Smalley (1959) applied to component species as follows: 1) If the net change between sampling periods was positive for both the live biomass (L) and dead biomass (D), then species production in the interval was equal to the sum ($\Delta L + \Delta D$); 2) if ΔL and ΔD were negative, production was assumed to be zero; 3) if ΔL and ΔD were + and −, respectively, then species production was equal to ΔL; and 4) if ΔL and ΔD were − and +, respectively, species production was assumed to be equal to the sum ($\Delta L + \Delta D$) if the sum was greater than zero, and equal to zero if the sum was negative. Net production for each species between harvests was summed to yield species annual net production, and macroplot annual net production was determined as the sum of component species production.

Physical Parameters

At the time of each vegetation harvest, soil water was analyzed for salt content with a Goldberg refractometer and oxidation-reduction potential (redox, as Eh in millivolts), ammonia, and pH was measured with an Orion specific ion meter (Behrens 1965; Banwart et al. 1972). Elevation of each macroplot with reference to National Geodetic Vertical Datum (NGVD) was established by survey and converted to potential mean high water (MHW) based on MHW for the nearest tidal bench mark (Warner Avenue bridge) and the work of Moffatt and Nichol (1971). All levels were double run with a closing error less than 0.2 cm.

Results

Vegetation

Four vascular plant species were recorded in quadrat samples. They were, in order of occurrence from high to low sites, *Frankenia grandiflora, Distichlis spicata, Salicornia virginica,* and *Spartina foliosa* (Fig. 3).

Net above-ground production varied from 4380 g m^{-2} yr^{-1} for a nearly pure stand of *Frankenia* (BB-1) to 164 g m^{-2} yr^{-1} for low-density *Spartina* (BB-5). More diverse stands (BB-2,3,4) were intermediate (2214, 3522, and 1561 g m^{-2} yr^{-1}, respectively). A sharp decrease in net production accompanied a decrease in elevation (Fig. 3), and the low-elevation *Spartina* appeared to be dying out as the study progressed despite the fact that this species is characterized by loss of aerials in the winter.

Physical Parameters

The sampling transect was 30 m long and extended from -0.57 to -1.12 m MHW (Fig. 3). Mean annual soil salinity for sample sites varied from 20 to 41 ppt with an increase toward lower sites (Fig. 4). The greatest annual range of soil salinity was recorded for BB-1 (7 to 45 ppt); for all sites minimum values occurred in the winter and early spring, while maximum values appeared in the summer.

Oxidation-reduction potential (redox) is a convenient measure of soil aeration (Brereton 1971). Values less than 200 mV indicate poor drainage and anaerobic conditions (Stolzy and Flühler 1978). Even though all macroplots recorded redox potentials greater than 200 mV in the early spring, annual means revealed persistent and increased anaerobiosis toward lower elevations along the transect (Fig. 4). Sampling sites were perpetually waterlogged, and disturbance of the peaty soil resulted in release of hydrogen sulfide.

Mean annual soil nitrogen (as NH_3) varied greatly along the transect with no clear relationship to elevation, although there was a tendency toward increased annual range for lower macroplots (Fig. 4). Minimum and maximum nitrogen occurred in the spring and summer, respectively.

Measurement of soil pH provides a general assessment of nutrient ion concentration, and variations in pH over time may indicate fluctuations in soil moisture (Neely 1962). Greater annual variation in pH for more elevated macroplots (Fig.

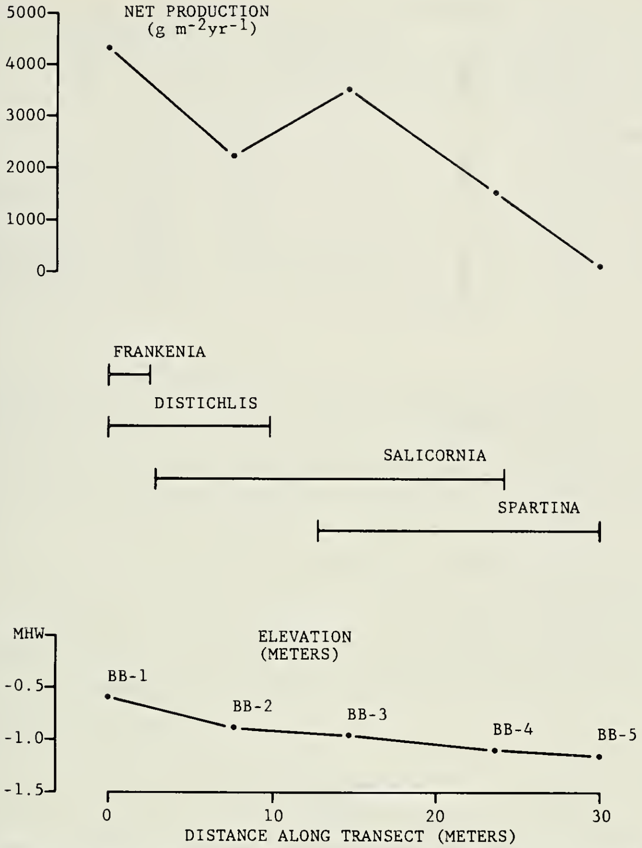

Fig. 3. Net production, species composition and macroplot elevation along sampling transect in Inner Bolsa.

4) suggested that some drying takes place near the summit of the transect. Annual mean pH reflected increased alkalinity at lower elevations.

Discussion

Vegetation and environmental measurements together suggested that the absence of tidal fluctuation for 80 years strongly influenced but did not totally alter the salt marsh system of Inner Bolsa Bay. Net production of vascular plants, except for *Spartina* at BB-5 was comparable to that observed elsewhere in southern California marshes (Winfield and Zedler 1976; Eilers 1980).

The presence of *Spartina* in Inner Bolsa was curious. This grass dominates low marsh environments from northern California (Humboldt Bay) to the southern most extent of salt marsh at Laguna Ojo de Liebre, Baja California (Phleger 1965; Macdonald 1969). A tall (1 m) rhizomatous grass with prominent aerenchyma tissue, *Spartina foliosa* is capable of withstanding long submergence (Purer 1942). Macdonald (1977) recognizes two distinct groups of estuaries and coastal lagoons in southern California based in part of the presence of this species. The first of these is characterized by having deep channels, large tidal prism, perennial

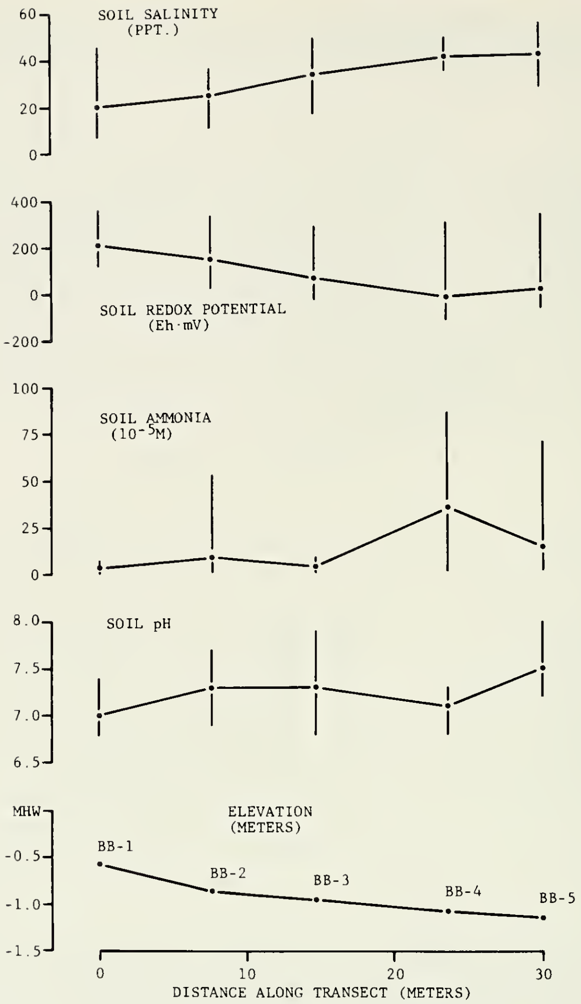

Fig. 4. Soil salinity, redox potential, ammonia and pH along sampling transect in Inner Bolsa. Annual means for sample macroplots shown as filled circles; vertical lines denote annual range.

ocean contact and well-developed, pure stands of *S. foliosa* directly above mudflat. The second group includes those with insufficient tidal prism to prevent seasonal or long-term closure of their ocean inlets. Invariably, according to Macdonald (1977), *S. foliosa* is absent from the second group. Vigorous stands of *S. foliosa* are present at open tidal sites such as Upper Newport Bay (Vogl 1966), Tijuana Estuary (Zedler 1977) and Anaheim Bay (Speth et al. 1976); *S. foliosa* is absent at Los Penasquitos Lagoon where tidal access is restricted to winter months (Mudie et al. 1974). The restricted distribution of *S. foliosa* at Mugu Lagoon where tidal fluctuation is reduced (Warme 1971), and its absence from diked marsh at La Ballona Creek (Clark 1979), lends further support to the Macdonald (1977) model. The occurrence of *S. foliosa* at Bolsa where tidal fluctuation was not permitted for 80 years is, therefore, difficult to explain. Perhaps the

Table 1. Mean redox potential of substrata in four southern California salt marshes obtained at harvest sessions in 1977–1978 (Eh·mV). After Eilers (1980).

	1977		1978				
Marsh	Oct/ Nov	Dec/ Jan	Feb	Apr	June	July	Aug
Bolsa Bay	65	307	−1	27	55	1	103
Upper Newport Bay	304	407	289	337	—	289	261
Los Penasquitos Lagoon	382	381	301	384	242	276	322
Sweetwater River Estuary	369	—	369	311	428	354	354

unique environment created by artificial removal of tides is a factor. Yet, because the salinity regime and soil alkalinity at BB-3,4,5 where this grass was sampled were characteristic of sea water, and because elevations there were well below MHW, it is likely that some sea water inflow through the permeable beach sands occurred and permitted *Spartina*, which was probably present in the bay before 1899, to persist.

Low redox potentials and attendant anaerobiosis were among the more significant effects of diking and removal of the tides. Redox measurements obtained in undiked southern California marshes were consistently higher than those for Bolsa Bay (Table 1). Peat accumulations 15 to 20 cm thick in each macroplot at Bolsa indicated poor nutrient turnover and restricted nutrient contribution to the adjacent mudflat and channel.

The relationship between plants and tide levels has been a central theme in salt marsh research since the pioneer investigations of Ganong (1903) and Johnson and York (1915), through the work of Hinde (1954) and Chapman (1960), and continuing to the present with studies, for example, by Zedler (1977), Eilers (1979) and Frenkel et al. (In press). Salt marsh macrophytes have been shown to occupy relatively narrow elevational limits and the vertical boundaries of salt marshes tend to be somewhat uniform from one coastal location to the next. Chapman (1934 in Hinde 1954) observed that none of the higher plant associations or species in the British marshes he investigated had a lower limit below mean sea level (MSL). Mahall and Park (1976) recorded *Spartina foliosa* in San Francisco Bay salt marshes from about MSL to MHW and *Salicornia virginica* from MHW to the upper limit of tidal fluctuation. Warme (1971) and Barbour et al. (1973) likewise noted the presence of salt marsh above MSL, and Macdonald (1969) generalized that most Pacific coast marshes become established at about mean lower high water (MLHW) regardless of local tidal range. The upper limit of salt marsh is often more difficult to define because a gradual transition between marsh and upland is frequently present (Harvey et al. 1978). The National Ocean Survey (NOAA 1980) surveyed 17 Pacific coast salt marshes and found a mean upper boundary (defined as the center of the transition zone) of 0.9 m above MHW for central and southern California locations.

Most if not all of the work to date concerning salt marsh plants and tide levels has been completed in estuaries, bays and lagoons where tidal fluctuation is unrestricted or is at least a seasonal event occurring over several months. Comparison of the vertical range of salt marsh vegetation at Inner Bolsa with that of

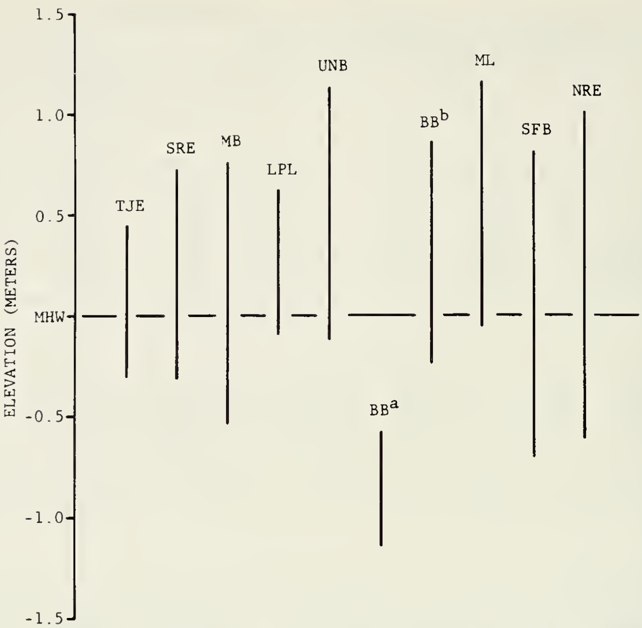

Fig. 5. Vertical range of salt marsh at Bolsa Bay compared to that of other Pacific Coast salt marshes. Abbreviations as follows: TJE, Tijuana River Estuary (Zedler 1977); SRE, Sweetwater River Estuary (Eilers 1980); MB, Mission Bay (Macdonald 1969); LPL, Los Penasquitos Lagoon (Eilers 1980); UNB, Upper Newport Bay (Eilers 1980); BBa, Inner Bolsa Bay; BBb, Outer Bolsa Bay; ML, Mugu Lagoon (Warme 1971); SFB, San Francisco Bay (Hinde 1954); NRE, Nehalem River Estuary, Oregon (Eilers 1979).

Outer Bolsa and other tidally influenced southern California marshes, therefore, provides some insight into the vertical distribution of plant species and marsh after long-term removal of tidal access (Fig. 5). Apparently, in the 80 year absence of periodic inundation, salt marsh plants abandoned positions at or above MHW and re-established at anomalously low elevations. *Frankenia*, for example, was located 0.3 to 0.9 m below its normal elevation and equal to or below the lowest *Spartina* or *Salicornia* found elsewhere as reported by Zedler (1977) and Hinde (1954).

This anomalous condition may not be due to the removal of tidal fluctuation alone but to a combination of tidal removal and subsidence (resulting from oil or ground water withdrawals or both). Moffatt and Nichol (1971) studied bench mark levels for the time period 1933 to 1964 and estimated subsidence at between 23 and 46 cm. Orange County bench marks along the west side of Inner Bolsa have been repeatedly surveyed and show continued loss of elevation. For example, bench mark IJ-29-68 near the sampling transect descended by 8.4 cm between 1968 and 1976. From the available data, a mean subsidence rate for Inner Bolsa may be estimated at about 1 cm per year. Subsidence could account for a marshland shift downward of approximately 80 cm since the removal of tidal fluctuation and, together with some re-establishment or vegetation extention of marsh plants to lower levels, may be responsible for the anomaly. Whatever the cause, however, it is obvious that restoration of unrestricted tidal access to Inner Bolsa will lead to prolonged inundation and disruption of the existing salt marsh.

Following the construction of a parking lot for visitors and a dike to prevent inundation of land owned by Signal (Fig. 1), partial tidal contact was returned to the Bolsa Chica Ecological Reserve in Inner Bolsa by removing flap valves on culverts through the old dike on 15 November 1978. The lower marsh at the time of writing (August 1979) was in an advanced state of decay and, due to the restricted nature of the culverts, water fluctuation (as recorded from a temporary staff gauge near the parking lot) was limited to 0.5 m above and below −0.75 m MHW.

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A General "Exact Test" for N × M Contingency Tables

Harrington Wells and Jack Lester King

Abstract.—A general "Exact Test" for n × m contingency tables by Harrington Wells and Jack Lester King, *Bull. Southern California Acad. Sci.*, 79(2):65–77, 1980. A generalized Exact Test for n × m contingency tables based upon methodology of the Fisher-Yates Exact Test for 2 × 2 tables and the chi-square statistic is presented. The General Exact Test is a multi-tailed statistic with no minimum expected matrix cell values required. A computer program for the General Exact Test is described and presented in the computer language BASIC. The number of possible tables that need to be considered for an Exact Test can be very large. However, when expected cell sizes are large the chi-square distribution can be used for an approximation to the probability. The generalized Exact Test should be very useful for n × m contingency tables where categories are nominally measured and some expected values are small (e.g. taxonomic problems involving type specimens, or protein electrophoretic data), since other available statistical tests require arbitrary lumping of categories and/or populations.

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Introduction

Experimental situations often occur in which only small samples may be obtained, or where some types of events are rare and others are not. For example, medical studies on human subjects are often limited to a few individuals. Similarly, an environmental impact study of a rare or endangered organism might be limited to small samples. In other cases the high cost of acquiring data may result in few observations being made. On the other hand, genetic and other types of research often involve investigation of rare events (e.g. rare allele occurrence). Although the sample size in this latter type of study may be large, the number of observations of a particular type of event is small. If the data are of nominal measure, and there are low expected numbers of observation for some event type, then the data are essentially untestable unless nonarbitrary lumping of sample populations or categories can be made, or unless the data form a 2 × 2 table and directional predictions are made *a priori*.

This article describes a generalized Exact Test for n × m contingency tables. Two variations of the Exact Test are presented; one based on the multinomial distribution and the other on the multivariate hypergeometric distribution. The method combines the technique of the Fisher-Yates Exact Test for 2 × 2 matrices (Fisher 1934; Yates 1934), and the chi-square statistic (Pearson 1900, 1911) to produce a multi-tailed statistical test with no minimum expected frequency requirements for any size matrix. The technique is presented as a computer program.

The investigator often obtains biological data from several independent samples and wishes to know whether they should be regarded as having come from the same statistical population. The problem is to determine whether the observed variation between samples is due to chance difference in random samples from the same population, or whether the variability signifies true differences among populations. If the researcher can assume that the samples are drawn independently from normally distributed populations of equal variance then the standard parametric F statistic can be used, which is the statistic for analysis of variance. However, if the assumptions of the parametric statistic cannot be made, a nonparametric alternative is required. For data which are at least ordinal there are several appropriate nonparametric statistics. However, there is basically only one general nonparametric statistic for nominal data in contingency tables larger than 2×2: the chi-square (Lehmann 1975).

The classic statistical test of the hypothesis that the sample populations have distributions which are homogeneous for data in a $n \times m$ contingency table has been the chi-square with $(n - 1)(m - 1)$ degrees of freedom. The chi-square test, however, requires that the expected values in each cell not be too small. When this requirement is violated the results of the test are meaningless since the chi-square distribution no longer is a good approximation to the sum of relative squared differences. Siegel (1956) recommends that fewer than 20 percent of the expected values for a χ^2 with df larger than 1 be less than 5, and that no cell should have expected values less than 1. More recent studies involving known distributions suggest that these criteria may be conservative and adequate criteria for the χ^2 test may be only that all expected values are greater than 1.333 (Yarnold 1970; Larntz 1978). In either case, if data do not meet the criteria, columns and/or rows must be lumped until the criteria are met. If there are only 2 categories of result and 2 populations in the problem, then the data are testable by the Fisher-Yates Exact Test regardless of expected cell values if the experimenter can use a one tail test (Siegel 1956). Frequently, studies involve more than two populations, or more than two categories of results, or are two tailed, and in addition deal with rare events. Genetic data often are untestable without lumping, since usually there are 1, 2, or 3 common alleles and an additional number of rare alleles. In other types of experiments it may be expensive to obtain large samples, or the data may have been collected by other researchers prior to conception of the current experiment. Taxonomic studies often can have this latter type of problem. Arbitrary lumping of data has been the only solution.

Methods and Examples

The data to be analyzed are assumed to consist of observations which can be placed into discrete mutually exclusive categories, and to be of either nominal or ordinal measure. Furthermore, the data are assumed to have come from two or more independent samples. Thus, random samples are drawn from n different sampling populations, and each observation in each sample can be classified as one of m different types. Then, the data can be expressed as the n by m contingency table (1); where k_{ij} represents the number of observations of the j*th* type in the random sample from the i*th* population for $i = 1, \ldots, n$ and $j = 1, \ldots, m$, $r_i = \sum_{j=1}^{m} k_{ij}$ for $i = 1, \ldots, n$ are the row sums, $c_j = \sum_{i=1}^{n} k_{ij}$ for

$j = 1, \ldots, m$ are the column sums, and $N = \sum_{i=1}^{n} \sum_{j=1}^{m} k_{ij}$ is the sum of all elements of the data matrix.

$$
\begin{array}{lcccc|c}
 & & \text{CATEGORY} & & & \text{ROW SUM} \\
 & k_{11} & k_{12} & \ldots & k_{1m} & r_1 \\
\text{POPULATION} & k_{21} & k_{22} & \ldots & k_{2m} & r_2 \\
 & \vdots & \vdots & & \vdots & \vdots \\
 & k_{n1} & k_{n2} & \ldots & k_{nm} & r_n \\
\hline
\text{COLUMN SUM} & c_1 & c_2 & \ldots & c_m & N
\end{array} \tag{1}
$$

The null hypothesis to be tested is that the proportion of individuals which can be classified as belonging to a given category is equal in all populations sampled, and that this supposition is true for each observation category. However, proportionately equal numbers of individuals of different types is not hypothesized to necessarily occur in the sampled populations. Let p_{ij} denote the true probability that an observation chosen at random from the *ith* sample population will be of type j for $i = 1, \ldots, n$ and $j = 1, \ldots, m$. Of course, the true probabilities $\{p_{ij}\}$ are not known. Since every observation can be categorized as one of the given possible types, $\sum_{j=1}^{n} p_{ij} = 1$ for $i = 1, \ldots, n$. Then, the hypothesis to be tested may be algebraicly expressed as (2).

$$
\begin{aligned}
&H_0\colon p_{1j} = p_{2j} = \ldots = p_{nj} \text{ for } j = 1, \ldots, m \\
&H_1\colon \text{The hypothesis } H_0 \text{ is not true.}
\end{aligned} \tag{2}
$$

As equation (2) states, the null hypothesis H_0 asserts that all the distributions from the n different samples are actually alike, which is to say they are homogeneous. When the null hypothesis H_0 is true the n random samples are drawn from the same distribution. Therefore, given that H_0 is true, the maximum likelihood estimator of p_{ij} is the same for all values of i, and this estimator is $\hat{p}_{ij} = c_j/N$ for $j = 1, \ldots, n$. It follows directly that under H_0 the maximum likelihood estimator of the expected number of individuals of type j to be experimentally observed from the *ith* sample population is $\hat{e}_{ij} = r_i\hat{p}_{ij} = r_i(c_j/N)$ for $i = 1, \ldots, n$ and $j = 1, \ldots, m$.

The crucial question in defining a general Exact Test is, what criteria does one choose to determine how deviant a given table is from the results expected if the null hypothesis is true? The difference between the actual number of observations recorded of type j from population i, and the expected number under H_0 will tend to be smaller when H_0 is true than when H_0 is not. It seems reasonable, therefore, to base a test of the hypothesis (2) on values of the difference $\Delta = (k_{ij} - \hat{e}_{ij})$. However, it is obvious that the importance of a given deviation from expected is dependent on the expected value, and that since deviation can be either positive or negative from the expected value, a simple summing of the relative differences will result in cancellation of differences. We have chosen to use the statistic Q in (3) to correct for the summation and weighting difficulties because it has been shown to be a good test of difference by Pearson (1900, 1911), and others, irrespective of the fact that the chi-square distribution is a good approximation to (3) when $\{\hat{e}_{ij}\}$ are large. For our purposes, the fact that the chi-square test gives a good approximation of the probability of obtaining a value of Q as large or larger than that observed when expected cell frequencies are large, is an additional reason for choosing (3).

$$Q = \sum_{i=1}^{n} \sum_{j=1}^{m} (k_{ij} - \hat{e}_{ij})^2/\hat{e}_{ij} \tag{3}$$

The probability of obtaining a known table by random samples, given that the null hypothesis is true, can be found by using equation (4) since the sampling distribution is multinomially distributed under H_0; where x! is x factorial.

$$\text{Probability} = \frac{\prod_{i=1}^{n} r_i!}{\prod_{i=1}^{n} \prod_{j=1}^{m} k_{ij}!} \prod_{j=1}^{m} \left(\frac{c_j}{N}\right)^{\sum_{i=1}^{n} k_{ij}} \tag{4}$$

The generalized Exact Test finds the probability of observing a table with Q value greater than or equal to Q of the table actually obtained by the investigator. The fact that Q is the divergence measure of the widely used χ^2 statistical test, attests to its appropriateness as a measure of deviation from results expected under H_0. The exact test is performed by creating all possible tables that have the same row (population) sums as the observed data matrix.

If both the row (population) and column (category) marginals can be fixed then the probability of obtaining a known table by random samples, given that the null hypothesis is true, can be found by using equation (5) since the sampling distribution is multivariate hypergeometrically distributed under H_0; where x! is x factorial.

$$\text{Probability} = \frac{\prod_{i=1}^{n} r_i! \prod_{j=1}^{m} c_j!}{N! \prod_{i=1}^{n} \prod_{j=1}^{m} k_{ij}!} \tag{5}$$

Methodologically, the Exact Test using the multivariate hypergeometric distribution is performed by creating all possible tables that have the same row and column marginal sums as the observed data matrix. The technique, then, is analogous to the procedure of the Fisher-Yates Exact Test for 2 × 2 tables, though the criteria for determining what is a more deviant table differ.

Using either distribution, for each table the Q statistic and probability of obtaining the table when the null hypothesis is true are found. The probability of obtaining a table with value of Q as large or larger than Q of the observed data matrix, then, is the sum of the probabilities of those tables which have Q values greater than or equal to Q of the table actually obtained in the investigation. The General Exact Test is non-directional, so no *a priori* directional assumptions are required. Table 1 gives an example for a small matrix, and Table 2 for a large matrix.

Exact Test problems are best solved by use of a computer (TRS-80 in our case), since the larger n, m, and N become the more tables need be considered

Table 1. Relation between occurrence of individuals of morphological type defined by the *3rd* principal coordinate analysis axis and grassland habitat location (from Wells 1979).

	Observed Data		
	Principal Coordinate Axis III		
Grassland Location	+ Cluster	− Cluster	Total
Main Group	14	83	97
Pine Forest Isolated	1	10	11
Total	15	93	108

Multinomial Exact Test $P = .8964$
Hypergeometric Exact Test $P = .7072$
$\chi^2 = .2357$ DF = 1 $P = .803$

1176 Tables were Created for the Multinomial Test
12 Tables were Created for the Hypergeometric Test

and the more difficult it becomes to calculate each table's probability. Unfortunately, even with the fastest computers it is not practical to test some problems with the Exact Test statistic method. There simply are too many tables to be considered.

Use of the multinomial distribution for the Exact Test requires generation of many more tables than when the multivariate hypergeometric distribution is used, since the latter has only row marginals fixed. For example, Table 1 analyzed by use of the multinomial Exact Test requires generation of 1176 tables while the multivariate hypergeometric Exact Test requires generation of only 12 tables. Thus, the multinomial variation of the General Exact Test is more often impractical to perform than is the hypergeometric version of the Exact Test. However, the criteria for the hypergeometric distribution are rarely truly met. That is, resampling the same set of populations, with population sample sizes equal to those of the first sample will, due to sampling error, often give results differing from those of the original sample. Even so, for the reasons shown by Fisher (1956) for the Fisher-Yates 2 × 2 Exact Test, the multivariate hypergeometric distribution will give a good approximation. Enumeration techniques (Wilson

Table 2. Relation between occurrence of individuals of electrophoresis alkaline phosphatase phenotypes and habitat type (from Wells 1979).

	Alkaline Phosphatase				
	Individual Phenotype				
Habitat	N	S	F	FS	Total
Oak Forest	52	4	0	0	56
Grassland	88	5	3	6	102
Chaparral	100	3	1	0	104
Total	240	12	4	6	262

Hypergeometric Exact Test $P = .02343$

Table 3. Relation between occurrence of individuals of electrophoresis acid phosphatase phenotypes and habitat type (from Wells 1979).

	Acid Phosphatase		
	Individual Phenotype		
Habitat	S	F	Total
Oak Forest	15	24	39
Grassland	51	105	156
Chaparral	29	77	106
Total	95	206	301

Hypergeometric Exact Test $P = .412$
χ^2 Estimated $P = .416$

1941; Barnard 1945) seem only to enhance the apparent significance of the data. Therefore, use of the multivariate hypergeometric distribution for the Exact Test when the multinomial distribution may be impractical is conservative and closely approximates the multinomial probability.

Finally, many cases in which tables are too large to be efficiently tested via either Exact Test method will have large expected matrix cell values. When the expected numbers of all cells are large the Q statistic is approximately distributed as χ^2, and a chi-square table can be used to obtain a close estimate of the true probability. For example, consider Table 3. The Exact Test probability (hypergeometric) of an as likely or less likely table (value of Q) is .412 while the probability obtained by using the χ^2 distribution is .416 (by interpolation). Remember though that the Exact Test does not require large expected values whereas the chi-square approximation does.

An exact test for 3 × 2 contingency tables has previously been proposed in a book by Pierce (1970). However, Pierce simply defined his Exact Test probability as the sum of the probabilities of the tables which have a probability of occurrence less than or equal to that of the observed data table. His method has no quick approximation when expected cell values are large, is only for 2 × 2 or 3 × 2 tables, the power and efficiency have not been calculated as has been done for the χ^2, and the probability obtained by Pierce's method is not necessarily equal to that obtained with the χ^2 method. Using the actually observed data of Table 1 as an example, Pierce's method gives a probability of 1.000 which is larger than either Exact Test probability (multinomial $P = .8963$, hypergeometric $P = .7072$), or the chi-square ($\chi^2 = .2357$, df = 1, $P \simeq .803$).

Finally, consider a one tail modification of the hypergeometric Exact Test for 2 × 2 tables, and how the results compare to those of the Fisher-Yates Exact Test for 2 × 2 tables. For 2 × 2 tables the value of Q is equal to zero and is the minimum when the observed values are equal to the expected numbers. Furthermore, the value of Q is strictly increasing monotonically in either direction from the expected value. The proof is as follows. Let $\{\hat{e}_{ij}\}$ be the expected values, and x and y be some deviation from expected; where $x = y + z$ for any $y \geqslant 0$ and $z > 0$. Q_x and Q_y are then given by equation (6). Since the rows may be interchanged without changing the answer, and since reversing the rows reverses the sign on y and z, the proof for any $y \leqslant 0$ and $z < 0$ is also given by (6).

Table 4. Hypothetical example demonstrating how program initiates matrix and how all possible tables are formed.

Hypergeometric (4a)

Population	Categories A	B	C	D	Total
X	−1	7	4	2	12
Y	5	0	← 0	← 2	5
Z	5	0	← 0	← 0	5
Total	9	7	4	2	22

Observed Table

Population	Categories A	B	C	D	Total
X	5	4	2	1	12
Y	3	1	0	1	5
Z	1	2	2	0	5
Total	9	7	4	2	22

Multinomial (4b)

Population	Categories A	B	C	D	Total
X	12	0	← 0	← 0	12
Y	5	0	← 0	← 0	5
Z	5	0	← 0	← 0	5
Total	22	0	0	0	22

$$Q_x = [(\hat{e}_{11} - x)(\hat{e}_{22} - x) - (\hat{e}_{21} + x)(\hat{e}_{12} + x)]^2/S$$
$$> [(\hat{e}_{11} - y)(\hat{e}_{22} - y) - (\hat{e}_{21} + y)(\hat{e}_{12} + y)]^2/S = Q_y$$

because $[\cdot] > [\cdot]$ can be reduced to $zN(N + 2y) > 0$, which is greater than 0 since $z > 0$; where $\{\hat{e}_{11}, \hat{e}_{12}, \hat{e}_{21}, \hat{e}_{22}\}$ are the expected frequencies, and S = product of all row and column sums. (6)

Now, if a sign is given to Q corresponding to the direction which the table deviates from expected, then Q changes strictly monotonically with the corresponding deviation of the Fisher-Yates test. Q is more extreme than the value of Q for the observed table if: 1) it is greater than the observed Q, given that a positive *a priori* prediction was made; or 2) it is less than the observed Q, given that a negative *a priori* prediction was made. Therefore, for 2 × 2 tables, by assigning a sign to Q values based on an *a priori* directional prediction the results obtained via the multivariate hypergeometric Exact Test are identical to those obtained via the Fisher-Yates Exact Test.

Exact Test Computer Program

We have designed a program to perform the Exact Test using either the multinomial or multivariate hypergeometric distributions on any table of n populations and m categories (see the appendix for the actual program). The program begins by entering the data table. Next a table of Log factorials is created. Probabilities are calculated using logarithms so that the numbers do not get too large due to the factorials. Creating the factorial table at the beginning of the program allows the problem to be solved much more rapidly. The third step is to calculate the value of Q (subroutine 400) and the probability of the table (subroutines 200 and 250 for the multivariate hypergeometric distribution, subroutines 300 and 350 for the multinomial distribution). Finally, all possible tables must be created. To do this, start by initializing the matrix. For the multivariate hypergeometric Exact Test this is done by setting all elements $k_{ij} = 0$ for $i > 1$ and $j > 1$, set k_{1j} = *jth* column sum for $j > 1$, set k_{i1} = *ith* row sum for $i > 1$, and set k_{11} = 1*st* column sum + 1*st* row sum − total sum. An example is illustrated in Table 4a. All elements k_{ij}, $i > 1$ and $j > 1$, are then systematically changed. When some element k_{ij} is changed to $k_{ij} + a$, also change k_{1j} to $k_{1j} - a$, change k_{i1} to $k_{i1} - a$, and change k_{11} to $k_{11} + a$. One only needs to test if $k_{11} \geqslant 0$ to see if the table is a legitimate matrix of the Exact Test. For the multinomial Exact Test matrix initialization is done by setting all elements $k_{ij} = 0$ for $i > 1$, and setting $k_{i1} =$ *ith* row sum for $i = 1, \ldots, n$. An example is illustrated in Table 4b. All elements k_{ij}, $i > 1$, are then systematically changed. When some element k_{ij} is changed to $k_{ij} + a$, also change k_{i1} to $k_{i1} - a$. One needs only to test if $k_{i1} \geqslant 0$ to see if the table is a legitimate matrix of the Exact Test. For Exact Tests based on either distribution, the statistic Q and the probability of observing each legitimate table are calculated. If Q is greater than or equal to Q of the observed data matrix the probability is summed. A version of this program written in the computer language BASIC for the TRS-80 Level II micro-computer (Radio Shack) is given as the Appendix.

Conclusions

The generalized Exact Test for n × m contingency tables is applicable to data of either nominal or ordinal measure. However, we expect that its primary use will be for nominal data where some cells have expected frequencies too small for traditional statistical testing of the data without lumping categories and/or populations (e.g. Wells and Wells 1980). As table size and row and column sums increase so do the number of tables that must be considered for the exact test. Thus, only the advent of widespread computer use has allowed this technique to be a realistic statistical method for researchers. Even so, very large contingency tables cannot be tested via either multinomial or multivariate hypergeometric Exact Tests in a reasonable length of time on even the fastest of contemporary computers. However, on large tables that have large expected frequencies the chi-square distribution gives a good approximation to the Exact Test probability.

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Appendix

A computer program for the generalized Exact Test which is written in the computer language BASIC. The program will perform both the multinomial and multivariate hypergeometric variations of the Exact Test. The program will run on the Radio Shack TRS-80 Level II computer without modification. Odd number lines may be deleted without affecting the program. Lines are skipped to isolate sections of the program so that interpretation is easier.

The program is interactive with the user. Requested are the data matrix and a decision as to the distribution on which to base the Exact Test (multinomial or multivariate hypergeometric). The user need only respond to the commands as they appear to use the program. P, P4, and P5 (see program comments 1–21) are printed for each legitimate table. Q1, T1, T2, P3, P4, and P5 (see 1–21) are printed when the Exact Test is completed.

```
1      REM    EXACT TEST FOR ANY SIZE MATRIX.
3      REM    VARIABLES BEGINNING WITH I,J,K,L,M, AND N ARE INTEGER
              VARIABLES BEGINNING WITH P ARE DOUBLE PRECISION TYPE.
5      REM    WE FIND MOST PROBLEMS DO NOT REQUIRE THAT THE FUNCTIONS
              LOG AND EXP BE DOUBLE PRECISION.
7      REM    RESERVED VARIABLE LIST.
              T1 = # OF TABLES WITH SAME ROW AND COLUMN SUMS.
              T2 = # OF TABLES WITH VALUE OF Q > OR = Q1.
9      REM    Q = "CHI-SQUARE" VALUE OF A TABLE.
              Q1 = "CHI-SQUARE" VALUE OF THE OBSERVED DATA MATRIX.
              M1 = # OF ROWS IN THE DATA MATRIX = # OF POPULATIONS.
11     REM    M2 = # OF COLUMNS IN THE DATA MATRIX = # OF CLASSES.
              N = MATRIX OF DATA WITH DIMENSIONS M1 BY M2.
              N1 = COLUMN MATRIX OF ROW SUMS WITH DIMENSION M1.
13     REM    N2 = ROW MATRIX OF COLUMN SUMS WITH DIMENSION M2.
              N3 = TOTAL SUM.
              E = TABLE OF EXPECTED VALUES WITH DIMENSIONS M1 BY M2.
15     REM    F = MATRIX OF LOG FACTORIALS, F(J)=LOG(J!).
              P = PROBABILITY OF A GIVEN MATRIX OCCURRING.
              P1 = LOG OF VARIABLE PORTION OF PROBABILITY FUNCTION.
17     REM    P2 = LOG OF CONSTANT PORTION OF PROBABILITY FUNCTION.
              P3 = OBSERVED TABLE PROBABILITY.
              P4 = PROBABILITY OF TABLES WITH Q > OR = TO Q1.
19     REM    P5 = TOTAL SUM OF PROBABILITIES = 1.0 AT END OF RUN.
              J AND K ARE RESERVED POINTERS IN MATRIX OPERATION.
              J1,J2,K1,K2, AND K3 ARE LOOP VARIABLES.
```

Appendix

Continued

```
21    REM     VARIABLES TO BE ENTERED ARE M1, M2, AND THE MATRIX N.
23    REM     CLEAR SCREEN AND DEFINE VARIABLE TYPES.
24    CLS
26    DEFINT I,J,K,L,M,N
28    DEFDBL P
29    REM     ENTER MATRIX SIZE AND DIMENSION MATRICES.
30    PRINT “ENTER NUMBER OF POPULATIONS = ROWS” : INPUT M1
32    PRINT “ENTER NUMBER OF CLASSES = COLUMNS” : INPUT M2
34    DIM N(M1,M2), N1(M1), N2(M2), E(M1,M2)
35    REM     INITIATE VARIABLES BY SETTING THEM EQUAL TO ZERO.
36    T1=0 : T2=0 : P4=0 : P5=0 : N3=0
38    FOR J=1 TO M1 : N1(J)=0 : NEXT J
40    FOR K=1 TO M2 : N2(K)=0 : NEXT K
41    REM     ENTER DATA MATRIX AND CALCULATE ROW SUMS, COLUMN SUMS,
              AND THE TOTAL SUM.
42    FOR J=1 TO M1
44    FOR K=1 TO M2
46    PRINT “ENTER ELEMENT”; J; K : INPUT N(J,K)
48    N1(J)=N1(J)+N(J,K) : N2(K)=N2(K)+N(J,K) : N3=N3+N(J,K)
50    NEXT K
52    NEXT J
53    REM     CALCULATE EXPECTED FREQUENCIES.
54    FOR J=1 TO M1
56    FOR K=1 TO M2
58    E(J,K)=N1(J)*N2(K)/N3
60    NEXT K
62    NEXT J
63    REM     DIMENSIONS MATRIX OF LOG(FACTORIAL) AND CALCULATE ITS
              ELEMENTS.
64    DIM F(N3) : F(0)=0
66    FOR J=1 TO N3 : F(J)=F(J-1)+LOG(J) : NEXT J
67    REM     DECIDE WHICH DISTRIBUTION TO USE - MULTINOMIAL OR
              MULTIVARIATE HYPERGEOMETRIC.
68    PRINT “ENTER 1 TO USE THE MULTINOMIAL DISTRIBUTION”
70    PRINT “ENTER 2 TO USE THE HYPERGEOMETRIC DISTRIBUTION”
72    INPUT J : IF J=1 THEN 134
74    IF J=2 THEN 76 ELSE PRINT “INVALID ENTRY” : GOTO 68
75    REM     STATISTIC WILL BE BASED ON MULTIVARIATE HYPERGEOMETRIC
              DISTRIBUTION.
76    CLS : PRINT “EXACT TEST USING HYPERGEOMETRIC DISTRIBUTION”
77    REM     CALCULATE Q AND PROBABILITY FOR OBSERVED TABLE.
78    GOSUB 200 : GOSUB 250 : P3=EXP(P2-P1) : GOSUB 400 : Q1=Q
79    REM     INITIATE MATRICES FOR THE PROCESS OF CREATING ALL POSSIBLE
              TABLES.
80    FOR J=2 TO M1 : N(J,1)=N1(J) : NEXT J
82    FOR K=2 TO M2 : N(1,K)=N2(K) : NEXT K
84    FOR J=2 TO M1 : FOR K=2 TO M2 : N(J,K)=0 : NEXT K : NEXT J
86    N(1,1)=N1(1)+N2(1)-N3
87    REM     INITIATE POINTERS AND BEGIN PROCESS OF TABLE GENERATION.
88    J=M1 : K=M2 : GOTO 102
```

Appendix

Continued

```
89    REM    FORM A NEW MATRIX BY INCREASING ONE ELEMENT OF THE
             MATRIX BY 1.
90    N(J,K)=N(J,K)+1
92    N(1,K)=N(1,K)-1 : N(J,1)=(J,1)-1
94    N(1,1)=N(1,1)+1
95    REM    TEST MATRIX TO SEE IF IT IS LEGITIMATE, IF IT IS CALCULATE Q
             AND THE PROBABILITY ASSOCIATED WITH IT.
96    IF N(J,1)<0 THEN 112
98    IF N(1,K)<0 THEN 112
100   J=M1 : K=M2
102   IF N(1,1)<0 THEN 90
104   GOSUB 250 : P=EXP(P2-P1) : P5=P5+P : T1=T1+1
106   GOSUB 400 : IF Q<Q1 THEN 110
108   P4=P4+P : T2=T2+1
110   PRINT TAB(63), “P = ”; P, “P4 = ”; P4; TAB(63), “P5 = ”; P5 : GOTO 90
111   REM    POINTERS J AND K NEED TO BE RESET, AND ELEMENTS OF THE
             MATRIX NEED TO BE RESET.
112   K=K-1 : If K>1 THEN 116
114   J=J-1 : K=M2 : IF J<2 THEN 178
116   FOR J1=J TO M1
118   IF J1=J THEN K2=K+1 ELSE K2=2
120   IF K2>M2 THEN 130
122   FOR K1=K2 TO M2
124   N(J1,1)=N(J1,1)+N(J1,K1) : N(1,K1)=N(1,K1)+N(J1,K1)
126   N(1,1)=N(1,1)-N(J1,K1) : N(J1,K1)=0
128   NEXT K1
130   NEXT J1
132   GOTO 90
133   REM    STATISTIC WILL BE BASED ON MULTINOMIAL DISTRIBUTION.
134   CLS : PRINT “EXACT TEST USING MULTINOMIAL DISTRIBUTION”
135   REM    CALCULATE Q AND PROBABILITY FOR OBSERVED TABLE.
136   GOSUB 300 : GOSUB 350 : P3=EXP(P2+P1) : GOSUB 400 : Q1=Q
137   REM    INITIATE MATRICES FOR THE PROCESS OF CREATING ALL POSSIBLE
             TABLES
138   FOR J=1 TO M1 : N(J,1)=N1(J) : NEXT J
140   FOR J=1 TO M1 : FOR K=2 TO M2 : N(J,K)=0 : NEXT K : NEXT J
141   REM    INITIATE POINTERS, BEGIN PROCESS OF TABLE GENERATION.
142   J=M1 : K=M2 : GOTO 150
143   REM    FORM A NEW MATRIX BY INCREASING ONE ELEMENT OF THE
             MATRIX BY 1.
144   N(J,K)=N(J,K)+1 : N(J,1)=N(J,1)-1
145   REM    TEST MATRIX TO SEE IF IT IS LEGITIMATE, IF IT IS CALCULATE Q
             AND THE PROBABILITY ASSOCIATED WITH IT.
146   IF N(J,1)<0 THEN 158
148   J=M1 : K=M2
150   GOSUB 350 : P=EXP(P2+P1) : P5=P5+P : T1=T1+1
152   GOSUB 400 : IF Q<Q1 THEN 156
154   P4=P4+P : T2=T2+1
156   PRINT TAB(63), “P = ”; P, “P4 = ”; P4; TAB(63), “P5 = ”; P5 : GOTO 144
157   REM    POINTERS J AND K NEED TO BE RESET, AND ELEMENTS OF THE
             MATRIX NEED TO BE RESET.
```

Appendix

Continued

```
158  K=K-1 : IF K>1 THEN 162
160  J=J-1 : K=M2 : IF J<1 THEN 178
162  FOR J1=J TO M1
164  IF J1=J THEN K2=K+1 ELSE K2=2
166  IF K2>M2 THEN 174
168  FOR K1=K2 TO M2
170  N(J1,1)=N(J1,1)+N(J1,K1) : N(J1,K1)=0
172  NEXT K1
174  NEXT J1
176  GOTO 144
177  REM    PRINT FINAL SOLUTION.
178  CLS
180  PRINT “Q1 = ”; Q1, “P3 = ”; P3
182  PRINT “T2 = ”; T2, “P4 = ”; P4
184  PRINT “T1 = ”; T1, “P5 = ”; P5
186  END
199  REM    SUBROUTINE TO CALCULATE CONSTANT PORTION OF
            HYPERGEOMETRIC PROBABILITY FUNCTION.
200  P2=0
202  FOR J2=1 TO M1 : P2=P2+F(N1(J2)) : NEXT J2
204  FOR K3=1 TO M2 : P2=P2+F(N2(K3)) : NEXT K3
206  P2=P2-F(N3)
208  RETURN
210  END
249  REM    SUBROUTINE TO CALCULATE VARIABLE PORTION OF
            HYPERGEOMETRIC PROBABILITY FUNCTION.
250  P1=0
252  FOR J2=1 TO M1
254  FOR K3=1 TO M2
256  P1=P1+F(N(J2,K3))
258  NEXT K3
260  NEXT J2
262  RETURN
264  END
299  REM    SUBROUTINE TO CALCULATE CONSTANT PORTION OF
            MULTINOMIAL PROBABILITY FUNCTION.
300  P2=0
302  FOR J2=1 TO M1 : P2=P2+F(N1(J2)) : NEXT J2
304  RETURN
306  END
349  REM    SUBROUTINE TO CALCULATE VARIABLE PORTION OF
            MULTINOMIAL PROBABILITY FUNCTION.
350  P1=0
352  FOR K3=1 TO M2
354  P=0
356  FOR J2=1 TO M1
358  P1=P1-F(N(J2,K3)) : P=P+N(J2,K3)
360  NEXT J2
362  P1=P1+P*LOG(N2(K3)/N3)
364  NEXT K3
366  RETURN
368  END
```

Appendix

Continued

```
399    REM    SUBROUTINE TO CALCULATE Q = ''CHI-SQUARE.
400    Q=0
402    FOR J2=1 TO M1
404    FOR K3=1 TO M2
406    Q=Q+(N(J2,K3)-E(J2,K3))↑2/E(J2,K3)
408    NEXT K3
410    NEXT J2
412    RETURN
414    END
```

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Research Notes

Morphological Variation of the Carinal Plate of the Stalked Barnacle *Pollicipes polymerus* Sowerby

The intertidal area of Southeast Farallon Island, San Francisco County, California (37°42′N, 123°00′W) is riddled with numerous caves at sea level. Although the majority of these penetrate less than 8 m, a few reach lengths of over 60 m. The biota of these caves differ markedly from that occurring at corresponding tidal levels outside. While many organisms are thought to occur in caves because of reduced illumination, others appear to occupy caves because of the benefits derived from the cave's topography. The decreasing dimensions of a cave with length, combined with acute and oblique side channels, deep fractures and wall protuberances, tend to intensify and concentrate the waves that enter the cave. In these areas of considerable wave action the stalked barnacle *Pollicipes polymerus* Sowerby (1833) occurs in large aggregations. This barnacle is generally associated with, and is considered indicative of high energy intertidal areas along the coast of California (Ricketts & Calvin, 1968).

During a biological survey of Southeast Farallon Island, several aggregations of *P. polymerus* were examined. These aggregations occurred in a moderately exposed, dimly illuminated side channel which leaves the main chamber of the cave at an acute angle. The side channel also opens seaward, but the position and level of the opening is such that neither large scale water movement nor illumination is enhanced. Two aggregations, each of approximately 20 typical *P. polymerus,* contained two and three individuals respectively, having an elongate carinal plate (Fig. 1).

P. polymerus has been figured by Darwin (1851), Pilsbry (1907), Newman (1975), and others as having a carina that terminates below the apex of the tergum, a rostrum which extends above the accessory platelets, triangular accessory platelets and peduncular scales (Fig. 2). The membrane that surrounds the aperture has been described as being yellow to brown or red in color, the latter being associated with low illumination.

In the Southeast Farallon Island variants (Fig. 3) the carinae extend as much as one centimeter beyond the apex of the tergum; the rostrum is reduced; the terga and scuta show signs of erosion (exfoliation) and both accessory platelets and peduncular scales are sub-rectangular in shape. The membrane that surrounds the aperture is red.

Arnold Ross and William A. Newman (Scripps Institute of Oceanography) suggested that the elongate carina may only be apparent; the terga being reduced due to exfoliation of the laminae. Exfoliation of both terga and scuta is not uncommon, as can be seen in Figure 3.

To test the above suggestion we did a morphometric study of four variant and 59 typical specimens of *P. polymerus* to determine (1) if the elongate carinae result from plate exfoliation or allometric growth, and (2) if the specimens with elongate carinae are allometrically different from typical specimens. As a bio-

Fig. 1. *In situ Pollicipes polymerus* with elongated carina (arrow). Southeast Farallon Island, California. T. Niesen photographer.

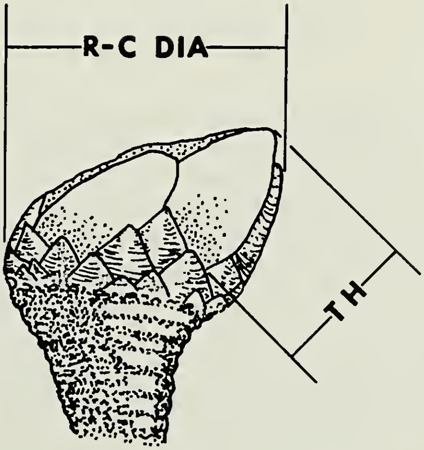

Fig. 2. Typical *Pollicipes polymerus* showing measurements used for capitular biometric index; R-C DIA = rostral-carinal diameter, TH = tergal height.

Fig. 3. Variant *Pollicipes polymerus* with elongated carinae. Southeast Farallon Island, California. Drawing by E. Hamburg.

metric index we used the relationship between the rostral-carinal (r-c) diameter and the tergal height (Fig. 2); specimens were measured to the nearest 0.01 mm with vernier calipers.

The scatter diagram of tergal height on r-c diameter for the 59 typical specimens indicates a linear relationship for the two variables (Fig. 4). An analysis of covariance showed no significant difference in the relationship of r-c diameter to tergal height between the variant and typical specimens. Thus the elongated carinae of the variant specimens are not a result of tergal exfoliation.

Fitted regression lines were then calculated for the four specimens with elongated carinae and the 59 typical specimens. Although the variants fall within the cluster of points defining the typical specimens, they do not appear to correspond to the fitted regression line for the typical specimens (Fig. 4). A Student's t-test of regression coefficients shows that the variant specimens are significantly different ($P < 0.01$) from the typical specimens. Therefore, the capitular growth of the variants is allometrically different from the typical barnacles. Allometric growth of these barnacles may result from competition between individuals in the aggregation. All four variant barnacles were found in the center of their respective aggregations and were surrounded by typical specimens.

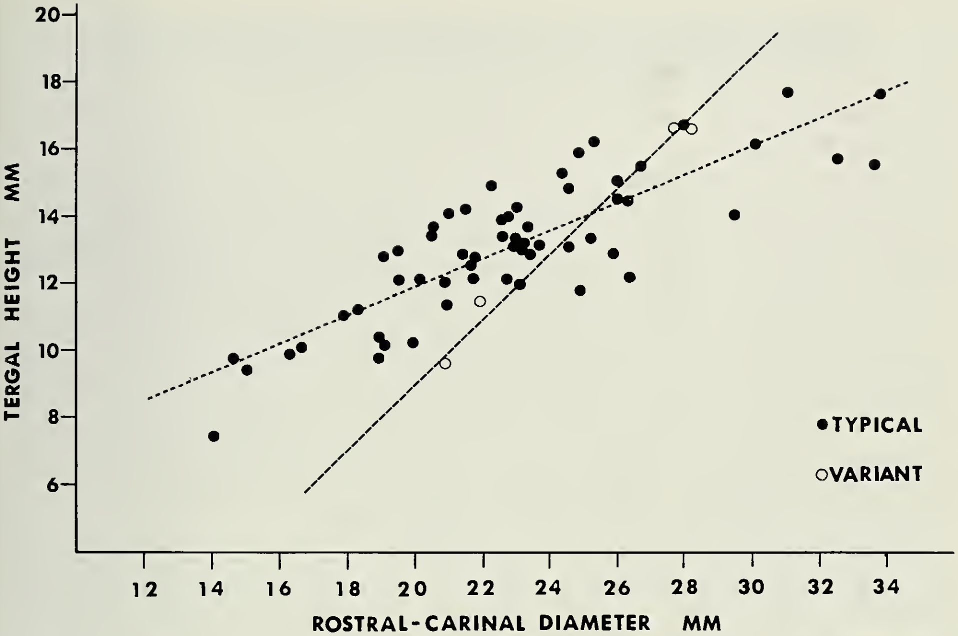

Fig. 4. Scatter diagram and fitted regression lines of tergal height on rostral-carinal diameter for typical and variant specimens of *Pollicipes polymerus*. Correlation coefficient for typical specimens = .8479; for variants = .9929.

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Observations of Feral Populations of *Xenopus laevis* (Pipidae) in Southern California

Xenopus laevis, a clawed frog native to Africa, is known to colonize areas outside its natural range. Extralimital populations have been reported in the United Kingdom, Ascension Island, and the United States (Wyoming, Wisconsin, Arizona, New Mexico, Utah, California, Florida, Nevada, and Colorado).

The characteristics that may have aided in the establishment of temporary or permanent populations outside of Africa appear to be: (1) distribution for scientific, medical, and pet uses; (2) ability to reproduce in a broad variety of conditions including temporary bodies of water, man-made ponds, and irrigation/drainage channels; (3) ability to avoid adverse conditions by short overland migrations, aestivation, and habitat modifications; (4) high reproductive potential; and (5) opportunistic feeding on a broad variety of food sources.

The precise date of introduction in California in unknown. The first official report of feral frogs in California is 1968 (St. Amant and Hoover 1969). However, it is likely that *Xenopus* existed in California waters before this time. Clawed frogs were widely used in the 1930's and 1940's for human pregnancy diagnosis and subsequently for medical research. A few years later, clawed frogs became popular as aquarium pets and were readily available to the general public through pet stores. The presence of *Xenopus* in Orange County near metropolitan Los Angeles before 1968 undoubtedly stems from accidental or intentional release of captive frogs by humans. Subsequent reports of feral clawed frogs in Los Angeles, San Diego, Yolo, and Riverside counties generated an often sensationalized interest within California that may have prompted further human dispersal of clawed frogs.

The San Diego Natural History Museum was often contacted by people seeking information on the frogs and the areas where they could be collected. However, few studies were conducted to gain insight into the potential impact of this exotic on the established fauna (see Munsey 1972; Zacuto 1975; Fritts and McCoid 1976).

From summer 1974 through spring 1977, we conducted a series of studies on the feeding habits, growth, and reproduction of *Xenopus* in California. During this period we made a number of incidental observations on population densities, dispersal, and aestivation. Because such data are important to understanding feral clawed frogs and to any eradication, control, or management of the species, the observations are summarized in this report.

Generally, when *X. laevis* was encountered in San Diego and Riverside counties, it was found in large numbers in restricted areas such as ponds and pools. In contrast to the broad distribution in the Sweetwater River drainage described on the basis of metamorphosing young by Mahrdt and Knefler (1973), we found clawed frogs to be conspicuous in only a few sites. We investigated several of the sites noted by Mahrdt and Knefler, but often found clawed frogs to be absent or present only as transients. The two sites we studied most intensively were: Site A—a pond at the junction of Avocado and Valencia streets, Spring Valley, San Diego County, California; and Site B—a pond 1.6 km southwest of Vail Lake, near Temecula, Riverside County, California. Site A was about 17 × 42 m with a maximum depth of 1.5 m. Site B was about 6 × 18 m with depths of 10–70 cm. Using a Peterson mark-recapture method, we computed population estimates of 602 and 494 adult frogs for Sites A and B respectively. Additionally, a far larger body of water in the flood plain of the Tijuana River in San Ysidro, San Diego County, California, was determined to have a large population of clawed frogs, but it was not studied.

That each of these major populations was in a different river system and not adjacent to similar aggregations suggests that human-aided dispersal is more important to colonization of clawed frogs in California than is natural dispersal of the frogs. The metropolitan San Diego populations possibly stem from a pet dealer who raised clawed frogs in outdoor tanks adjacent to the Sweetwater River in the mid-1960's (Douglas Ruth, pers. com.). The population at Site B was first reported to us in January 1975, shortly after the opening of a recreational vehicle park which encompasses Site B. Most of the campers and visitors to the campground and park come from the metropolitan Los Angeles area where established populations of clawed frogs have existed for several years. Campers and visitors may have brought pets which were introduced into the waters in the campground.

Within a stream system, clawed frogs are capable of dispersing over short distances (Mahrdt and Knefler 1973), perhaps in response to high population density and flooding conditions. After metamorphosis (generally in May but quite variable), large numbers of juveniles move downstream out of the source pond. We observed the colonization of a shallow pond 0.8 km downstream from Site B in May 1975 by 200–300 juveniles. Only a few juveniles were found in the intervening stream habitat despite our active search. Subsequently, we collected downstream from the second pond in a marsh area adjacent to Vail Lake but only one juvenile clawed frog was found on 4 May 1975. The majority of the frogs apparently stopped at the first available habitat. No adults were found in the downstream pond until several months after colonization.

Juvenile clawed frogs also used sheet flooding situations to disperse. In San Diego County near Site A, young frogs moved across fields and school playgrounds with runoff after a heavy rain. Only recently metamorphosed frogs were observed in actively running water. All sites occupied by *Xenopus* that we examined were noticeably disturbed habitats (i.e., directly altered by man in being artificially impounded, channelized, or excavated).

It is commonly thought that adult *Xenopus* are unpalatable to predatory fishes (James St. Amant, pers. com.). In our experience, *X. laevis* is conspicuously absent from waters with predatory fishes (centrarachids) in Riverside and San Diego counties. We failed to find clawed frogs in much of the Sweetwater River, or in the San Diego and Santa Margarita rivers. Frogs were also absent from a number of large ponds seasonally continuous with the Sweetwater River and from the margins of Vail Lake. Because of the continuity of the drainage and proximity to established populations of frogs, *Xenopus* is presumed to have had opportunities to colonize these areas occupied by fish species.

It is possible that *Xenopus* can be eliminated from a body of water by continuous predatory pressure on the larvae or smallest young. We have some circumstantial evidence to suggest that black crappie (*Pomoxis nigromaculatus*) and green sunfish (*Lepomis cyanellus*) were responsible for the extirpation of all *Xenopus* larvae from the spring reproduction of 1976 at Site B. Calling male frogs, amplexing pairs, egg masses, and young larvae, between the stages of 5 to 47, were observed during April and May 1976. However, no larvae older than stage 47, which coincides with the initiation of midwater schooling of clawed frog larvae, were found despite continued searches. Black crappie and green sunfish were present throughout the 1976 reproductive period. Clawed frogs did reproduce successfully in the same area in 1975, but to our knowledge no predatory fishes were present at that time.

In California (like Africa) *X. laevis* was subjected to occasional drought. During late summer and early fall, water levels dropped significantly at Site A. In 1974 and 1975 this further concentrated an already dense population and caused a marked behavioral shift in the frogs. Surface water temperatures exceeded 30°C and as the pond reached depths of 10–15 cm, bottom temperatures approximated those at the surface. During this period, clawed frogs were concentrated in the deepest water.

Upon examination of the actual areas occupied, we found the pond substrate had been excavated by the frogs, thereby increasing the vertical water column. Presumably in response to rising water temperatures, the frogs excavated pits in the soft mud. The pits were 30–40 cm deep and 10–45 cm wide. Each pit was occupied by one to two frogs but adjacent pits sometimes were connected in a reticulated pattern. The temperature at the bottom of the pits was much lower than nonexcavated areas and fluctuated around 20°C. Frogs often surfaced to breathe, but at other times remained in the pits.

During 1974 the pond did not completely dry, but if it had, the pits would have concentrated the available water for the frogs, delaying the need for aestivation or other evasive behavior. Under extreme drought conditions the pits would presumably be the site of further excavations for aestivation chambers (Balinsky et al. 1967).

To test this hypothesis, 11 frogs were removed from Site A on 10 September 1974, transported to the laboratory and placed in one-gallon jars (3.78 l) filled with mud from the substrate of Site A. The jars were covered with wire mesh and the contents allowed to dry slowly. The frogs immediately burrowed into the mud, constructing a small space at the bottom of the jar with a vertical tube opening to the surface. Over a 3 month period, all 11 frogs were sequentially removed, examined, and preserved. In each instance, the frog was found in vertical position with the head oriented upwards. The frog occupied a chamber not greatly exceeding the dimensions of the body. The chamber had a vertical connection with the surface of the now hardened soil, which presumably served as a source of air for the aestivating frog. During the confinement in jars, no food or water was added and only two animals died before they were removed from the experiment. It should be noted that the frogs were not dormant during their confinement and occasionally were seen with the tip of the snout projecting from the vertical opening. On 13 December 1974, the last frog gained 31.6 gm in weight, presumably due to water uptake.

Perhaps the greatest concern about the impact of *X. laevis* in California involves its feeding habits. The frogs have been characterized as voracious, nonspecific predators of vertebrates (St. Amant et al. 1973). However, only indirect evidence exists to support this belief. There have been only two feeding studies on California populations (Lenaker 1972; McCoid and Fritts 1980). The latter study refuted the conclusions of the former by demonstrating that Lenaker's method of collecting frogs inadvertently produced a bias in the stomach contents of the frogs. McCoid and Fritts concluded that *Xenopus* preyed almost exclusively on slow-moving invertebrates in southern California, a conclusion supported by laboratory studies (Avila and Frye 1978). Mahrdt and Knefler (1972) cited the absence of presumed vertebrate prey species in the areas occupied by *Xenopus,* implying the possibility of local extinctions due to predation by *Xenopus.* However, these authors gave no consideration to other factors that might affect the distribution of the prey species (i.e., habitat quality or seasonal variation in distribution).

During our investigations at Site A, *Gambusia affinus,* which was widely introduced in California for mosquito control, became extinct during a period of low water and high temperatures in 1974. There is little doubt that clawed frogs consumed some of the *Gambusia* as the water volume decreased. *Xenopus* is capable of capturing active vertebrates in confined situations (McCoid and Fritts 1980). An unknown percentage of the *Gambusia* at Site A died possibly as a result of high water temperatures in those shallow areas not occupied by clawed frogs. On the basis of our observations, the *Gambusia* were faced with two alternatives—to remain in hot shallow water or invade the small pits occupied by clawed frogs. The confinement of pits constructed by clawed frogs presented an opportunity for the frogs to exploit a food source otherwise unavailable. Therefore, the extinction of *Gambusia* was a result of unusual conditions associated with drought and the presence of clawed frogs. Whether *Gambusia* would have become extinct in the absence of *Xenopus* cannot be determined.

In view of our studies and a review of other data, we see the impact of *X. laevis* in a different light than other investigators. Our analysis of stomach contents (McCoid and Fritts 1980), distributions, and other aspects of the biology of feral clawed frogs, suggests that *X. laevis* is a nuisance species, but not a major threat to the established fauna (introduced or native) of California. In San Diego and Riverside counties, the frogs occupy marginal habitats and prey infrequently on aquatic vertebrates. The fact that reproduction of *Xenopus* is not always successful suggests that populations can be controlled and, perhaps with time, eradicated by game fishes. Certainly the failure of high concentrations of rotenone to remove a Los Angeles County population should not be used as testimony to the durability of an exotic frog that lacks gills and breathes air at the surface of the water (see St. Amant 1975; Zacuto 1975).

Because the major factor in dispersal of clawed frogs in California appears to be human transport, populations will likely continue to appear and spread. An alternative way to curb the spread of *Xenopus* in California is through education of the general public on the implications of exotic introductions.

Xenopus laevis is used widely in research laboratories and classroom instruction (Deuchar 1975). As an animal capable of reproducing and forming dense populations under proper conditions, a potential exists for the clawed frog to be reared for commercial distribution to research institutions that currently depend upon imported *Xenopus* and native *Rana* sp. harvested from natural habitats. A commercial biological supply company in Wisconsin is currently rearing *Xenopus* in their laboratory. On the basis of the success of feral populations in California, it may be possible in special situations to harvest feral clawed frogs without detrimental environmental effects.

Acknowledgments

We thank the Riverside County Fish and Game Commission for partial support of field work at Site B. We are indebted to D. Ruth, C. Crumly, and H. Snell for assistance with field work. R. Matheson, J. Sites, Jr., and J. Dixon provided editorial comments on an early draft of this paper.

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79(2), 1980, pp. 87–88

Extension of the Range of *Holothuria zacae*, Deichmann 1937

In October 1970, 20 unusual holothurians were found off Ship Rock, Santa Catalina Island, California (33°27′48″N; 118°29′26″W) on a shelly debris bottom, at a depth of 30 meters. One specimen was sent to the Smithsonian Institution and it was identified as *Holothuria zacae* (Deichmann 1937), a species previously known to range from Cedros and Guadalupe Islands off Baja California south to the Galapagos Islands, and into the Gulf of California.

The Panamic region of the west coast of North America was explored extensively for shallow water holothurians during the Hancock Expeditions of 1932–1939 and 1944–1954 (Deichmann 1958). A search of these reports and other available literature and collections leads us to believe that the Ship Rock population is the only one known from north of Guadalupe Island. The locality data from the Hancock Expeditions suggest a rather disjunct distribution of *H. zacae*, hence the occurrence of this species so far north of its known range may be unusual.

Additionally, Pawson (pers. comm.) has suggested that since the genus is known to have a pelagic larva, this is probably an isolated population at the northern extreme of the range and that it has merely escaped detection until recently.

The physical characteristics of the Ship Rock forms comply with the "forma


Holothuria zacae, adult. 90′ of water, base of Ship Rock, Santa Catalina Island.

iota" of *H. zacae* typical of the Baja California area (Pawson, pers. comm.). A representative individual (Fig. 1) was 40 cm long and 18 cm in circumference. Its basic coloration is a creamy background with two widely separated rows of dark brown papillae, each with a green tip. The rest of the dorsal surface is covered with closely spaced, lighter brown, warty projections. The numerous podia are green and distributed abundantly along the ventral surface. When disturbed, only a slight contraction of the body wall is exhibited and there is no evidence of evisceration.

Another large holothurian that occurs at Catalina, *Parastichopus parvimensis* (Clark 1913), is generally smaller, caramel-brown in color, has fewer dorsal papillae and fewer ventral podia than *H. zacae*. *P. parvimensis* has a great capacity for contraction and readily eviscerates when handled roughly.

More recent observations (March–May 1978) of the Ship Rock *H. zacae* population revealed only five individuals found exclusively on a shelly debris, around rocks, at depths of 25 to 35 meters. Some cursory investigations have been made for other populations in the southern California bight without success.

We would like to thank D. L. Pawson of the Smithsonian Institution for his assistance in identifying our material and for searching the available literature. Further, we thank the Institute for Marine and Coastal Studies of the University of Southern California for logistical support.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

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Research Notes

COVER: Aerial oblique view of Inner Bolsa Bay, California, June 15, 1979. Pacific Ocean at right; oil field operated by Signal, Inc. at upper left. Diked area at center is part of Bolsa Chica Ecological Reserve to which tidal fluctuation was partially restored in 1978.

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Notes on a Collection of Centrolenid Frogs from the Colombian Chocó

Marc P. Hayes and Priscilla H. Starrett

Abstract.—Notes on a collection of centrolenid frogs from the Colombian Chocó by Marc P. Hayes and Priscilla H. Starrett, *Bull. Southern California Acad. Sci.*, 79(3):89–96, 1980. A collection of 30 Chocoan centrolenids comprising 7 species is reported. *Centrolenella albomaculata, C. chirripoi, C. euknemos, C. fleischmanni,* and *C. ilex* are first reports from Colombia. *C. chirripoi* is reported for the first time outside the type locality in Costa Rica. Prepollical spines found in *C. spinosa* are shown to lack sexually dimorphic character. A distinctive protuberance of the third metacarpal in centrolenids is advanced as an apparently unique familial character.

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In 1968 and 1971, Philip A. Silverstone visited the Colombian Chocó in the course of work on dendrobatid frogs. Silverstone (1973) gives a thorough description of the 1971 study site. During these visits, a small, but significant collection of centrolenid frogs was made. This assemblage of 31 frogs was subsequently deposited in the herpetological collection of the Los Angeles County Museum of Natural History (LACM).

It is the purpose of this paper to report on this collection, as several of the species are new to Colombia, and further, to comment on significant characters, augmenting existing knowledge of selected species and the family Centrolenidae. A single specimen is omitted from the following accounts, as it is being reserved for possible description as a new species in a separate account. Localities of individual specimens are summarized in the appendix following the discussion.

Centrolenella albomaculata Taylor

Specimens.— LACM 72909.

Remarks.—This is the only specimen referable to this species and the first report from Colombia. We were struck by the superficial resemblance of this specimen to the Amazonian lowland slope form *C. medemi* (see Lynch and Duellman 1973). This specimen suggested a new species, were it not for some large-spotted variants in the Costa Rican collections at the University of Southern California. Specimens of *C. albomaculata* show an increasing size progression of spots from head to vent, the largest spots located on the upper surface of the thigh. Further, Costa Rican individuals examined exhibit considerable variation in spot size among individuals. However, thigh spots of this Colombian example attain maximum diameters of 2.5–3.0 mm, a condition found only in the Costa Rican specimens with the largest spots. In this respect, the Colombian specimen represents the extreme of pattern variants examined.

Centrolenella chirripoi (Taylor)

Specimens.—LACM 72929.

Remarks.—*C. chirripoi* was reviewed by Starrett and Savage (1973), who regarded it as a valid species. The only collections of this species are the holotype and paratype series from Río Cocolis, Provincia de Limón, Costa Rica (Taylor 1958). This single collection represents the first reported collection outside the type locality. We take this opportunity to emphasize the characters which separate *C. chirripoi* from its closest congeners, since centrolenids of the *fleischmanni* group (sensu Savage 1967) are notoriously difficult to separate in a preserved state. Starrett and Savage (1973) listed 8 characters, all of which are not equally important in characterizing this species. The characters most important are: 1) the distinctive webbing between fingers II and III, 2) the indentation between the nostrils when the head is viewed from above, 3) the only slightly protuberant eyes when viewed from above, 4) the slightly rounded nature of the snout when viewed in profile, 5) the long loreal region and 6) the weak canthus rostralis. The webbing character, perhaps the most distinctive, is superficially shared with *C. pulverata*. Figure 1 demonstrates the distinctive webbing in both species. The remarkable feature of this character is that it exhibits very little variation in all specimens examined. Starrett and Savage (1973) also noted that the color of the parietal pericardium was not known. Examination of the guanine distribution on this specimen and one of the paratype series (KU 36868) suggested that *C. chirripoi* has a transparent parietal pericardium. This was confirmed by Silverstone's field notes, taken on the specimen in life, which stated (quote):"bare heart." In this character and the indentation of the snout, *C. chirripoi* allies itself with *C. colymbiphyllum*.

Centrolenella euknemos Savage and Starrett

Specimens.—LACM 47066.

Remarks.—Savage and Starrett (1967) report this species from Costa Rica and Panama. This specimen represents the first published record from Colombia and extends the known range of the species over 400 km to the south and east.

Centrolenella fleischmanni (Boettger)

Specimens.—LACM 47067–9, 47071–4, 72930.

Remarks.—This is the most wide ranging of centrolenid species (Lynch and Duellman 1973), although some (Goin 1964; Starrett and Savage 1973) suggested that several cryptic species may be involved. Duellman (1973) reports the range as from Guerrero and Veracruz, Mexico to Surinam and Ecuador. Occurrence in Colombia is based on a statement of Goin (1964), where he postulates its presence based on geographic encirclement by documented localities. These collections, therefore, represent the first definitive records from Colombia.

Centrolenella ilex Savage

Specimens.—LACM 47063, 47070, 72910, 72914.

Remarks.—Starrett and Savage (1973) reported specimens from Costa Rica and Panama. Charles W. Myers (pers. comm.) recently informed us that the unlisted specimens of *C. ilex* reported by Lynch and Duellman (1973) are not referable to this species. These collections, therefore, represent the first definitive records

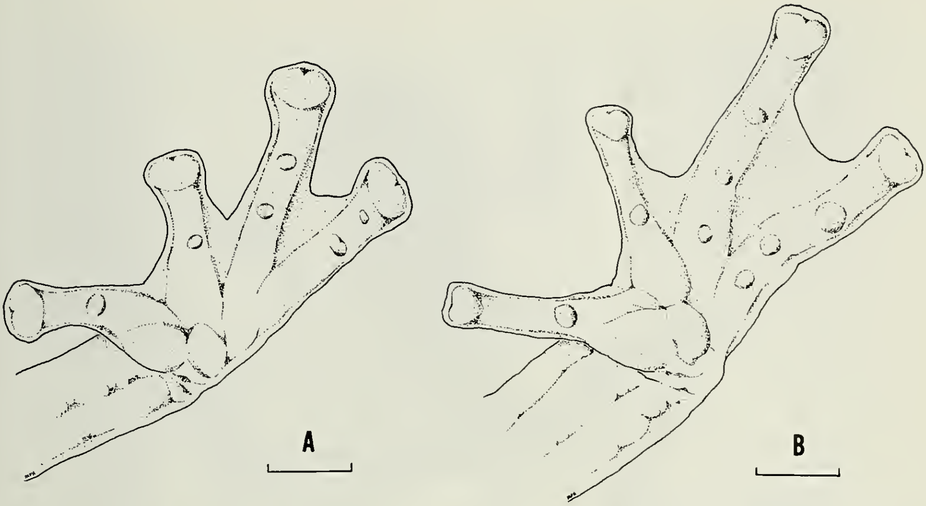

Fig. 1. A) Volar aspect of left manus of *Centrolenella chirripoi*. Drawn from specimen KU 36863. B) Volar aspect of left manus of *Centrolenella pulverata*. Drawn from specimen CRE 7155 (USC collections). Scale mark = 2 mm.

from Colombia. Radiographs of the males in this series confirm a previously unverified suspicion that the males of this species have distinctive humeral hooks (Fig. 2). Myers informs us that this is also the case in Panamanian *C. ilex*. The humeral hook in *C. ilex* is long, thin, lying parallel to the humerus and terminating in a sharp point (Fig. 3). It lies well-concealed by the arm musculature. This is in sharp contrast to the rather spatulate, flairing humeral hooks found in *C. prosoblepon*. Females have at most a small humeral boss, but no hook. We have also examined a specimen from Jaime Villa that was taken in the drainage of the Río Indio, Departamento Zelaya, Nicaragua, extending the known range north to this site.

Centrolenella prosoblepon (Boettger)

Specimens.—LACM 47065, 72923, 72925–6.

Remarks.—The three male specimens (LACM 72923,72925–6) lack the dorsal and tibial spots characteristic of most Costa Rican *C. prosoblepon*. Lynch and Duellman (1973) comment on the apparent continuum of variation between spotted and unspotted dorsal patterns which forced them to synonymize *C. parabambae* with *C. prosoblepon*. Furthermore, snout shape in these specimens is the extreme of variants observed in Central American *C. prosoblepon*, the canthal platform being less pronounced. This variability in pigmentation, snout shape and our own observations on the shape and degree of flairing in humeral hooks did not permit separation of these specimens as a new species. As with *C. fleischmanni*, cryptic species may be involved, but this is not determinable at this time. Lynch and Duellman (1973) cite specimens referable to this species from Departamento Cauca, Colombia, but these collections are the first reported from Departamento del Chocó.

Fig. 2. Radiograph of a male *Centrolenella ilex* (LACM 72910), venter up. Dark arrow denotes metacarpal bulge and light arrow points to humeral hook. Specimen length = 29.5 mm.

Centrolenella spinosa Taylor

Specimens.—LACM 47064, 72911, 72913, 72917–8, 72920–2, 72924, 72927–8.

Remarks.—Taylor (1949) described this species from an all male series and speculated on the presence of reduced prepollical spines in females. In a later paper (Taylor 1951), he notes that the spine is entirely concealed and restates that females have a less well developed spine, although he cites no new specimens. Savage (1967) mentions that *C. spinosa* males have both a free prepollex and prepollical spine and adds that females have a prepollex while implying they lack a prepollical spine. This Colombian series of *C. spinosa* includes 11 adults, 3 females and 8 males. Radiographs of both this series and Costa Rican *C. spinosa*

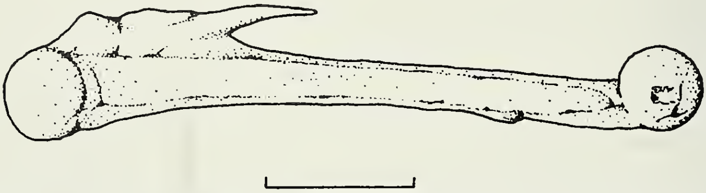

Fig. 3. Left humerus, ventral aspect of a male *Centrolenella ilex* (LACM 72910). Drawn from a radiograph. Scale mark = 2 mm.

Fig. 4. Radiograph of a female *Centrolenella spinosa* (LACM 72920), ventral aspect. Dark arrow denotes metacarpal bulge and light arrow points to the prepollical spine. Specimen length = 21.0 mm.

show that both males and females have a prepollex and prepollical spine (Figs. 4–5). Furthermore, the spine found in females is not significantly smaller than that found in males. Starrett and Savage (1973) report localities for this species from Costa Rica and Panama. Their addition that specimens examined from Colombia and Ecuador are referable to this species refers in part to the series being reported here. We concur with their determinations and confirm this series as the first definitive records of *C. spinosa* from Colombia.

Discussion

The species reported herein raise the total number of known Colombian centrolenids west of the Andean crest to 13, the others being *Centrolene geckoideum*, *Centrolenella antioquiensis*, *C. buckleyi*, *C. grandisonae*, *C. griffithsi* and *C. johnelsi* (Cochran and Goin 1970; Duellman and Lynch 1973). There is no reason to believe that the wet lowland tropical forest species, *C. pulverata* and *C. valerioi*, found in Panama (Starrett and Savage 1973), will not eventually be found in the Chocoan lowlands of Colombia. Similar predictions can be made for the mid-elevation Pacific slope species, *C. peristicta* and *C. ocellifera*, reported by Lynch and Duellman (1973) from Ecuador on biogeographic grounds. These species are expected in similar habitats on the Pacific slope of the Colombian Andes.

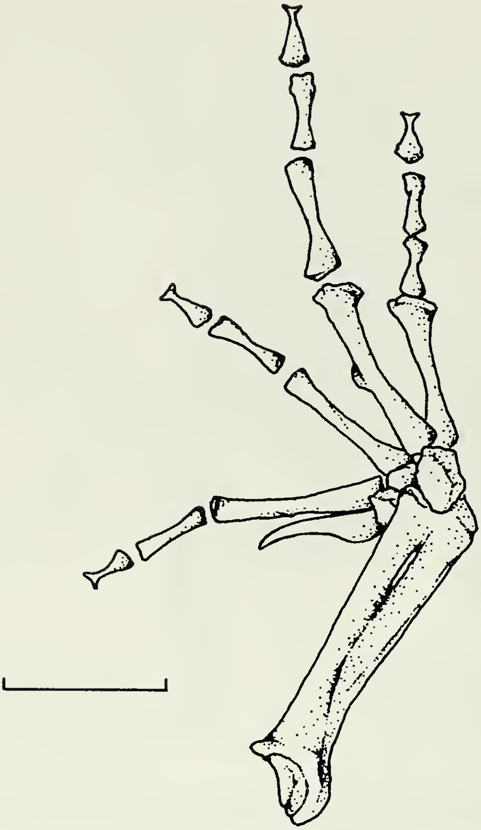

Fig. 5. Hard elements of left manus and forearm of a female *Centrolenella spinosa* (LACM 72920), ventral aspect. Drawn from a radiograph. Cartilaginous intercalated phalangeal elements are omitted. Scale mark = 2 mm.

Taylor (1951) defined the family Centrolenidae. His familial definition is based primarily on the nearly complete fusion of the astragalus and calcaneus, a fusion pattern shared only by the genus *Pelodytes* (Pelobatidae). Other characters used by Taylor are the presence of terminal T-shaped (or Y-shaped) phalanges, present in certain hyperoliids, leptodactylids, microhylids, rhacophorids and possibly bufonids (Trueb 1973; Liem 1970) and the digital intercalated cartilage, a character shared by the Hylidae, the Hyperoliidae and the African microhylid *Phrynomerus*. To this group, we add a character we believe will be useful in defining the family Centrolenidae. This is the presence of a distinct protuberance on the medial side of the third metacarpal (Figs. 2, 4 or 5). This protuberance was noted in all radiographed centrolenid material to date (both in *Centrolene* and 26 species of *Centrolenella*). This bulge, which varies in position from between two-thirds to one-third the distance from the distal end of the metacarpal, varies in size among species, protruding from ½ to 2 mm from its shaft. It was illustrated, but not discussed, in Eaton's anatomical study of *Centrolenella prosoblepon* (see Eaton 1958:466). Presumably, this feature was regarded as anomalous, as limited comparative material was then available. Radiographs of available dendrobatid, hylid, leptodactylid, pelobatid and ranid material show that, at least in the material examined, the metacarpal protuberance is absent. Liem (1970) discusses a bony knob on the third metacarpal of some rhacophorids and hyperoliids. His illustration (see Liem 1970:39) clearly shows this structure an extended expansion of the dorsolateral tip of the metacarpal, analogous to, but differing from the protuberance of centrolenids located on the midlateral metacarpal. Notably, the bony knob in rhacophorids and hyperoliids is associated with a slip of the humerodorsalis muscle in what Liem suggests as being the most derived condition of this muscle. In this condition, the muscle has two metacarpal slips inserting on the third and fourth digits. Liem suggests this condition is associated with arboreal life, noting the modification probably both increases extension efficiency of these digits and enables independent extension. A muscle dissection of *Centrolenella prosoblepon* shows the humerodorsalis with insertions with patterns paralleling those found in Liem's derived rhacophorids and hyperoliids. Further, the slip on metacarpal three apparently inserts on the protuberance previously described. Realizing the very arboreal nature of all members of the family Centrolenidae, we suggest that the condition of the humerodorsalis found in *C. prosoblepon* is an independently acquired adaptation to an arboreal life mode. The presence of the metacarpal protuberance suggests that the pattern of insertion of the humerodorsalis may be a character which is uniform throughout the family. We reserve judgment, however, upon examination of the balance of the family. We believe careful examination of anuran families, particularily those with arboreal members, will support the apparent unique state of the metacarpal protuberance found in the Centrolenidae.

Acknowledgments

We thank John W. Wright and Robert L. Bezy (LACM) for the loan of the Silverstone collection. Further, we would like to thank William E. Duellman for the loan of the paratype series of *C. chirripoi* and for allowing us to open one of the paratypes to examine guanine distribution. Thanks are due Charles W. Myers, whose comments on *C. ilex* and generous loan of an unpublished manuscript benefited this paper. We thank Jaime Villa for allowing us to examine and report on the Nicaraguan *C. ilex*. We also thank Jay M. Savage for allowing us to dissect a specimen of *Centrolenella prosoblepon,* and Roy W. McDiarmid, Craig Guyer and Michael M. Miyamoto for taking of their time to review and enhance the manuscript. Special thanks are due Philip A. Silverstone, who took the time to go over the details of his field notes with us and clarify our questions. Finally, we dedicate this paper to the late Charles F. Walker, who long ago pointed out to one of us (Starrett) that available centrolenid radiographs had an interesting little protuberance on the third metacarpal.

Appendix of Specimens Examined

Large series of Costa Rican material from the collections at USC were used as comparative material. This material is not listed here since Starrett and Savage (1973) give a thorough listing. All material is listed by country first and then province, both in alphabetical order.

Centrolenella albomaculata.—COLOMBIA: Chocó: Camino de Yupe in the drainage of the Río Opogadó, 420 m, LACM 72909.

Centrolenella chirripoi.—COLOMBIA: Chocó: upper Río Opogadó between Río Merendó and Río Yupe, 75 m, LACM 72929. COSTA RICA: Limon: Río Cocolis, near Suretka, KU 36862–4, 36866–70.

Centrolenella euknemos.—COLOMBIA: Antioquia: Río Arquia at Finca Los Llanos (above Vegaez), 100–200 m, LACM 47066.

Centrolenella fleischmanni.—COLOMBIA: Antioquia: Río Arquia, Finca 5 km w of Finca Chibiquí (40 km wsw of Urrao), 350–400 m, LACM 47067–9. Chocó: upper Río Opogadó above Ríos Yoto and Angostura, 60 m, LACM 47071–4; upper Río Opogadó, 75–120 m, LACM 72930.

Centrolenella ilex.—COLOMBIA: Antioquia: Belén, Río Arquia upstream from Vegaez, 100 m, LACM 47063. Chocó: trail between upper Río Napipí (near its juncture with Río Merendó) and upper Río Opogadó at 60–130 m, LACM 47070; Camino de Yupe, 420 m, LACM 72910, 72914. NICARAGUA: Departamento Zelaya: Río Indio, 75 m.

Centrolenella prosoblepon.—COLOMBIA: Antioquia: Belén, Río Arquia upstream from Puerto Palacios (also above Vegaez), 100 m, LACM 47065. Chocó: Camino de Yupe, 420 m, LACM 72923, 72925–6.

Centrolenella spinosa.—COLOMBIA: Antioquia: Río Arquia at Belén (upstream from Vegaez), 100 m, LACM 47064. Chocó: Camino de Yupe, 420 m, LACM 72911, 72913, 72917–8, 72920–2, 72924, 72927–8.

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Five Insects Believed to be Newly Established or Recolonized on Santa Cruz Island, California (Dermaptera, Lepidoptera)

Jerry A. Powell

Abstract.—Five insects believed to be newly established or recolonized on Santa Cruz Island, California (Dermaptera, Lepidoptera) by Jerry A. Powell, *Bull. Southern California Acad. Sci.*, 79(3):97–108, 1980. An earwig, 2 moths, and 2 butterflies not recorded in 1939–41 and 1966–69 surveys of S.C.I. insects, became established during 1969–78. Evidence suggests that 3 were introduced by man. Sudden appearance of the butterflies, however, is not easily interpreted. Either might have immigrated often during 50–100 years S.C.I. has had their weedy hostplants. It is hypothesized that such species periodically colonize, are eliminated during stress such as overgrazing by feral sheep in drought years, then recolonize. An undersaturated nature of the insect fauna of offshore islands, especially badly perturbed ones, is proposed. Extinction presumably is higher than natural, immigration low, and/or colonization improbable owing to reduced patch sizes of native hostplants.

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Santa Cruz Island (S.C.I.) is the largest of the northern tier of California's Channel Islands and is the most diverse geographically and faunistically. Lying 30 km off the coast of the mainland, about 40 km south of Santa Barbara, the island is approximately 34 km long, ranging from 3 to 10 km wide, with an area of ca. 249 km^2.

There is no record of the native insect fauna prior to extensive disturbance of the natural flora by feral sheep and pigs. Sheep and hogs may have been introduced in the early 1800s. Cattle were grazed on the island as early as 1865 (Hillinger 1958), and according to Holder (1910) the Caire ranch was managing more than 30,000 head of sheep around the turn of the century. During the early era of insect exploration in California (1860–1930) inaccessibility of the Channel Islands and ownership visitation policies discouraged collecting visits. Sporadic survey by entomologists and sporadic collections by other biologists were made during the late 1800s and after the turn of the century, but most of these were on Santa Catalina and San Clemente Islands (see Miller and Menke 1980, for review of entomological investigations). No comprehensive systematic list of insects was produced for S.C.I. from these early visits. Even on the one major, organized Channel Islands survey, that of the Los Angeles County Museum in 1939–41, Santa Cruz Island was relatively neglected, considering its size, with only a one-week visit in August (with 3 entomologists), and a 5 day visit in March, mainly at Pelican Bay by one entomologist, with some collecting at other sites by two persons (Comstock 1939, 1946). Therefore extensive overgrazing had taken place for 80 years or more before any appreciable insect survey occurred.

A cooperative effort, beginning in 1940, between the Stanton family, owners of the island, and the Department of Biological Control, University of California, Riverside, to control prickly pear cactus, preceded the establishment of the U.C. Santa Cruz Island Reserve and field station on the Stanton property. According to Goeden et al. (1967), Mr. Stanton estimated that approximately 40% of the rangeland of the island had been rendered useless for grazing by dense growth of native prickly prears. After 24 years of efforts involving releases of several native southwestern Nearctic species of Hemiptera, Homoptera and Lepidoptera, a considerable degree of control was effected, primarily by cochineal scales, *Dactylopius* (Goeden et al. 1967).

Presence of the field station, beginning in 1966, opened the door for much more diverse and intensive entomological survey work, so that a picture of the island's insect fauna has begun to emerge during the past 15 years. In general the insect fauna has been found to be depauperate relative to that of the mainland (Powell 1967; Miller 1971; Opler 1974; Weissman and Rentz 1976). For example, only 33 species of butterflies have been discovered in rather intensive search during all months of the year (Langston 1980; C. L. Remington pers. comm.; California Insect Survey unpubl. data), while more than twice that number occur in a comparable area of adjacent mainland around Santa Barbara (Emmel and Emmel 1973; S. Miller in litt.). The fauna contains only a few endemic species (Alexander 1973; Gordon 1976; Powell 1967; Opler 1971, 1977; Rentz and Weissman 1973). Probably those mostly are relics of past extensive mainland distributions, as is believed to be true of endemic plants (Thorne 1969). However, Rentz and Weissman (1973) give evidence for island speciation in one genus of sand-burrowing crickets.

The establishment of a U.S. Naval operation on the island in the 1940s—and later the field station—has caused a considerable increase in the traffic of personnel, foodstuffs, and equipment in recent decades. As a result, the chance of introduction and establishment of mainland species has increased. Five species appear to have become established on the island during the past 15 years, based on survey work carried out in 1966–1969 compared with more recent collections.

No doubt the insects of Santa Cruz Island are incompletely surveyed, but comparison of collections from different institutions indicates that there has been sufficient seasonal coverage to enable reasonable confidence in statements about easily obtained species. Additions to the faunal list are expected in taxa where the insects are small or require specialized collection techniques (e.g., Berlese samples of litter dwellers, rearing of leaf miners, etc.), but the appearance of previously unrecorded, yet easily observed species can be taken as evidence of recent establishment or expansion of populations on the island.

During 1966 and 1969, personnel of the California Insect Survey, University of California, Berkeley, made three general collecting trips to the island. The first, 25 April to 2 May, involved 6 staff and graduate students, who devoted approximately 36 Full Time Equivalent (FTE) collector days. The second, 7–10 June 1966, was made by two participants, an equivalent of 8 FTE days. The third trip took place 14–17 March 1969, with 5 experienced collectors, about 15 FTE days. All three visits were blessed with good weather and adequate transportation facilities so that diverse habitats were surveyed, from Christi Beach near the western end to the vicinity of Chinese Harbor in the northeastern portion of the island. Subsequent collecting has shown that many species were overlooked, especially those active as adults only in late summer, fall, and winter. However, five species encountered during the 1970s are insects that likely would have been observed during our 1960s trips had they been present, as documented below.

DERMAPTERA

Forficula auricularia (Linnaeus)

Although the European earwig was not discovered in California before 1923, it rapidly spread throughout the northern half of the state at low to moderate elevations during the 1930s. The earliest record in southern California was 1931, but the species was not considered established there until 1940 or later (Langston and Powell 1975). It was collected around Santa Maria during 1945–1947 and at Santa Barbara as early as 1952, but we were unable to document its established occurrence in the 1960s for most of southern California (Langston and Powell 1975). Only one record was known from the Channel Islands at that time, a collection in 1972 on San Clemente Island.

Langston and I made special efforts to look for earwigs on both of our 1966 trips to Santa Cruz Island, as this was during the data-gathering years for the C.I.S. bulletin. Searches were made around the ranch buildings, the vegetable garden, and other likely sites, but we found no Dermaptera.

In September 1978, M. E. Buegler and I found adults and immatures of *Forficula* common around the field station. Therefore it appears that the European earwig was introduced to S.C.I. during the 1970s. Similarly, this earwig has recently turned up on Santa Rosa Island, the earliest specimen having been collected in 1971 (Langston and Miller 1977). That it was not introduced earlier to either island probably can be attributed to the fact that *F. auricularia* is better adapted to more mesic, northern habitats in California than arid ones. As a result this insect is not as abundant in southern California as is the ring-legged earwig, *Euborellia annulipes* (Gerstaecker), and probably it was not established in mainland areas adjacent to the islands before the 1950s or later.

Euborellia annulipes, a wingless species, has been widely established in southern California since the 1880s and is known from several of the Channel Islands, but still has not been discovered on S.C.I. (Langston and Powell 1975; Langston and Miller 1977). Although earwig colonies may be overlooked owing to seasonal dormancy or other causes of restricted occurrence, the flightless *E. annulipes* is more likely to remain localized and therefore undiscovered than is *Forficula*.

LEPIDOPTERA

Pieris rapae (Linnaeus)

The cabbage white butterfly occurs abundantly throughout California, except at the highest elevations and in the deserts, and is particularly common in coastal urban and agricultural situations. It is an Old World insect that was introduced into eastern North America about 1860 and is believed to have spread rapidly across the country (Holland 1898; Wright 1906). There is a possibility that it was introduced separately into California. In any event, *P. rapae* has been established in southern California coastal areas since before the turn of the century, the first specimen having been taken in 1883 (Wright 1906). Thus it was surprising when we did not find this species on Santa Cruz Island in 1966. Each trip included two lepidopterists, and other collectors were alerted to take samples of all butterflies seen. Moreover, *P. rapae* flies near the coast in southern California in every month of the year (Emmel and Emmel 1973). Thus, it is inconceivable that we could have overlooked the cabbage white even at a low population density.

Known from Santa Barbara as early as 1916 (Coolidge 1923), it seems unlikely that this butterfly has never immigrated to S.C.I., yet there appear to be no records prior to 1969. There are no specimens in the Los Angeles County Museum of Natural History from the 1939–41 faunal survey (S. Miller *in litt.*), and none could be located in the U.C. Riverside collection, which has some general insect survey material from the fieldwork associated with the biological control of prickly pear cactus on the island. Of course it is possible that *P. rapae* is such a weedy and ubiquitous insect that no voucher specimens were retained by early collectors who may have observed it.

Subsequently *Pieris rapae* has become common in weedy habitats along the main water courses in the Central Valley and Prisoners Harbor Creek. Specimens were collected in early August 1969, by D. B. Weissman; C. L. Remington (*in litt.*) encountered the species in the early 1970s; and we found it numerous in September 1978. If the species had been unable to cross the channel on its own for nearly 90 years following its establishment in California, it is possible that it was inadvertently introduced, perhaps as larvae on garden nursery stock, during the late 1960s. Why this event did not occur during a much earlier ranching era is a mystery.

Pyrgus communis albescens Ploetz

The western checkered skipper is a homodynamic insect that occurs throughout southern California, especially in weedy areas where *Malva* is adventive. Thus it should not have been surprising when we found this species at scattered places on S.C.I.—Cañada Cervada near the western end, Willow Cove on the south shore, and Prisoners Harbor on the north shore—during 26–29 September 1978. Those collections, however, evidently were the first records of *P. communis* on the island.

We did not encounter this species during our 1966–69 trips, when 26 species of butterflies were taken; D. B. Weissman did not collect it among 16 species taken in early August 1969; and G. A. Gorelick failed to record it among 22 species logged in June 1978 (Langston 1980 and *in litt.*). In addition, S. E. Miller (*in litt.*) did not find S.C.I. specimens in the LACM from the 1939–41 Channel Islands Biological survey.

Spring and summer collections cannot be ruled out as seasonally asynchronous unless a markedly differing voltinism has been fixed genetically in the island population, limiting it to a fall flight. On the mainland, *P. communis* has been recorded from every month and commonly flies from February to October (Emmel and Emmel 1973). Individuals are often seen by mid-March even in the San Francisco Bay area.

Moreover, data from other Channel Islands suggest a restricted flight period is unlikely. *Pyrgus communis* has been known on Santa Catalina Island at least since 1932 (LACM) and has been taken during the winter (Meadows 1936). There are specimens from Santa Rosa Island taken in 1939 and 1941 according to Miller (*in litt.*) who encountered this species on his earliest visits to other northern

Channel Islands, on tiny, remote Santa Barbara I. in June 1978, and on East Anacapa in August 1978. Therefore failure of *P. communis* to appear in S.C.I. collections prior to September 1978 is perplexing. The widespread distribution on the island at that time suggests either that populations expand in numbers and in range as the season progresses, or that the species had quite recently (since June 1978) reached the island, rapidly populating various parts of it. Neither hypothesis seems plausible, considering the overall distribution and voltinism of this insect.

Laetilia coccidivora (Comstock)

This pyralid moth was described from Washington, D.C. and is widespread through the southern and southwestern states, including southern California (Heinrich 1956). The larvae feed on various Coccidae, especially cochineal scales on cactus, and occasionally on the flowers of prickly pear.

Cochineal insects, species of *Dactylopius,* were introduced to Santa Cruz Island from the mainland between 1940 and 1951 for control of prickly pear cactus (Goeden et al. 1967). Successful introductions apparently occurred in 1951 with colonies from Hawaii, via Riverside, of cochineal insects descended from a series of introductions from Mexico to Australia beginning in 1927. Distributions of *Dactylopius*-infested *Opuntia* pads from the ranch headquarters area of the original introduction were carried out in 1955–1960, and observations from 1961 to 1966 indicated that *Dactylopius* had spread throughout the island and had effected substantial control of the cactus (Goeden et al. 1967). Goeden and his coworkers attributed the success of this biological control agent in part to the apparent exclusion of two of its natural predators, a coccinellid beetle (*Hyperaspis*) and *Laetilia coccidivora*. The latter was encountered at all mainland stations where *Dactylopius* was surveyed, but it was absent from their collections on Santa Cruz Island, although Goeden et al. admit the inadvertent introduction of these predators during the course of the biological control work could not be ruled out.

Laetilia coccidivora was first collected on Santa Cruz Island in October 1972, when C. L. Remington took a series of adults at lights at the U.C. field station. He collected another series in August 1974 at the same station, and I took them in blacklight traps at all sites sampled in late September 1978. Larvae collected by D. S. Green in June 1977 produced adults in mid-July. One *Dactylopius*-infested *Opuntia* pad I collected in late September 1978, at Willows Creek, produced adult *Laetilia* in October and November and again the following May and June (JAP 78J7). Heinrich (1956) cites collection dates throughout the year in Texas and Arizona and for March, October and November in southern California. The life cycle does not seem to be carefully documented, but the records suggest either a bivoltine pattern or continuous generations are possible in warmer areas.

In addition to our negative evidence from blacklight trapping at the field station in May and June 1966, Remington sampled a diversity of microlepidoptera at the station in late July 1967 and 1968, and mid-August 1968, but did not find *L. coccidivora*. Presuming that population numbers build up during the season and that adults appear at lights only in exceptionally warm weather, our spring and June work could be ruled out as adequate for discovery of this species. However, the moth sampling by Remington in July and August 1967–1968, should have revealed *Laetilia*, had it become as abundant in the area as collections during 1972–1978 indicated.

It appears that *Laetilia coccidivora* was introduced to Santa Cruz Island during the biological control program in 1951–1961, or by some other means subsequently. Probably the moth did not build up in population numbers or was localized on the island in areas remote from the vicinity of the ranch headquarters and field station, until the early 1970s.

The deleterious effect on *Dactylopius* as a biological control agent of prickly pear cactus by appreciable levels of this predaceous moth have yet to be assessed. My rearings produced 15 adult *Laetilia* and one Chalcidae, presumably a parasitoid of *Laetilia*, from a single *Opuntia* stem.

Platynota stultana Walsingham

The "omnivorous leaf roller" was described in 1884 from Sonora, Mexico, and its native range probably included adjacent parts of the southwestern U.S., as it was collected in Cochise County, Arizona in the 1890s by F. H. Snow (specimens, AMNH). As the common name implies, a vast array of larval hosts has been recorded (e.g., Atkins et al. 1957), most of which are in nursery and agricultural situations, whence the insect has expanded its geographical range during the past 80 years. *Platynota stultana* seems not to be native in cismontane southern California because it was not encountered by Coquillett and others in the early years of citrus investigations, yet it had become a pest of citrus by 1913 (Woglum 1920). The earliest record in California I have seen is at La Mirada, Los Angeles County, where it was reared from tomato in 1898 (specimen, NMNH). By 1913–1915, *P. stultana* had become an economic problem in various citrus and cut flower growing areas of southern California (Woglum 1920; Bohart 1942).

The species reached coastal Santa Barbara County by 1940, although the date of initial establishment and continuous residency there is unknown. There is one record for Carpinteria (40 km NW of S.C.I.) (NMNH), and *P. stultana* was reared from larvae collected by Henne on Anacapa Island during the LACM Channel Islands Biological Survey in 1940. About 1960 this species apparently underwent a change in physiological tolerance and during the following several years greatly expanded its geographic and ecological range in California (Powell 1981).

Adults of *Platynota stultana* readily come to lights, so presence of a population is easily detected. I collected the moths at Goleta (45 air km N of S.C.I.) in June 1965 and on both Santa Catalina and San Clemente Islands on my first visits to them, in April 1968 and March 1972, yet no collections were made on Santa Cruz Island prior to 1975. The adults fly virtually throughout the year in southern California, so that seasonal exclusion cannot be the reason.

The first record for S.C.I. was a female taken at UV light at the field station in late July 1975, by C. L. Remington and R. Priestaf. We found the adults common at lights around the station, and one was taken in a blacklight trap at Prisoners Harbor in late September 1978. Therefore it seems probable that *Platynota stultana* was introduced in the early 1970s, possibly via cut flowers or potted nursery plants, and is established on the island.

This species has been reared from *Eriogonum grande*, a native endemic plant, at Isthmus Station on Santa Catalina Island, by G. A. Gorelick, so it will be interesting to monitor its invasion of the native flora on Santa Cruz. There are no undoubted records of the occurrence of *P. stultana* in native plant communities on mainland California, except in desert areas (Goeden and Ricker 1976a). The same authors (1976b, and earlier references) encountered the omnivorous leafroller on several native ragweed species (*Ambrosia*) in cismontane southern California, but it appears that most or all these records are from roadsides, abandoned cropland and similar artificial expansions of *Ambrosia* habitat. It was not discovered on *Ambrosia chamissonis* in native situations by Goeden and Ricker or by me on Santa Cruz Island or at many other coastal sand dune localities.

Discussion

Probability of introduction by man.—There is reasonable evidence to indicate the recent introduction by man of 3 of the species recorded here, *Forficula auricularia, Laetilia coccidivora,* and *Platynota stultana.* The sudden, recent appearance of the remaining two butterflies, however, is not easily interpreted. No data are available to explain the long period during which they apparently failed to colonize.

Pieris rapae could have been imported on cabbage or other garden crucifers during the late 1960s, but an immigration via this route much earlier, when production and transport of agricultural products were less controlled, seems more plausible. *Pyrgus communis* is an unlikely candidate for accidental transport by man. Both species seem to be sufficiently strong fliers to have made the trip on their own many times during the 80–100 years their weedy hostplants surely must have been available on the island. Both have been resident for more than 50 years on Santa Catalina, a comparable sized island situated the same distance off the southern California coast (Meadows 1936).

Depauperate nature of the fauna:—One of the most fascinating aspects of the Channel Islands fauna is its depauperate nature. While reasonable hypotheses can be proposed to explain absence of many species that occur on the adjacent mainland, others seem missing by chance. In the best documented insect group, the butterflies, Miller (*in litt.*) has recorded about 70 species in an area the size of S.C.I. in the Santa Ynez Mountains-Santa Barbara coastal shelf, but of these, only 33 have been discovered on S.C.I., only 40 km away (Langston 1980; present data). Among the absentees, some can be theorized as either lacking from the original community at the time of separation from the mainland or subsequently eliminated and too sedentary to have immigrated (e.g., the lycaenids *Euphilotes battoides* and *Philotes sonorensis,* which have been demonstrated to possess low vagility rates, (Arnold 1980; Keller et al. 1966). Others might be missing because their restricted larval food preferences are for plants not found or too limited on the island to maintain insect populations (e.g., *Colias eurydice* on *Amorpha californica, Habrodais grunus* on *Quercus chrysolepis*). Overgrazing by feral sheep in dry years might account for the paucity of grass feeding Lepidoptera, explaining the absence of 6 or 7 Santa Barbara Hesperiinae and the Satyrid *Coenonympha california,* which occurs in weedy areas throughout most of California.

On the other hand, non-residents include several widespread, apparently vagile butterflies whose larval hosts are common on S.C.I. For example, *Papilio rutulus,* one of California's largest butterflies, and *Limenitis lorquini,* seem imponderably absent from suitable appearing willow-lined creek habitats; *Phyciodes mylitta,* a homodynamic species which feeds on weedy and native Asteraceae, occurs abundantly in disturbed situations at low elevations throughout the state north of Santa Barbara but not on S.C.I.; *Incisalia iroides* is polyphagous on native plants, both monocot and dicot, and would seem to be as likely a colonist as another lycaenid, the resident *Celastrina argiolus*, which has similar larval food preferences. Four *Eriogonum* (Polygonaceae) specialists, the lycaenids *Lycaena gorgon*, *Euphilotes battoides*, *E. enoptes*, and *Apodemia mormo*, do not occur on S.C.I., yet all live along the coast of the mainland, often in sympatry. Among *Cercocarpus* (Rosaceae) feeding Lepidoptera, two moths, *Acleris folianus* (Tortricidae) and *Ethmia discostrigella* (Oecophoridae) are common on S.C.I., but a butterfly, *Strymon tetra* (Lycaenidae) is absent. All 3 are sympatric in scattered parts of California, such as at San Diego. Many such examples could be listed.

Compliance to island biogeographic theory.—Orthoptera on the Channel Islands conform fairly well with the species numbers/area aspects of island biogeographic theory (Weissman and Rentz 1976), and species numbers of butterflies are remarkably similar (S. Miller *in litt.*). Preliminary sampling of S.C.I., San Nicolas, Santa Catalina, and San Clemente islands indicates that diversity for Lepidoptera as a whole will follow this pattern. Thus it is tempting to suggest that the Channel Islands possess dynamic equilibrium levels in insect species, that an extinction curve-immigration curve intersect has been reached. According to this hypothesis, the low species numbers compared to the mainland are a function of island area and ecological diversity. Theoretically, aspects of community complexity, including competitive displacement, interact to maintain the insect fauna near its present diversity. In birds, area by itself is a relatively poor predictor of numbers of species on the Channel Islands compared to ecological parameters such as numbers of native plant species (Power 1972). For insects, a list of plant species provides a crude index to potential niche diversity in larval foods in some phytophagous groups but not necessarily in Orthoptera, many of which are scavengers or general plant feeders. The insular fauna of Orthoptera may be at or near equilibrium, with numbers of species related to ecological diversity, expressed by complexity of vegetation types, which is roughly correlated with area. By contrast, in Lepidoptera and other phytophagous insects having many species that depend upon particular plants, extinction and colonization rates presumably are much more sensitive to disturbance, particularly overgrazing and invasion of weeds. Such perturbance favors homodynamic, especially polyphagous species, which are often alien, and these become dominant in population numbers per unit area. Native, host specific species are selected against by elimination or restriction of host plants to small habitat patches. As a result, although insect species numbers may be generally correlated with area and environmental complexity, in most taxa they are likely to be low compared to the original and potential equilibrium levels.

The best documented studies of extinctions and turnover rates of insular animals have concentrated on birds, primarily because they can be censused with confidence, and often long term data are available (e.g., Diamond 1969; Diamond and May 1977; Power 1976). Coincidentally, birds are vagile and presumably more easily capable of immigration than most animals. Therefore the supposition that such turnover rates represent a dynamic equilibrium of the MacArthur-Wilson (1967) interpretation may be valid. With most insects, however, recent extinction rates likely are higher than natural due to decimation of the plant community or to fragmentation of larval host populations. Colonization rates may be low owing to low immigration rates and/or reduced patch sizes of suitable habitat. Thus, the extinction rate in large part is independent of the colonization rate.

Population lifetime under natural conditions is a fundamental problem in population biology, and extinctions and recolonization of local populations due to natural causes have been recorded in butterflies (e.g., Ford 1945; Ehrlich et al. 1975). A species can survive such periodic fluctuations at a colony site provided that it is established nearby in sufficiently large numbers to ensure recolonization. Thus normal periodic cycles in abundance resulting in local extinctions may not have lasting effects in continental populations but may be disastrous to populations in isolated localities such as islands.

Problem of census in insect communities.—The primary problem in drawing inferences about extinction or other faunal changes in insects is a practical one, that of accurate census. It is essentially impossible to inventory the insects of a complex island such as S.C.I. with confidence. Year around effort would be needed to cope with seasonality, an array of collectors with differing specialized experience would be required to sample adequately the variety of habitats, and the expertise of an army of taxonomists would have to be recruited to provide specific discrimination, irrespective of nomenclatural decisions. Many of the smaller forms are undescribed, whether or not they are known to occur on the mainland. Moreover, prolonged diapause, the ability of individuals to postpone emergence for more than one season, is much more widespread in temperate zone insects than has been appreciated (Powell 1974).

Therefore, except in the simplest possible communities, such as the mangrove islands manipulated by Simberloff and Wilson (1969), several years are needed to census with any degree of completeness. Based on sporadic surveys representing nearly all months, I have recorded about 400 species of Lepidoptera on S.C.I. Comparing that figure to those given for the North American fauna (Daly, Doyen, and Ehrlich 1978), one can extrapolate an estimate of at least 3500 species of insects on the island, and probably the real count is much higher. As a result, efforts to assess extinction or turnover rates in insects must be confined to well known taxa with conspicuous, relatively easily sampled species, such as butterflies. When an animal such as *Pieris rapae* appears at several spots on the island, it can be inferred that recent colonization or recolonization has occurred. By contrast, the apparently sudden appearance of a native insect species more often is likely the result of inadequate past field survey. For example, when I discovered the univoltine, autumnal tortricid moth, *Decodes fragarianus*, on S.C.I. in September 1978, a plausible explanation is that we had overlooked the larvae during spring surveys of *Quercus* in 1966–1969, negating the statement by Opler (1974:22) that this species does not occur on the Channel Islands.

Undersaturated state of the insect fauna.—While it is true that the number of species on S.C.I. is the product of colonization and extinction rates superimposed upon the original community at the time of separation from the mainland, the number does not appear to be at equilibrium in phytophagous insects. It seems probable that a suppression of the original number has occurred through restriction of the islands' sizes during the Pleistocene (Johnson 1978) and through man's influence, especially grazing of domestic and ultimately feral animals, during the past 150 years. Most native insect species are not highly vagile and/or are dependent upon a narrow larval food preference. As a result, in contrast to birds, colonization rates almost certainly are too low to balance extinction rates, and a dynamic equilibrium is not attained. Severe disturbance of the flora has fragmented and reduced the size of many phytophagous insect populations on the island, enhancing chances of local extinction due to natural fluctuations in abundance.

Therefore it is probable that insect diversity has declined since the advent of introduced mammals and weedy plants, and the island's insect fauna is undersaturated. The situation is comparable to defaunation experiments with mangrove islands except the relaxation time required to reach equilibrium (or 90% of equilibrium $t_{0.90}$, of MacArthur and Wilson) is much longer. Feral sheep were removed and excluded from a large portion of S.C.I. during the 1950s, which can be envisioned as the end of the defaunation process, with gradual establishment and expansion of formerly resident and new colonist plants and phytophagous insects having progressed since that time.

The relaxation time for the fauna to return to equilibrium following perturbation (including immigration of alien species), may be very long (examples cited by Simberloff 1974). Thus the insect fauna of S.C.I., and probably most islands inhabited by Western man, may be interpreted as undersaturated and out of equilibrium, a state that will continue indefinitely. Cessation of overt disturbance (grazing, grading, farming, etc.) may mark the beginning of the return to an equilibrium, but immigration effects of the disturbance (colonized weedy plants and animals) prevent return to the original equilibrium and together with differential rates of immigration and abilities to colonize by mainland species that have not yet colonized, preclude return to the original community composition.

Insects that need specific plants as larval food, such as native bunch grasses or *Eriogonum,* may have dropped out of the fauna, and immigration from conspecific populations on the mainland or on nearby islands has not occurred and/or remaining patches of suitable habitat are too limited to have enabled colonization by chance. Homodynamic species that are more vagile and often weed-feeding, such as *Pieris rapae* and *Pyrgus communis,* also may have undergone extinction in times of climatic or grazing stress, but if so, have been able to recolonize.

Thus the insect community of S.C.I. is transitional in species membership, consisting primarily of two cohorts: a) relics of the original California mainland community, and b) species that have been able to colonize in spite of or even because of the disturbance by man. The latter group consists mostly of homodynamic, weed-feeding or polyphagous species, some of which may colonize and disappear periodically. Included are both alien (e.g., *Forficula auricularia* and *Pieris rapae*) and native species (e.g., *Platynota stultana* and *Pyrgus communis*).

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Crustaceans in the Shrimp By-catch from off the Coasts of Sinaloa and Nayarit, México

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Abstract.—Crustaceans in the shrimp by-catch from off the coasts of Sinaloa and Nayarit, México by R. K. G. Paul and M. E. Hendrickx, *Bull. Southern California Acad. Sci.*, 79(3):109–111, 1980. Samples of the shrimp by-catch were obtained from boats operating off the northwest Pacific coast of Mexico. The crustacean component of the by-catch was separated and examined. Twenty-four species of crustacean were found in the by-catch and several, including 5 species of large portunid crabs, have considerable commercial value but are presently unexploited in this region of Mexico.

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Introduction

For many years a large commercial fishing fleet of shrimp trawlers has operated in the Gulf of California and off the Pacific coast of Mexico. Shrimps of the genus *Penaeus* form the basis of this fishery (Snyder-Conn and Brusca 1977; Edwards 1978) and constitute more than 10% of the total catch (Chavez and Arvizu 1972; Rosales 1976). The rest of the total catch consists mainly of fish, crustaceans and mollusks and is often referred to as the shrimp by-catch. Very little published information exists concerning the composition of the by-catch and, of the studies that have been made, many are limited to fishes.

Research on the shrimp by-catch is important since, apart from the ecological information that can be obtained, the by-catch represents an important potential food source which is being vastly underutilized at present.

In this paper the crustacean component of the by-catch is considered and qualitative data are presented.

Materials and Methods

Two trips were made on commercial shrimp trawlers during November 1978 and February 1979 between Mazatlán (Sinaloa) and San Blas (Nayarit). In the first trip samples were obtained from three trawls, and in the second trip from 6 trawls. All the trawls were made within five miles of the coast at depths of 14 to 48 metres. The average duration of each trawl was 4 hours. The nets used by commercial shrimp trawls are benthic otter trawls with a 15 metre wide mouth and a 6.5 centimetre stretched mesh size.

Results

Table 1 gives a list of the crustaceans which occurred in the trawl samples. For purposes of comparison, the presence or absence of these organisms is also indicated for Mazatlán Bay (based on monthly samples taken for one year with a small benthic trawl), and from the study of Rosales (1976) on the by-catch off the whole coast of Sinaloa.

Table 1. Crustaceans occurring in the shrimp by-catch from the present study. For comparison, the presence (+) or absence (−) of these organisms is indicated for Mazatlán Bay samples and the by-catch samples of Rosales (1976).

Order	Section	Family	Species	Bay of Mazatlán	By-catch Rosales (1976)
Stomatopoda		Squillidae	*Squilla panamensis* Bigelow	+	+
			Squilla parva Bigelow	+	−
			Squilla mantoidea Bigelow	+	−
Decapoda	Macrura	Scyllaridae	*Evibacus princeps* Smith	−	+
		Palinuridae	*Palinurus gracilis* Streets	+	+
	Penaeidea	Penaeidae	*Sicyonia disdorsalis* (Burkenroad)	+	+
			Trachypenaeus similis pacificus Burkenroad	+	+
			Solenocera florea Burkenroad	−	−
	Brachyura	Portunidae	*Callinectes arcuatus* Ordway	+	+
			Callinectes toxotes Ordway	−	+
			Callinectes bellicosus (Stimpson)	−	+
			Portunus asper (A. Milne Edwards)	+	+
			Portunus acuminatus (Stimpson)	−	+
			Portunus xantusii affinis (Faxon)	−	−
			Euphylax robustus Milne Edwards	+	+
			Euphylax dovii Stimpson	+	−
		Majidae	*Leiolambrus punctatissimus* (Owen)	−	−
			Stenocionops ovata (Bell)	−	+
			Stenorhynchus debilis (Smith)	+	+
		Calappidae	*Hepatus kossmanni* Neumann	+	+
			Persephona townsendi (Rathbun)	−	+
			Calappa convexa de Saussure	+	−
	Anomura	Diogenidae	*Petrochirus californiensis* Bouvier	−	−
		Porcellanidae	*Porcellana cancrisocialis* Glassell	+	−

Discussion and Conclusions

A total of 24 species of crustaceans representing 2 orders, 4 sections and 9 families were identified from the by-catch samples. Rosales (1976) reported 34 species of crustaceans from the by-catch, but it should be noted that the samples in this study were taken over a two year period (1964–66) and from a much larger area. Many of the species reported by Rosales, and not in the present study, occurred in one trawl only and from outside the area covered by the present study.

Several species of commercial value occurred in large numbers in samples, including five species of swimming crabs: *Callinectes arcuatus* Ordway; *Callinectes toxotes* Ordway; *Callinectes bellicosus* (Stimpson); *Euphylax robustus* A. Milne Edwards; and, *Euphylax dovii* Stimpson. At present no fishery exists for crabs on the Pacific coast of mainland Mexico and large quantities are wasted during shrimp-fishing operations, since when the catch is sorted the crabs are often killed and thrown overboard. Fishermen believe them to be important predators of penaeid shrimp. Other species with possible commercial value include the stomatopods (*Squilla* spp.) and species of Penaeidae such as *Sicyonia dis-*

dorsalis (Burkenroad), *Trachypenaeus similis pacificus* Burkenroad and *Solenocera florea* (Burkenroad), none of which are commercially exploited at present.

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Research Notes

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Notes on Seasonal Collections of Sharks Near Point Conception, California

This note describes the results of eleven quarterly, week-long gill net collections of sharks between June 1974 and December 1976 at three stations near Point Conception, California. These collections were part of an extensive marine environmental survey (Dames and Moore 1977) encompassing quantitative sampling of fish, benthos, plankton, and intertidal organisms.

The Cojo Anchorage study area is approximately 25 km west of Santa Barbara and 5 km southeast of Point Conception, California. Three stations, designated PC-1, PC-2, and PC-3, were sampled at depths of approximately 17, 12 and 8 m MLLW, respectively. The three station locations corresponded approximately to the outer, middle, and inner boundaries of an extensive kelp bed dominated by *Macrocystis* sp. The dominant substratum at all stations was a shale pavement overlain with scattered shale or a veneer of sandy silt, with some higher rocky areas present at the inshore stations.

In June and September 1974, sampling consisted of one to three 24 hr sets of single mesh 3.8 cm bar mesh surface and bottom gill nets at Station PC-2. These nets measured 30.5 × 3.1 m, and were constructed of braided nylon line. In December 1974 and March 1975, the sampling effort was expanded to include three stations with night and day sets of approximately 12 hr each.

Since diver observations in the area indicated a more varied community of fishes than was represented in the collections from the single mesh gill nets, surface and bottom multimesh (1.3 to 6.4 cm bar mesh in 1.3 cm increments) monofilament nets were deployed for two 12 hr day and night sets at each of the three stations in June 1975. The multimesh nets measured 30.5 × 2.4 m; consisting of two 3.1 m wide panels of each mesh, and were constructed of monofilament line of varying thickness. Panels were in progressive size sequence. For comparative analysis, the single mesh nets were deployed coincidentally with multimesh nets during the June 1975 survey. From September 1975 through December 1976, multimesh nets were deployed with surface and bottom nets fished concurrently at each station.

Upon retrieval of the nets, specimens of sharks were recorded as to species, total length, and sex. Additional notes included the recording of the mesh size and location (surface or bottom) in which each specimen was caught.

A total of 2190 hr of gill net fishing time resulted in the capture of 673 sharks, representing eight species (Table 1). Due to the concentration of effort for the first two 1974 surveys at Station PC-2, almost 50% of the total fishing time was at that station. Surface and bottom net fishing times were evenly distributed, with 1075 hr for surface nets, and 1116 for bottom nets.

Spiny dogfish[1] (*Squalus acanthias*) and swell sharks (*Cephaloscyllium ven-*

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[1] Common and scientific names in accordance with American Fisheries Society (1970).

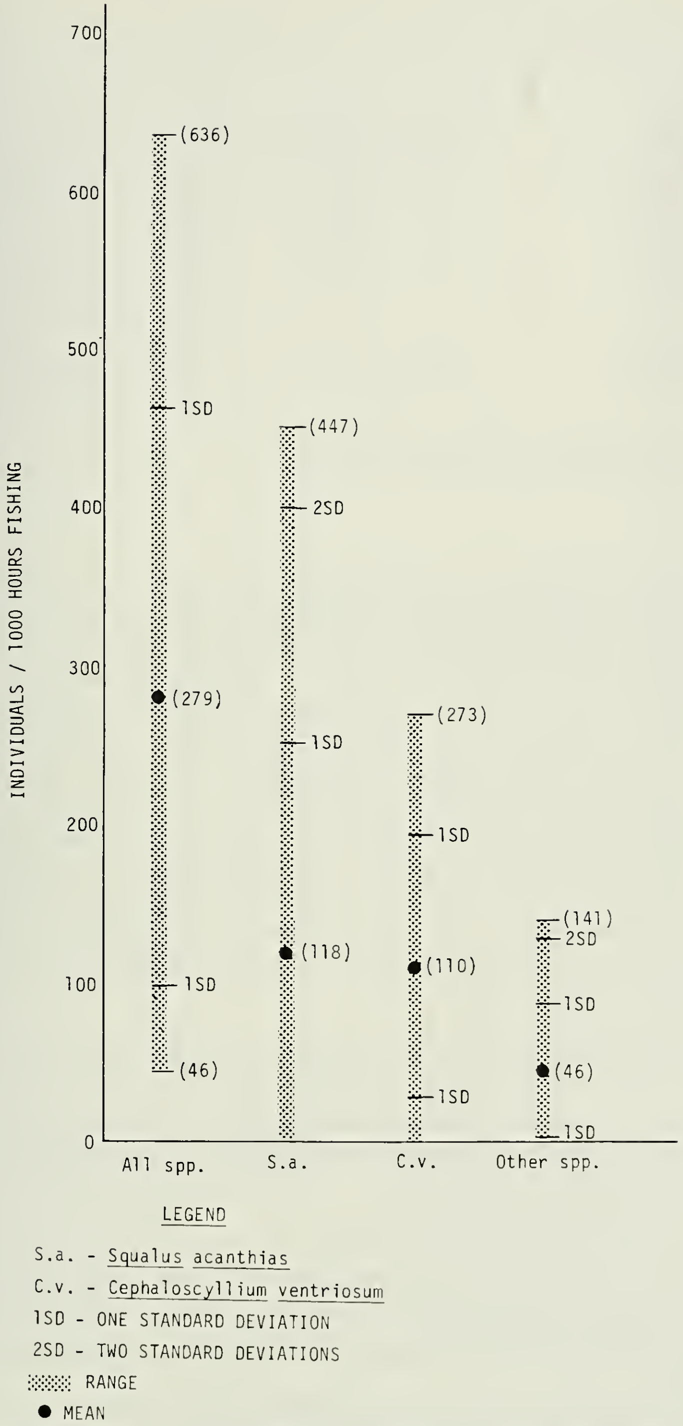

Fig. 1. Mean and range of number of individuals caught/1000 hours fished by species (all stations/depths and seasons combined).

Table 1. Catch per 1000 hours fished by season (all stations combined).

Species	Season				
	Spring	Summer	Fall	Winter	Mean[1]
Squalus acanthias	7.6 (3)[2]	349.4 (181)	127.6 (81)	54.6 (35)	137
Cephaloscyllium ventriosum	63.1 (25)	148.7 (77)	192.1 (122)	70.2 (45)	123
Triakis semifasciata	—	17.4 (9)	6.3 (4)	51.5 (33)	21
Galeorhinus zyopterus	—	5.8 (3)	29.9 (19)	4.7 (3)	11
Squatina californica	2.5 (1)	30.9 (16)	11.0 (7)	—	11
Mustelus californicus	—	—	3.2 (2)	7.8 (5)	3
Prionace glauca	—	1.9 (1)	—	—	<1
Heterodontus francisci	—	—	1.6 (1)	—	<1
Total catch/1000 hr	73.2 (29)	554.1 (287)	371.7 (236)	188.8 (121)	307 (673)
Total hours actually fished	396	518	635	641	2190

[1] Sum of actuals divided by 2190 multiplied by 1000.

[2] Actuals.

triosum) were nearly equal in abundance and accounted for about 85% of the total catch (Fig. 1). Leopard sharks (*Triakis semifasciata*), Pacific angel sharks (*Squatina californica*) and soupfin sharks (*Galeorhinus zyopterus*) accounted for a combined total of 14% of the catch, with *T. semifasciata* being twice as abundant as the other two. A blue shark (*Prionace glauca*), a horn shark (*Heterodontus francisci*), and seven grey smoothhounds (*Mustelus californicus*) accounted for the remainder of the sample. Combining the data on all species, females outnumbered males during all but the spring (March) surveys by as much as 2.3:1.

Due to the nonrandom grid sampling and variations in methodology, the collected data are not suitable to rigorous statistical analysis. However, the data have been standardized to catch per unit effort (here equalling number of individuals per 1000 hr fishing), and the significance of seasonal, spatial (station preference) and compositional changes in the shark populations has been inferred assuming a normal data distribution.

When the 11 sample periods are considered separately, the mean catch per 1000 hr of all species combined was 279 individuals with a range of 46 to 636 (Fig. 1). Although there was no significant difference in the means of catch per unit effort between *C. ventriosum* and *S. acanthias* (110 and 118/1000 hr, respectively), these two species dominated the catches and the combined mean of these two species was significantly greater ($\alpha \leq 0.001$, one tailed) than all other species combined ($\bar{x}$, all other species = 46).

The seasonal mean shark density ranged from 73 to 554 per 1000 hr of fishing (Table 1) over the year with the summer catch the highest. *C. ventriosum* catch/effort in the spring, fall and winter was significantly ($\alpha \simeq 0.05$) greater than the mean of any other species for those seasons as was the *S. acanthias* catch/effort in the summer.

By station, catch/effort of all sharks ranged from 151 to 414, but was not significantly different between stations. *C. ventriosum* mean catch/effort was significantly ($\alpha \simeq 0.05$) greater at Station PC-1 (offshore) than the mean for all other species at that station, and the *S. acanthias* mean catch/effort was significantly

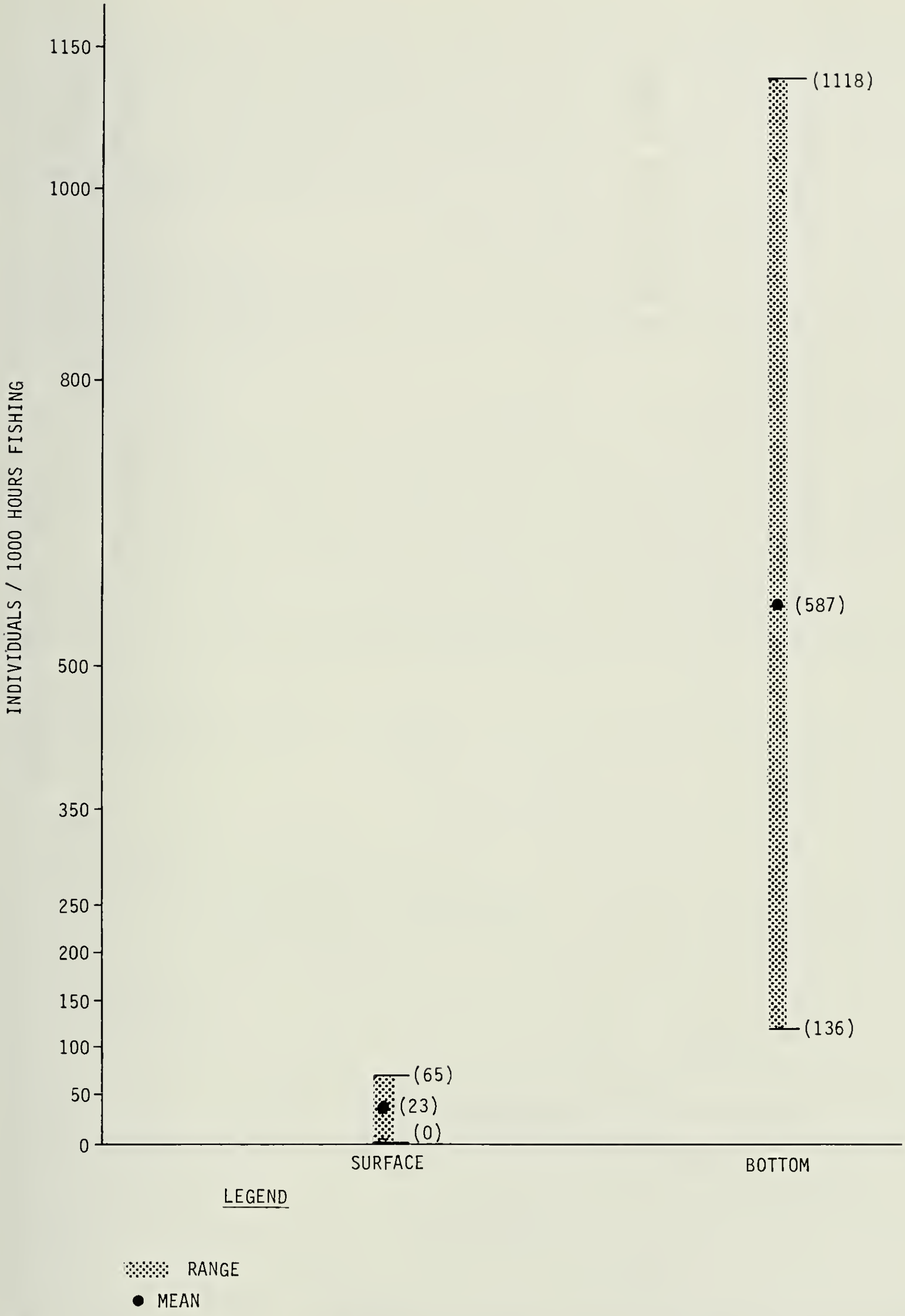

Fig. 2. Number o individuals caught/1000 hours fished by depth (all stations, species and seasons combined).

($\alpha \simeq 0.05$) greater at PC-3 (inshore) station. Both species were abundant (means greater than 1 SD above mean of all other species) at the mid-depth station.

Mean catch/effort of male sharks was not significantly different from the mean for females; however, males were least abundant in the spring and females most abundant in the summer. Mean catch/effort of male and female *C. ventriosum* and *S. acanthias* showed no significant increase during any season, but female *S. acanthias* mean catch/effort showed a substantial increase (>1 SD above the mean for all species) in the summer season.

The mean of seasonal surface (depth of 0 to 3.1 m) caught sharks per 1000 hr of fishing was 23, compared with 587 for bottom (to within 3.1 m of bottom) caught sharks. Since the ranges do not overlap, the estimated 95% confidence limits would also not overlap (Fig. 2), so that it is clear that the bottom associated sharks dominated.

Seasonal length frequency distribution for *S. acanthias* is shown in Figure 3. These data indicate (1) a substantial increase in the number of females in the summer months, (2) the majority of the females and males are beyond the length at which 98% of the individuals of this species are mature, and (3) the majority of the females are between 90 and 104 cm TL irrespective of season.

The data collected during this study indicate that the shark populations of this site are predominantly demersal, with two species (*S. acanthias* and *C. ventriosum*) dominating the overall catch. Seasonal data indicate that the summer catch consists of more species and individuals with increases in the number of *S. acanthias*. *C. ventriosum* is relatively constant in catch/unit effort at the study area, with a higher abundance at the mid-depth (12 m) and outer (17 m) stations than nearshore. *S. acanthias* dominates the inshore catch. All other species show a more varied seasonal and station abundance.

Feder et al. (1974) state that *P. glauca*, *C. ventriosum* and *T. semifasciata* have been observed to be associated (to varying degrees) with southern California kelp beds. They also report that *T. semifasciata* is gregarious and may appear in large aggregations for only short periods of time. The data in this report tend to support the documented gregariousness of *T. semifasciata* (24 of the 53 individuals were collected during one bottom net setting at PC-3) and the association of *C. ventriosum* with the kelp bed habitat. The relatively large numbers of *S. acanthias* reported here are greater than what would be expected based on other reports (Feder et al. 1974; Quast 1968). Multiple sightings of *S. acanthias* have been made, however, within the kelp beds near Big Fisherman's Cove, Catalina Island (Ted Hobson, pers. comm.) and this species historically supported a limited local gill net fishery in a nearshore sedimentary bottom area offshore Ventura, California (John Richards, pers. comm.). Large scale migrations and preference for inshore areas by *S. acanthias* have been documented by Templeman (1944) and Alverson and Stansby (1963); and increases in numbers of *S. acanthias* in San Francisco Bay during winter months have been reported by de Wit (1975). Although no fecundity data were collected during this study, it is possible that Cojo Anchorage is conducive to breeding and pupping activities for this species during the summer months. The relatively large numbers of this species appear, however, to be unreported for southern California kelp beds.

The lack of substantial suitable habitat for *S. californica* (sandy bottom near rock areas; see Feder et al. 1974) may be the primary reason for the relative

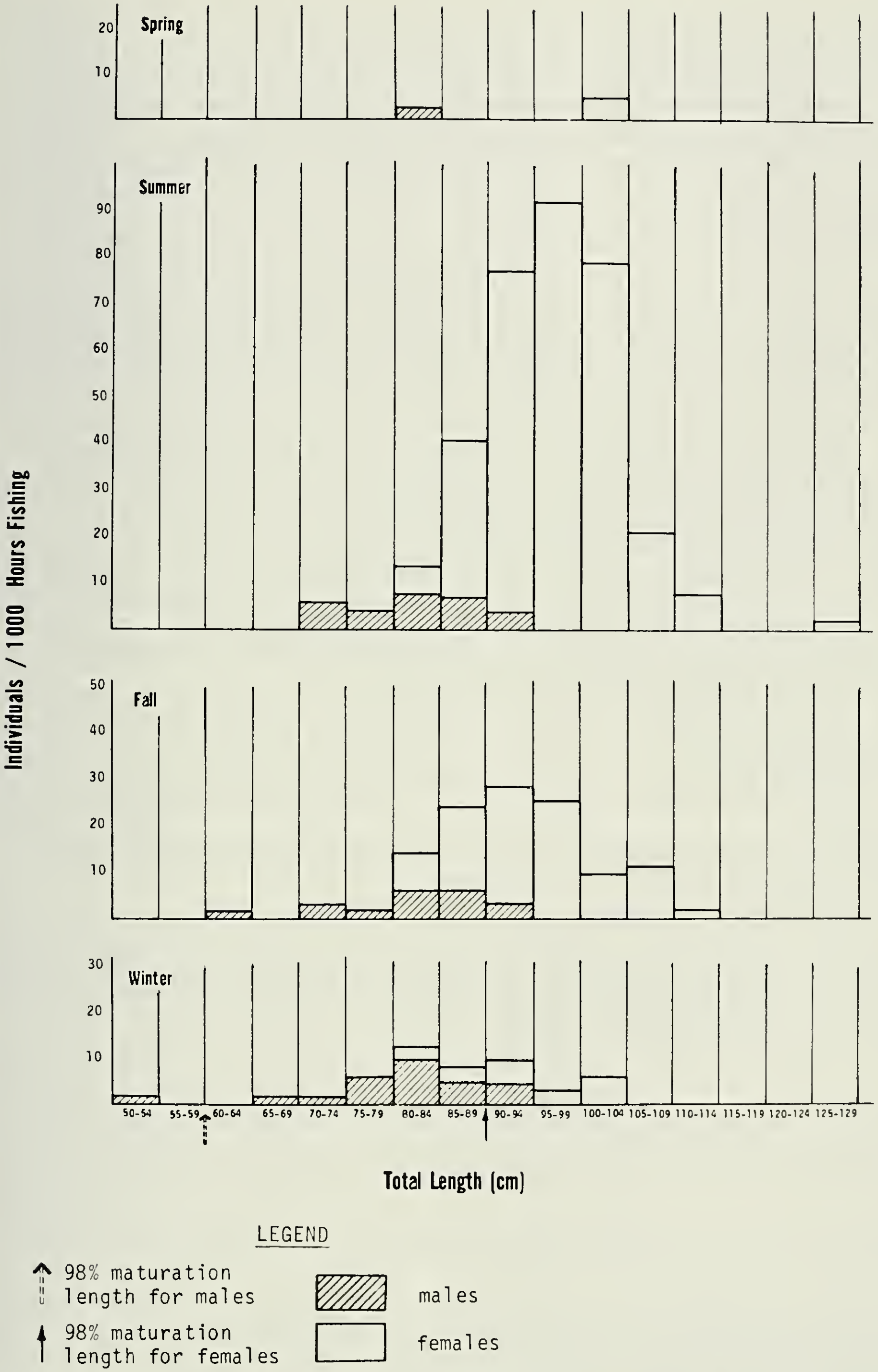

Fig. 3. Number of male and female *Squalus acanthias* caught/1000 hours fished by season (all stations combined).

paucity of this species. This species was most common at the offshore station where kelp cover is minimal and expanses of sedimentary bottom are present.

The study documents shark population distribution similar to those cited in Feder et al. (1974), but our data indicate the presence of some species that are more characteristic of bays and other protected waters. The paucity of *P. glauca* in these samples may have been due to the location of all the stations within the bounds of the kelp bed, as *P. glauca* is usually considered typical of open ocean habitats (Feder et al. 1974; Tricas 1979).

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Bull. Southern California Acad. Sci.
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A Remora, *Remilegia australis,* Attached to an Atlantic Spinner Dolphin, *Stenella longirostris*

On 8 November 1979, in the eastern Caribbean Sea, off Venezuela (10°25′N, 64°30′W), in about 180 m of water, a herd of approximately 250 dolphins was observed. They were identified as Atlantic spinner dolphins (*Stenella* cf. *S. longirostris* Gray), on the basis of their cape, elongated rostrum, triangular dorsal fin, and other pigmentation evidence (Perrin 1972). For about 30 minutes groups of dolphins rode the bow of the boat, a "Morgan 41," which was moving at about 9 km/hr. Individuals were easily observable.

One individual, whose behavior differed from the others in erratic changes of direction, caught our eye during a spinning leap, and was subsequently photographed. The animal approached the boat to swim alongside, dashed ahead crisscrossing in front of the bow, and finally moved away with several leaps. Throughout this period there was a remora firmly attached to the dolphin's side. Figure 1 shows the location of the attached fish.

The remora was a pale sky-blue, about 40 cm long and 10 cm wide. We tentatively identified it as a whalesucker, *Remilegia australis* Bennett (Echeneididae), the only remora reported to utilize cetaceans as hosts (Rice and Caldwell 1961). This species appears to have a world-wide distribution in temperate and tropical waters. It has been reported as far north as Vancouver Island, British Columbia (49°N), and as far south as Cape of Good Hope (34°S) (Follett and Dempster 1960).

Whalesuckers have been reported on the following cetacean species: *Balaenoptera musculus* (Follett and Dempster 1960; Rice and Caldwell 1961; Rice 1978); *Balaenoptera borealis* (Rice and Caldwell 1961); unidentified rorqual (Nicklin 1963, later identified as *Balaenoptera edeni,* Morejohn and Rice 1973); *Eubalaena* sp. (Gudger 1922); *Physeter macrocephalus* (Gudger 1922; Follett and Dempster 1960); *Delphinus delphis* (Follett and Dempster 1960); *Delphinus bairdii* (= *D. delphis*) (Radford and Klawe 1965); *Stenella plagiodon* (Mahnken and Gilmore 1960); *Stenella attenuata* (Linehan 1979); *Tursiops truncatus* (Wallace 1977; Shane 1978); and an unidentified pelagic dolphin (Townsend 1916; Caldwell 1961).

We are aware of additional unpublished observations of whalesuckers attached to *Globicephala* sp. and *Steno bredanensis* (W. E. Evans, personal communication), and to *Lagenorhynchus obliquidens* (S. Leatherwood, personal communication).

Stenella cf. *S. longirostris* is now added to this list of cetacean hosts for remoras.

In most accounts, remoras have been reported to move about on a cetacean host, changing position frequently. In contrast, during the period of our observation, this one seemed to cling tenaciously to one spot. Close to the attachment site, we observed several oval pink spots about the size of the remora's sucker disc. The aerial acrobatics of *Stenella longirostris,* its characteristic high-speed spinning leaps, rapid turns and fast swimming would seem to require adhesive

Fig. 1. Atlantic spinner dolphin, *Stenella longirostris*, with a suckerfish attached to its left side. Photo by William A. Watkins.

strength sufficient to account for both the unusual tenacity of the specimen observed and the oval abrasions of the dolphin's skin. Scars from suckerfish attachment on cetaceans have been mentioned by Krefft (1953) and Radford and Klawe (1965).

The observation of remora on the spinner dolphin were corroborated by Karen E. Moore and Romaine Maiefski, on board during a radio tracking experiment on *Balaenoptera edeni*.

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Stereotyped Motor Patterns in Two Captive Bull Sharks, *Carcharhinus leucas*

Various motor patterns and the associated social activities have been described for the bonnethead shark, *Sphryna tiburo* (Myrberg and Gruber 1974) and the gray reef shark, *Carcharhinus amblyrhynchos* (Johnson and Nelson 1973). The sterotyped nature of these body movements and postures, as well as their departure from normal swimming behavior, were similar to those the authors observed in two captive bull sharks, *Carcharhinus leucas*. This report describes the behavior of these two bull sharks when the proper releasing situation occurs.

Both bull sharks were males, and were caught in the area of the Florida Keys. At capture in April 1978, the smaller was 180 cm total length (TL), and the larger was 218 cm TL upon his capture in October of the same year. Each shark was transported approximately one and one-half months after capture to Sea World San Diego, where they were placed in a 1,500,000 liter, filtered sea-water aquarium. This facility was designed and built specifically for the maintenance and study of sharks (Keyes 1979). The general dimensions of this aquarium are 30.4 m long, 10.7 m wide and 4.6 m deep. The observations were carried out daily, both from top side and through the underwater tank windows, from March through June 1979.

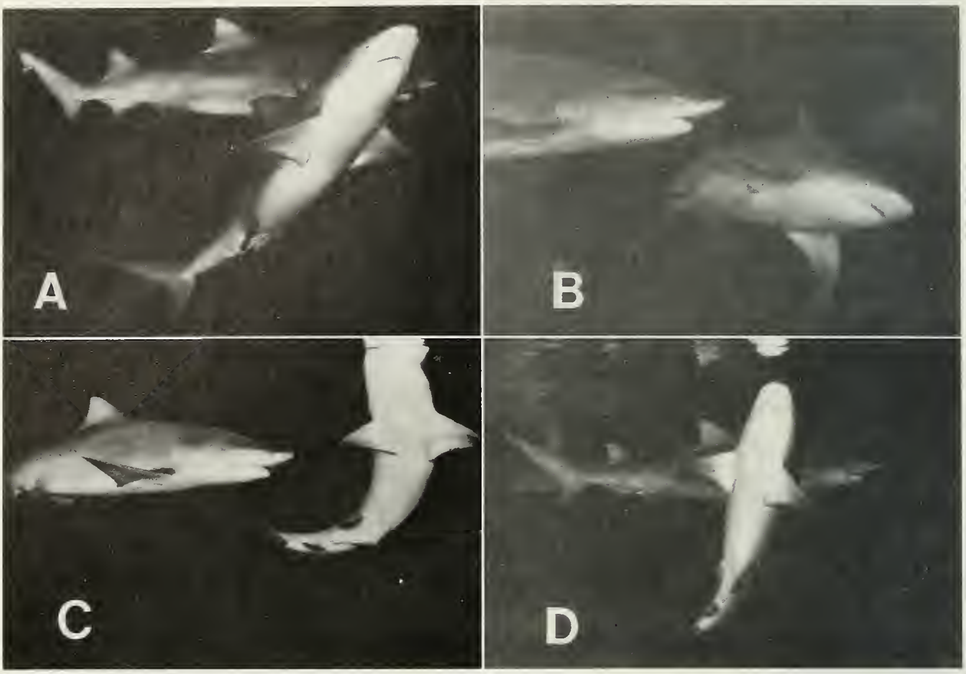


Fig. 1. Comparison of the postures exhibited by the bull sharks: A. angle-up; B. sustained lean; C. roll-arc and D. the common vertical orientation.

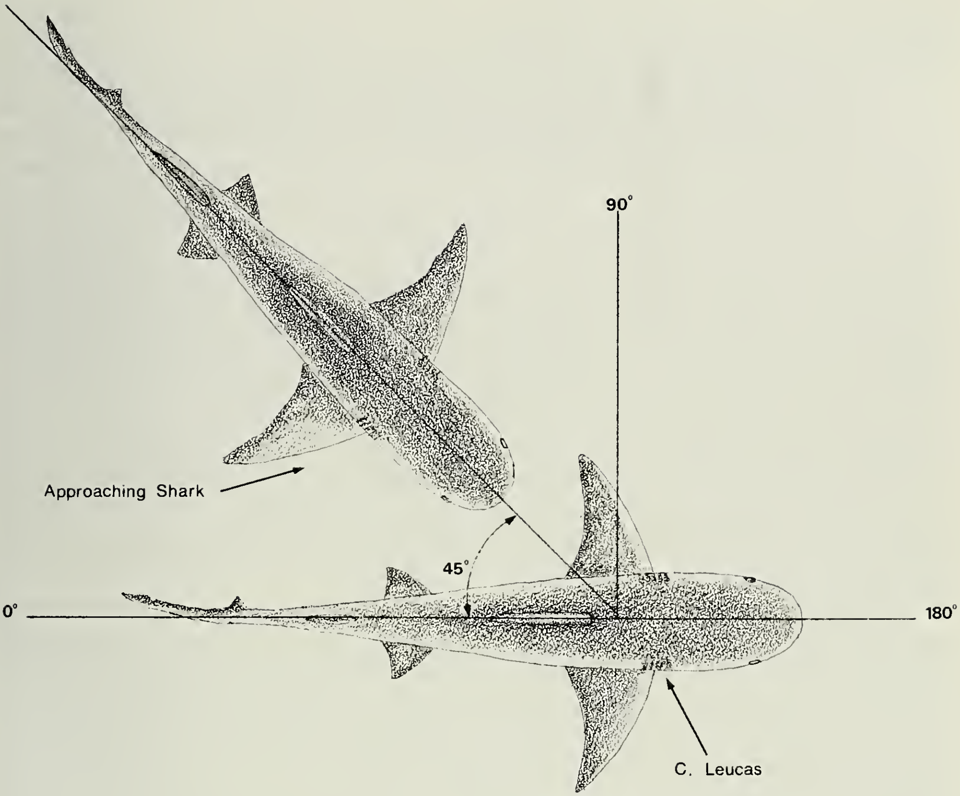
In addition to the bull sharks, this facility housed the following: 1) seven nurse sharks, *Ginglymostoma cirratum,* three males and four females (≃1.5 to 3.0 m TL), 2) five Atlantic lemon sharks, *Negaprion brevirostris,* two males and three females (≃2.0 to 3.0 m TL), 3) four sandbar sharks, *Carcharhinus plumbeus,* all females (≃2.0 to 2.5 m TL), 5) six cleaner wrasse, *Labroides dimidiatus.* All of the above-mentioned sharks, excluding the two Pacific lemon sharks, had lived in this aquarium for at least seven months.

During regular locomotion, both bull sharks swam with relatively smooth, slightly stiff body movements. When closely encountering another shark under specific circumstances, explained later in this paper, the bull sharks involved veered to one side and performed one or more of the following postures:

Angle-up (Fig. 1A).—a sharp and sudden upward change of attitude, ranging from 35° to 90° from the horizontal swimming path. The swimming strokes of the tail did not stop.

Sustained-lean (Fig. 1B).—a prolonged roll (less than 90° from horizontal) along the longitudinal body axis. This lean was usually held for approximately three seconds while the shark continued swimming.

Roll-arc (Fig. 1C).—most abrupt change from normal swimming, this posture began with a lean of the body to one side. The head and tail were then simultaneously thrown laterally toward the opposite side of the body lean. This resulted in a posture with the head and tail directed upward in relation to the shark's original horizontal orientation. In most cases the dorsal surface of the bull shark



Sophia Ann Dawes

Fig. 2. Typical releasing situation, in which the approaching shark passes over the *C. leucas* at an angle of 45°, at point of intersection.

faced the other shark. Near vertical orientation of the bull shark's body in the water column was common (Fig. 1D). Many times the head of the bull shark broke the surface of the water. All swimming motion was halted during this posture.

Each of these postures was culminated by the bull shark either swimming or gliding away, and eventually returning to normal swimming behavior. The glides varied in descending angles, sometimes actually becoming a nose dive, straight down to just above the tank floor.

The bull shark postures were released when another shark's approach direction and body orientation satisfied all of the following three criteria: 1) traveled approximately on the same level or above the bull shark's body in the water column, 2) swam close to the bull shark's body ($\approx$0 to 2.4 m distance, averaging .7 m), 3) achieved either a sustained parallel, a close trailing, or an angular intersecting travel with reference to the bull shark's body. When the bull shark reacted to instances of intersecting angle, the angle between the two sharks' bodies was less than approximately 90°, as shown in Figure 2.

All of the shark species in the aquarium released postures in our bull sharks. Out of 158 recorded cases, 95 (60%) were released by the five Atlantic lemon sharks. The two bull sharks stimulated each other in 16 (10%) instances. The sandbar, Pacific lemon and nurse sharks were involved in 33 (21%) instances, while in 14 (9%) cases the observer could interpret no influence by any individual.

This disproportionate number of postures exhibited toward the Atlantic lemon sharks can be explained largely by the existence of a general depth stratification of shark species at the Sea World facility. The bull sharks, along with the sandbar sharks, tended to occupy the mid depths of the aquarium, although the latter species will usually swim below a nearby bull shark. The nurse and Pacific lemon sharks most often rested on, or swam along the floor. Except when being cleaned by the cleaner wrasse (Keyes in prep.), or rummaging along the bottom after feeding, the Atlantic lemon sharks usually circled in the upper quarter of the aquarium water column. This preference for the area above the bull sharks placed the Atlantic lemon sharks in more posture inducing situations.

The sharks at which the bull sharks directed their postures sometimes made obvious responses, such as change of course and/or speed. Quantified data concerning these responses are presently insufficient to allow the authors to present a conclusion as to the effect these postures have on the other sharks' behavior. Without this conclusion, an assignment of function to the bull shark postures is impossible.

The bull shark is native to inshore and estuary areas of the Atlantic Ocean and Gulf of Mexico (Bohlke and Chaplin 1968), and occurs world wide in both fresh and salt water. The postures exhibited by the two Sea World bull sharks may be a result of such conditions as the mixture and high concentration of shark species in the aquarium. Yet, the occurrence of similarly exaggerated and repetitive behaviors of *Sphyrna tiburo* and *Carcharhinus amblyrhynchos* in their natural environment (Myrberg and Gruber 1974; Johnson and Nelson 1973) promotes the possibility that the bull shark postures may also occur in the wild.

Acknowledgments

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Possible Cleaning Behavior by a Juvenile California Sheephead, *Semicossyphus pulcher* (Labridae)

Cleaning behavior has been observed in a number of marine fishes inhabiting the nearshore waters of California. This group includes six species of embiotocids, two species of labrids, two species of kyphosids, one pomacentrid, and one scorpidid (Limbaugh 1955, 1961; Feder 1966; Gotshall 1967; Turner et al. 1969; Hobson 1969, 1971, 1976; Hixon 1979; DeMartini and Coyer 1981). These fishes possess a small mouth and are generalized (*sensu* Hobson 1971) "substrate-pickers" or "plankton-pickers" as juveniles or adults. For some of these species, cleaning behavior is confined to the juvenile phase and/or to relatively few, specialized individuals (Hobson 1971; DeMartini and Coyer 1981). This note reports possible cleaning by a juvenile California sheephead, *Semicossyphus pulcher* (formerly *Pimelometopon pulchrum*), a behavior previously unreported for this species.

During an early afternoon dive on 2 December 1976, I observed a juvenile sheephead apparently cleaning a blacksmith, *Chromis punctipinnis*. The event occurred above a small algae-encrusted boulder at a depth of 4–5 m in a dense kelp (*Macrocystis*) forest at Starlight Beach, near the west end of Santa Catalina Island, California. Two blacksmiths (approximately 60 and 120 mm total length) with no obvious discolorations or wounds, hovered 0.5 m above the small boulder. The juvenile sheephead was approximately 90 mm total length and possessed the normal juvenile coloration: a brilliant red orange body with a yellow stripe along the lateral line, two black spots on the dorsal fin, a single black spot at the base of the caudal fin, and black pelvic and anal fins trimmed with white.

When first noticed, the larger blacksmith was 10–15 cm from the juvenile sheephead and had assumed a conspicuous head-up, tail-down posture with fins motionless and erect. During the subsequent observation period, the sheephead briefly inspected the posing blacksmith, then picked once at the region just posterior to the right pectoral fin. The blacksmith reacted positively to the contact by continuing to pose for an additional 15–20 s. During this period, the sheephead continued to inspect, but did not approach the posing blacksmith. The event was terminated when the sheephead slowly swam away (perhaps because of my presence). This individual was not captured and could not be located on later dives within the area. The smaller blacksmith hovered near the larger blacksmith during the apparent cleaning event, but did not pose and was not approached by the sheephead. Neither blacksmith followed the retreating sheephead.

I believe this represents cleaning behavior for the following reasons:

1) blacksmith vigorously solicit and accept cleaning by cleaning fishes (Limbaugh 1961; Hobson 1971)
2) the observed blacksmith assumed a pose typical of cleaning solicitation in this species (Limbaugh 1961; Hobson 1971)
3) the pose resulted in a brief inspection and subsequent oral contact by the

juvenile sheephead, behaviors consistent with other reported instances of cleaning (Hobson 1971)

4) the blacksmith continued to pose after interspecific contact, a positive response frequently observed in cleaning events (Limbaugh 1961; Hobson 1971)

During numerous subsequent observations of sheephead, I did not notice such apparent cleaning behavior among either juveniles or adults. Therefore, the behavior seems restricted to juveniles and is either an occasional activity for a very few individuals, or is a rare event among all juveniles.

It is reasonable to expect some degree of cleaning behavior in juvenile sheephead. Cleaning is widespread among labrids throughout the world (Randall 1958; Feder 1966; Ayling and Grace 1971) and is restricted to the juvenile phase in the temperate *Pseudolabrus miles* and *Coris sandageri* (Ayling and Grace 1971) and the tropical *Bodianus pulchellus, B. rufus,* and *B. diplotaenia* (Randall 1968; Hobson 1969). Furthermore, juvenile sheephead are small-mouthed, substrate-pickers, and cleaning behavior appears to be widespread among small-mouthed fishes that pick food items from a substratum or the water column (Hobson 1971).

Acknowledgments

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Use of Incisors to Identify Rodent Genera in Owl Pellets

Analysis of owl pellets has been used for predator food studies (e.g. Cunningham 1960), determining species distributions (e.g. Twente and Baker 1951), interpreting paleontological finds (e.g. Brain and Brain 1977), and for estimating mammalian populations (e.g. Cabon-Raczynska and Ruprecht 1977). The senior author has used owl pellets in environmental impact studies, reducing the cost of the rodent species list and the impact of the assessment itself on the living fauna of the area. Owls may preferentially select prey species (Voight and Glenn-Lewin 1978); thus, pellet analysis is useful for verifying what species are in an area, not as proof of their absence. Owl pellet analysis is also a simple but rewarding laboratory exercise in ecology classes.

Presently, Ingles (1965) provides the best known key for identifying the mammals of California; it is predominantly based on cranial characteristics. Great Horned Owls (*Bubo virginianus*) and Barn Owls (*Tyto alba*) are known to regurgitate 95–100% of the crania of their prey (Dodson and Wexlar 1979). The mandible, however, is seen as often as the cranium in the pellets but no concise key appears to be available for this bone.

We asked six college biology majors with no previous experience to key out nine rodent crania (from owl pellets) to genera using Ingles' key which included only likely local species; they took an average of 13.6 minutes per item and were correct 75% of the time. The identification of these species had been verified against a reference collection of skulls kept at California State University, Fullerton. In this paper we present a new key (with an emphasis on incisor arcs) for rodent species from coastal sage scrub and disturbed (urban) habitats of Southern California. We think our method is adaptable to other localities; it is designed for individuals with limited experience in the use of mammal keys. Our method reduced the students' handling time to below two minutes per item and their identification accuracy rose to 85 and 89% on crania and on mandibles.

Our method is based primarily on both upper and lower incisor characteristics with a limited number of cranial and mandibular characters. A basic piece of equipment needed is a multiple-circle plastic template (circles in $^1/_{32}$ inch sequences; templates may not be in metric), readily available from art and graphic supply stores. We assume that the incisor is an arc of a circle. As Landry (1957) pointed out, this assumption is not accurate since incisor curvature occurs in two planes "so that the curve produced is not a flat circle but a shallow spiral or, more properly, a helix." One only needs to place an incisor on a flat surface and try to match its outer curvature to the inner curvature of an appropriate circle on the template. The best match occurs when the entire outer surface of the incisor is in contact with the inner curvature of the proper diameter circle; the diameter of the incisor arc can then be recorded from the template and used on our key. Upper incisors approximated an 180° arc of a circle while lower incisors were less than 135° of a circle for our species. Upper incisor morphology and

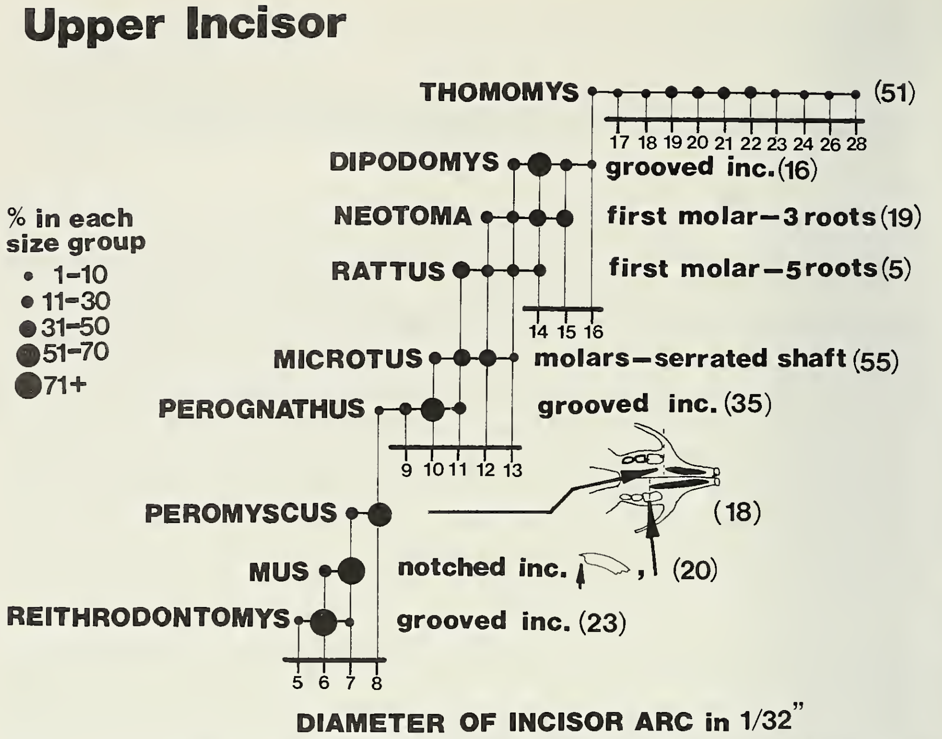

Fig. 1. Key to upper incisors, with cranial characters as needed, of the rodents found in owl pellets from coastal sage scrub and urban/disturbed habitats of Southern California. Taxa represent *Reithrodontomys megalotis*, *Mus musculus*, *Peromyscus* sp., *Perognathus* sp., *Microtus californicus*, *Rattus* sp., *Neotoma* sp., *Dipodomys agilis*, and *Thomomys bottae*. Sample sizes are in parentheses. Inc. = incisor.

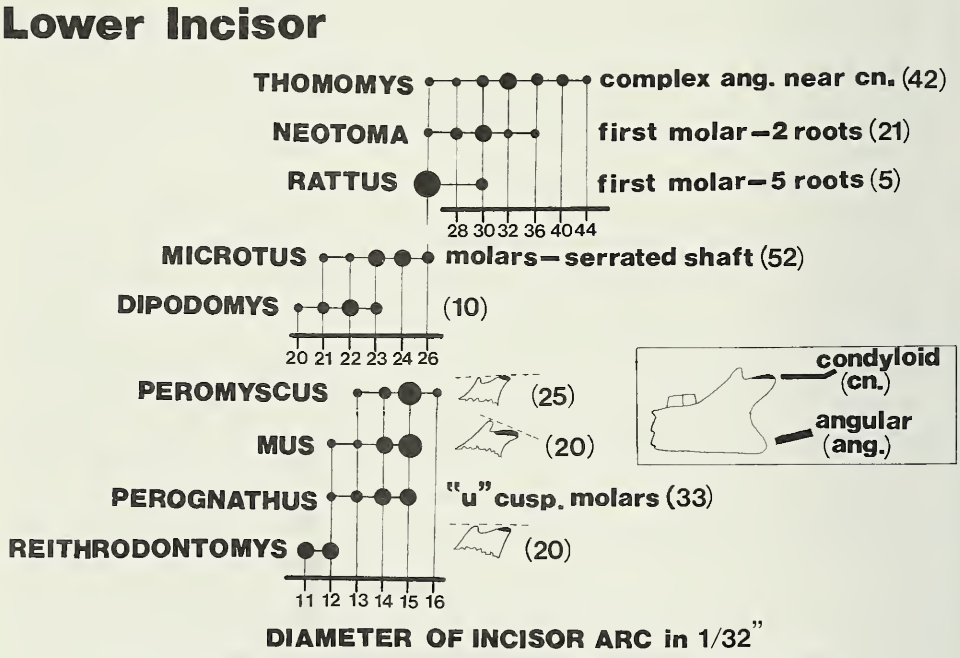

Fig. 2. Key to lower incisors, with mandibular characters added as needed.

diameter of arc can be used to separate out six of nine rodent genera found in the owl pellet samples. We used the right incisor for our measurements whenever possible. Most owl pellets were from Barn Owls in western Riverside, Orange, and southeastern Los Angeles counties of California in coastal-sage scrub and urban/disturbed habitats.

Figures 1 and 2 show the key for upper and lower incisors with cranial or mandibular characters added if needed. The user first finds the column corresponding to the diameter of the incisor arc which narrows the possible rodent species; a second incisor character or a mandible/cranial character allows the identification of the specific genus. Our method cannot separate out closely related species which are the same size (i.e. *Rattus rattus* versus *R. norvegicus*, *Neotoma fuscipes* versus *N. lepida*). Thus for our sampling area the following taxa can be identified; *Reithrodontomys megalotis*, *Perognathus* sp., *Dipodomys agilis*, *Thomomys bottae*, *Microtus californicus*, *Neotoma* sp., *Rattus* sp., *Mus musculus*, and *Peromyscus* sp. Another difficulty with this method is removing incisors from *Reithrodontomys* and *Perognathus*; it may be necessary to remove some of the cranial bones in the process.

Acknowledgments

We thank the fall, 1979 Animal Ecology class of California State University, Fullerton for their help, especially Greg Jakust and Gordon Owens. Dr. Bayard Brattstrom provided some of the owl pellet material. Dr. Gene Jones provided helpful criticism on the figures.

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79(3), 1980, pp. 130–132

On the Status of the Eastern Pacific Cymothoid Fish Parasite *Braga occidentalis* Boone, and Its Synonymy with *B. patagonica* Schioedte and Meinert (Crustacea: Isopoda: Cymothoidae)

Amid the various collections examined by the naturalist Pearl Lee Boone in her lifetime, is a single specimen of cymothoid isopod she chose to name *Braga occidentalis*. The specimen was allegedly collected from an unspecified locality "off the west coast of California" by James D. Dana and John L. Le Conte in 1866 (Boone 1918). This species has not been reported since and its validity has been seriously questioned by Lemos de Castro (1959), who suggested the possibility that it is in reality a synonym of *Braga patagonica* Schioedte and Meinert, 1884, a South American freshwater species. Lemos de Castro apparently did not examine the type of *B. occidentalis*. Our examination of this type specimen (deposited as a holotype in the Peabody Museum of Natural History, Yale University, YPM No. 302) has confirmed Lemos de Castro's suspicions and we herein synonymize *Braga occidentalis* Boone, 1918 with *B. patagonica*.

There is no original collection label associated with the type specimen, and considerable doubt is cast upon the data associated with it by Boone. First, there is no record of Dana and/or Le Conte having participated on any oceanic or coastal expeditions in the alleged year of the collection (1866). Secondly, the five other known species of the genus *Braga* are restricted in their distribution to freshwater habitats within the eastern drainage of South America (Trilles 1973). Lastly, no other specimens of *B. occidentalis,* or any congeners, have been reported from the Pacific or any other marine habitat.

During the year 1866, when the specimen was reported by Boone to have been obtained, neither Dana nor Le Conte were in a position to make such a collection. Just a year after the Civil War, Le Conte (ending an appointment as Surgeon of Volunteers) was acting geologist on an overland survey for the extension of the Union Pacific Railroad. Dana was gradually recovering from a severe physical breakdown following his completion of the United States Exploring Expedition Report on the Crustacea and Zoophytes, and was never again capable of extended travel.

The possibility still exists that either Dana or Le Conte collected the specimen Boone designated as *B. occidentalis,* but not in the year she reported. Le Conte traveled on an expedition to California in 1850–1851 collecting a considerable variety of material in many marine taxa, including crustaceans. The list of Crustacea was subsequently published by Dana (1854), but contained only intertidal and terrestrial species, suggesting that offshore collections were not made. There appears to be no record of Le Conte ever accompanying an expedition to the east coast of South America (although he did travel as far south as Honduras).

Dana, on the other hand, traveled extensively around the world as a geologist and naturalist for the U.S. Exploring Expeditions of 1838–1842, collecting along both the Atlantic and Pacific coasts of South America. Dana might have collected the specimen in question from a freshwater or estuarine habitat along the east coast of South America, failing to describe it in his report on the Crustacea (Dana 1853). The Crustacea listed in his report included five genera of cymothoid isopods: *Cymothoa* and *Lironeca* (3 species each), collected from Rio de Janeiro and the Hawaiian Islands; *Nerocila* (6 species) from Rio de Janeiro; *Aegathoa* (2 species), from the Bahamas, Rio de Janeiro, and Tierra del Fuego; and *Ceratothoa* (2 species), from the Atlantic coast of North America and the Indo-Pacific. All 16 of these species are strictly marine in distribution, and none were reported from the eastern Pacific. Unfortunately, Dana did not include collection dates for any of the species he discussed.

We believe there are two possible explanations regarding the collection data reported by Boone for *Braga occidentalis*. First, one of Le Conte's South American colleagues may have sent the specimen to him, Le Conte subsequently forwarding it to Dana. Second, Dana may have collected the specimen along the Atlantic coast of South America while on the U.S. Exploring Expedition and later sent it to Le Conte for examination. Le Conte then would have returned the specimen (unidentified) years later, after the completion of Dana's report. The year presently associated with the specimen might then be the year Dana received the specimen back from Le Conte, and/or the year it was accessioned into the Yale Peabody Museum. Many years passed until Pearl Boone found the specimen on the shelves of the Yale Peabody Museum and described it, assuming it to be part of the Le Conte-Dana California collection.

Ho (1975) reported the only other record of *Braga* (n. sp.) from the eastern Pacific. His specimen subsequently has been lost and recent communication with Ho suggests that it was probably a case of mistaken generic identification. Based on his description it appears to have been a juvenile *Lironeca*.

We thank Thomas E. Bowman and Ernest W. Iverson for their critical review of this paper.

This is contribution no. 387 of the Allan Hancock Foundation, University of Southern California.

Appendix

I. Chronology of J. L. Le Conte pertinent to the present paper (1825–1883)

1850–1851	Expedition to California; stopped at Panama to make collections. Extended explorations through Colorado desert.
1857	Accompanied the Honduras Inter-Oceanic Survey, under J. C. Trautwine. Visited Fuente de Sangu.
1862–1865	Appointed Surgeon of Volunteers during Civil War.
1867	Geologist, surveyed for extension of Union Pacific Railroad southward to Fort Craig, Colorado.
1869–1872	Traveled in Europe, Algiers and Egypt.
1874	President of American Association for the Advancement of Science.

Comments: Although Le Conte worked extensively in the field of entomology (particularly the Coleoptera), he also contributed numerous scientific articles to the fields of vertebrate paleontology and mammalogy.

II. Chronology of J. D. Dana pertinent to the present paper (1813–1895)

1834	Upon graduation from Yale appointed as Instructor of Mathematics to the midshipmen of the United States Navy. Traveled extensively.
1836–1838	Chemical assistant at Yale College.
1838–1842	Served as geologist and naturalist to the U.S. Exploring Expedition to the southern and Pacific Oceans under Comm. Charles Wilkes. The next 13 years were devoted largely to the study of the material collected by the expedition and preparation of his report.
1850	Appointed Professor of Geology and Natural History at Yale College.
1859	Suffered a severe physical breakdown. Traveled abroad in Europe for a year to regain health.
1862–1872	Published several books: *Manual of Geology* (1862), *Text Book of Geology* (1864), *Systematics of Mineralogy*, fifth edition (1868), *Manual of Geology*, new edition (1874), *Corals and Coral Islands* (1872).
1887–1890	Revisited the Hawaiian Islands (the "Sandwich Islands") and the Volcano of Kilauea.

Comments: Dana's principal publications dealt with hermatypic corals ("zoophytes"), crustaceans and geological formations. He was the first to propose the concept of cephalization in animals (1852), "The domination of the brain in determining the development of an animal organism," and he proposed a subsidence theory of atolls independently of Darwin's. His zoogeographical analysis and techniques (1853) represent a landmark in marine biogeographical studies.

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One Mass Stranding, Not Two, of Sperm Whales at La Paz, Baja California, 1954

In January 1954, news arrived in San Diego of a mass stranding of sperm whales at La Paz, southern Baja California, gulf side.

I visited La Paz on 6 February 1954, and found three sperm whales in advanced stages of decomposition, on an inner, shallow beach, just east of the city of La Paz. I also received details of the mass stranding from two informants in La Paz: Mrs. Margaret Waters, stringer for the New York Times, and teacher of English; and Sr. Luis Collins, manager of Hotel Mision. Collins also gave me photos.

Waters and Collins agreed on all essential details: The date was 16 January; 22 individuals had stranded at the same time; all were males, 35 to 40 feet in length; nineteen had been towed to an outer beach before my arrival. Photos showed partial flensing of many carcasses by local inhabitants to obtain blubber to render for the waxy oil, good for lubrication.

In May 1956, Cockrum reported two mass strandings at La Paz, as follows: "An Associated Press dispatch datelined February 13, 1954, from San Diego, California . . . reported [that] Mr. Marvin Grisby, a pilot from San Diego, . . . saw 24 sperm whales stranded in the shallow cove at La Paz . . . and, two weeks later, at the same place, 34 more . . ."

In early 1957, appeared my report on the stranding. It had been submitted prior to Cockrum's publication. It had all the details and the photos that I gathered on 6 February 1954.

In 1959, I recorded all the known mass strandings in the world that I was able to obtain at that time. In it, I included the stranding at La Paz of 16 January 1954. I also stated that I had no information of a second stranding a short time after the first and at the same place; and that the dispatch of the Associated Press that Cockrum had used was in error.

All this is important because: 1) I visited La Paz, 6 February 1954, while some sperm whales were still on the beach. I also gathered what I considered accurate information on the mass stranding. I continued correspondence and conversations with Mrs. Waters, and visited La Paz again in February 1955, 1956, 1957, and in December 1959; 2) Cockrum used a newspaper dispatch of doubtful accuracy—no accuracy, as it turned out; 3) the report of two strandings has now entered the popular literature (Nayman 1973); and 4) two recent mass strandings of sperm whales have raised much interest in the phenomenon, often with references to earlier cases. The two recent mass strandings were: 1 January 1979, 56 sperm whales, 9 of which were females, at a beach between Mulegé and Santa Rosalia, eastern coast of mid Baja California (see Payne 1979); and 16 June 1979, 41 sperm whales—16 males and 25 females—near Florence, Oregon (Rice 1979).

I met Mr. Marvin Grisby some time in the early or mid 1950s. He operated a small plane out of San Diego for charter service to Baja California, and possibly was using his and rumored information to obtain business.

Cockrum in 1956 also briefly mentioned another mass stranding of sperm whales in Golfo California—this case accurately. In 1957, I gave full details with photos of this stranding: nine sperm whales, all males, at Cabo Tapoca, Sonora side of the upper Golfo, 12 April 1953.

My visit to La Paz on 6 February 1954 was during air census of the Californian population of gray whales with Dr. Gifford C. Ewing, owner and operator of a plane at Scripps Institute of Oceanography, La Jolla, California.

Incidentally, Nayman mentioned two dates for the alleged two mass strandings of 1954: 3 February for 24 whales, and 27 February for 34. These dates were not in Cockrum's report, and presumably, from the context of his report were not in the dispatch from the Associated Press. All this adds to the confusion of Grisby, Associated Press, Cockrum, and Nayman.

I am indebted to Mr. Robbin B. Patten for the reference to and the quotation from Nayman.

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79(3), 1980, pp. 135–136

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INSTRUCTIONS FOR AUTHORS

he BULLETIN is published three times each year (April, August, and November) and includes articles in English any field of science with an emphasis on the southern California area. Manuscripts submitted for publication iould contain results of original research, embrace sound principles of scientific investigation, and present data a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide r contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, hieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous ference of pronouns, and logically placed modifiers.

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It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The ithor is requested to submit *at least two additional copies with the original,* on 8½ × 11 opaque, nonerasable iper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the manuscript.*** ootnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to ie author.**

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* company a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into ie following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, and terature cited. Avoid using more than two levels of subheadings.

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Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the ULLETIN. **Omit periods after standard abbreviations:** 1.2 mm, 2 km, 30 cm, but Figs. 1–2. Use numerals *before* nits of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of eights and measurements should be used wherever possible.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54:452–458.

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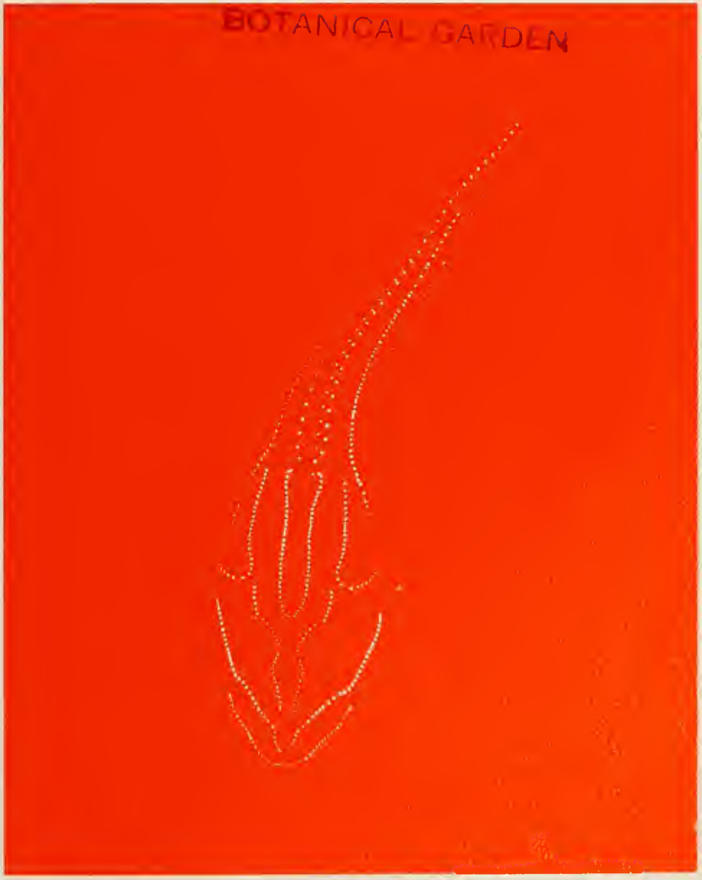
SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

BULLETIN

Volume 80 Number 1



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Date of this issue 16 December 1981

Bull. Southern California Acad. Sci.
80(1), 1981, pp. 1–12

A New Species of Murre, Genus *Uria,* from the Late Miocene of California (Aves: Alcidae)

Hildegarde Howard

Abstract.—A new species of murre, genus *Uria,* from the late Miocene of California (Aves: Alcidae) by Hildegarde Howard, *Bull. Southern California Acad. Sci.,* 80(1):1–12, 1981. A new species of murre, *Uria brodkorbi,* is represented by impressions of the skull and incomplete skeleton of one individual on two slabs of diatomite from the late Miocene Sisquoc Formation, exposed near Lompoc, California, U.S.A. This is the seventh species of fossil bird to be described from this formation. *Uria brodkorbi* is very similar morphologically to the Recent *Uria aalge* that is common along the California coast today, but differs in being of heavier build and having a shorter beak, a stronger sternum and more massive wings.

Introduction

A previously unrecorded fossil bird specimen from the diatomite deposits of the Sisquoc Formation near Lompoc, California, was recently made available to me for study and description through the generosity of Dr. Pierce Brodkorb, of the University of Florida. The new fossil consists of the impressions of the skull and the anterior elements of the skeleton on two contiguous slabs of diatomite; it represents a new species of murre, family Alcidae.

Six species of marine birds were described from the same late Miocene deposits at Lompoc by Miller (1925). These include three species of the booby-gannet family (Pelecaniformes: Sulidae): *Miosula media, Sula willetti* and *Morus lompocanus*; a shearwater (Procellariiformes: Procellariidae), *Puffinus diatomicus*; a godwit (Charadriiformes: Scolopacidae), *Limosa vanrossemi*; and an auklet (Charadriiformes: Alcidae), *Cerorhinca dubia,* of smaller size than the alcid specimen now at hand and related to the puffins rather than to the murres.

Although the number of fossil bird specimens collected from the Sisquoc Formation has nearly doubled since the time of Miller's report (1925), no additional species have been described from the deposits. The holotypes and many of the referred specimens are in the collections of the Museum of Paleontology at the University of California, Berkeley. The others are in the Natural History Museum of Los Angeles County and the California Academy of Sciences. Most of the approximately 20 avian specimens now known from these deposits are skeletal imprints in diatomite with no bones remaining. One specimen, assigned to *Cerorhinca dubia* (LACM 74068), retains badly fragmented wing bones.

The specimen now at hand is in the collection of Dr. Pierce Brodkorb (PB 7960). It was acquired by Dr. Brodkorb many years ago under a Cooperative Agreement with the Florida State Geological Survey. Dr. Brodkorb was unable to learn particulars regarding the collection of the specimen. The label data read, "Sisquoc Formation, Santa Barbara Co., Cal. Diatomaceous earth quarries in this area. Johns Manville Co."

Photographs of PB7960 viewed in certain lights cause the image of the impressions to be reversed, so that the skeletal elements appear in relief (Figs. 1 and 2). In this aspect the skeleton so closely resembles that of the present-day murres, genus *Uria*, that had the deposit been of Pleistocene age, the specimen might have been identified as the Common Murre, *Uria aalge*, that is found along the California coast today. More detailed study, however, reveals important differences. Therefore, a new species is here described.

Methods and Materials

In order to observe more closely the details of the skeleton of this fossil murre, latex molds were made of the impressions in the diatomite. Two sets of molds were prepared, each made directly from the slabs in an effort to assure maximum accuracy of detail. One set remains with the holotype, the other is in the cast collection of the Natural History Museum of Los Angeles County. Although the skeletal impressions in the diatomite slabs were checked for measurements, the actual study of the specimen was based largely on the latex molds.

Abbreviations.—The following acronyms are used for specimens cited in the text: ANSP, Academy of Natural Sciences, Philadelphia; CSULB, California State University, Long Beach; LACM, Natural History Museum of Los Angeles County; PB, Pierce Brodkorb collection; USNM, National Museum of Natural History, Smithsonian Institution.

Bone terminology follows Howard (1929).

Comparative material.—Recent: Complete skeletons of *Uria aalge californica* (17), *U. a. inornata* (6), *U. lomvia lomvia* (2, one lacking complete skull), *U. l. arra* (10), from the collections of CSULB, LACM and PB. Also disassociated elements of *Uria* spp. from Aleut middens in Amchitka, Alaska (CSULB): 48 humeri, 45 coracoids and 36 carpometacarpi. With the exception of the genus *Alle*, specimens representing all other North American genera of Alcidae were also compared.

Fossil: *Uria antiqua* (Marsh 1870), cast of holotype humerus (ANSP 13357); *Uria affinis* (Marsh 1872), cast of holotype humerus (ANSP 13358); *Australca* cf. *grandis* Brodkorb 1955, proximal and distal ends of humeri (USNM 192758 and 178136) and ulnae (USNM 193326 and 215652, complete coracoid (USNM 215513) and proximal end of carpometacarpus (USNM 215906) from the Lower Pliocene Yorktown Formation, Lee Creek, North Carolina; *Miocepphus* cf. *mcclungi* Wetmore 1940, humerus (USNM 25668) from the Middle Miocene Calvert Formation, Maryland; ?*Uria* sp., proximal end of humerus (LACM 52018) from the late Miocene Monterey Formation, Orange County, California.

Systematics

Class Aves Linnaeus 1758
Order Charadriiformes (Huxley 1867)
Family Alcidae Vigors 1825
Subfamily Alcinae (Vigors 1825)
Genus *Uria* Brisson 1760

In the fossil specimen from Lompoc, as exposed on the diatomite slabs and shown in the latex molds, the following characters shared with *Uria, Alca* and

Pinguinus (genera that Storer (1960) groups together in the tribe Alcini) are observable: sharply ridged temporal fossa of the cranium, carpometacarpus with long process of metacarpal I, and humerus with depressed, ovoid pectoral attachment and with external tuberosity projecting anconad.

The straight beak and well developed wing elements immediately distinguish the fossil specimen from *Pinguinus*. The straight beak also distinguishes the fossil from the genus *Alca*. Other distinctions from *Alca* include the more rounded shaft of the humerus and the less acute bend in the anconal profile of its distal end, and a narrower coracosternal connection. In all of these characters, as well as in the general proportions of the skeleton, the fossil resembles the murres of the genus *Uria*.

Uria brodkorbi new species
Figures 1–4

Holotype.—PB7960, consisting of impressions of skull and anterior portion of skeleton on two slabs of diatomite. Slab PB7960A contains the skull in lateral aspect, and seven cervical vertebrae: slab PB7960B contains the incomplete furcula, sternum, coracoids, scapula, ribs and wing bones.

Plastotypes.—Latex molds made from the holotype PB7960A and PB7960B are stored with the holotype and at LACM.

Formation and age.—Sisquoc Formation, late Miocene, Clarendonian land mammal age.

Locality.—Johns Manville diatomite quarry near Lompoc, California. Collector and date of collection unknown.

Etymology.—The new species is named in honor of Dr. Pierce Brodkorb.

Diagnosis.—Premaxillary symphysis shorter than in *Uria aalge* or *U. lomvia arra,* closer to *U. lomvia lomvia.* Height of mandible at angular greater than in either Recent species of *Uria.* Sternum with broadly curved anterior margin, in contrast to straight contour dorsal to forward thrust of the carinal apex typical of Recent *Uria*; tip of carina more truncated and anterior carinal margin more protruded anteriorly. Coracoid with well developed procoracoid as in Recent *Uria,* but with the tip sharper and more upturned; scapular facet more deeply cup-shaped than in *U. aalge,* and rounder, less oval than in *U. lomvia*; glenoid facet broader than in either Recent species. Humerus with area below head narrowed by flange extending mediad from pectoral attachment below external edge of head, and, internally, by raised area marking medial extent of capital groove; line of M. latissimus dorsi anterioris not paralleling shaft as in Recent species of *Uria,* but slanting palmad from distal edge of pectoral scar along external side of shaft, nearly 20 mm in length. Distal metacarpal symphysis of carpometacarpus with metacarpal III sloping distad rather than forming distinct right angle as in *U. aalge*; closer to *U. lomvia,* but distal margin more raised.

Measurements (in millimeters).—Because of the condition of the specimen, many of the measurements are based on the latex mold, with the skeletal impressions used as a check. At best all measurements are approximate.

Skull: Greatest length 93.6; length of rostrum 53.0; length of premaxillary symphysis 25; greatest height of mandible 12.5.

Sternum: Length from carinal apex to tip of posterior lateral process 122; height from carinal apex to ventral lip of coracoidal sulcus 36.

Fig. 1. *Uria brodkorbi*, holotype in diatomite slabs PB7960A (top) and PB7960B (bottom). Lighting of photograph makes impressions appear in relief. Length from tip of beak to posterior tip of sternum 338 mm.

Fig. 2. *Uria brodkorbi*, holotype slab PB7960B showing impression on left side. Depending on the angle viewed, the skeletal elements appear raised or impressed. Length of complete carpometacarpus 47.5 mm.

Coracoid: Length from foremost (anterior) edge of coracohumeral surface to external tip of sternal facet 42.5; depth of shaft to tip of procoracoid 11.5; breadth of glenoid facet 6.5; length of glenoid facet 8.0; distance from procoracoid to foramen 6.6.

Humerus: Greatest length 90 approx.; breadth of proximal end across external and internal tuberosities 18; proximodistal height of head 7; length of pectoral attachment through external tuberosity 12; greatest breadth of pectoral attachment 4; greatest distance from distal end (externally) to point of contact of ectepicondylar prominence with shaft 12.3; depth of external side of distal end 8.0; depth of shaft above distal end 7.5.

Ulna: Depth of distal end, externally, 8.0.

Radius: Length 66 approx.

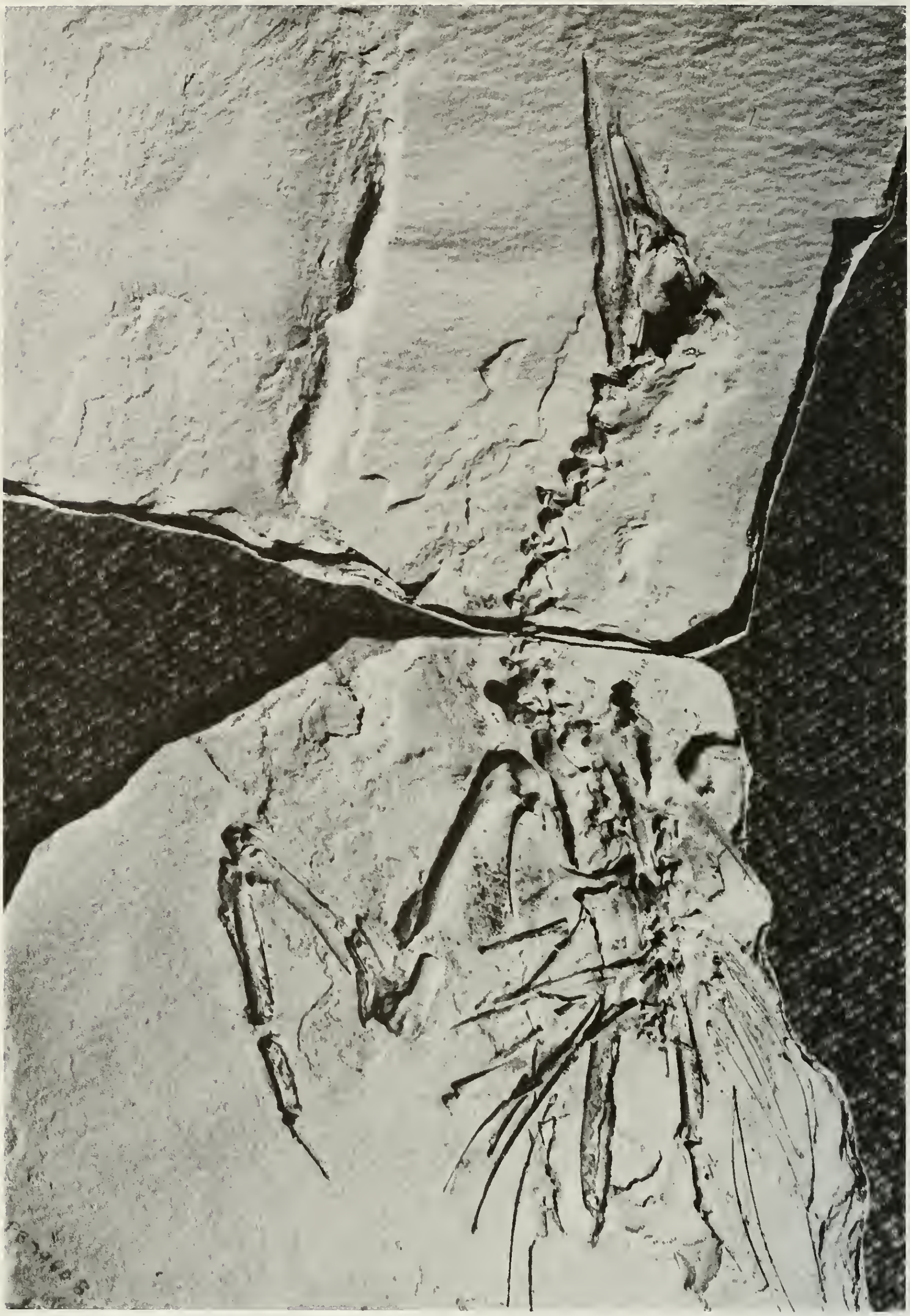

Fig. 3. *Uria brodkorbi,* latex molds of holotype showing left side. Length from tip of beak to posterior tip of sternum 338 mm.

Fig. 4. *Uria brodkorbi,* humerus on latex mold of holotype. Approximately natural size.

Carpometacarpus: Greatest length, externally, 47.5; length of process of metacarpal I, 9.3; depth of distal end from internal tuberosity of metacarpal II through distal metacarpal symphysis, measured on right carpometacarpus, 8.0.

Wing phalanges: Lengths: digit I, phalanx 1, 21.2; digit II, phalanx 1, 20.8; digit II, phalanx 2, 21.5; digit III, phalanx 1, 9.3.

Description.—As exposed on the diatomite slabs and shown in the latex molds, the left side of the skull and sternum and the elements of the left side of the skeleton are best preserved.

Although the cranial part of the skull is incompletely preserved, the rounded posterior contour of the supraoccipital and the narrow, sharply ridged temporal fossa are distinguishable. The latex mold (Fig. 3) defines the extent of the short beak, which more closely resembles that of *Uria l. lomvia* than any of the adult specimens of either *U. l. arra* or *U. aalge* at hand. The mandible depth is even greater than in *U. l. arra* (see Table 1).

The position of the furcula is indicated on holotype slab PB7960B by two holes anterior to the coracoids. Filled with latex in preparing the molds, the poorly defined tips appear, but reveal no dependable characters.

The sternum is damaged posterior to the coracoidal sulcus, and the area of the costal ridges is pushed forward and folded onto the carina so that from this point to the posterior end the dorsal surface is exposed. Because of this damage, the total length as measured on the specimen (and given above) could be as much as 10 mm less than the actual length of the sternum. The anterior contour of the carina shows clearly in lateral view (Fig. 2) as a broad arch, in contrast to the straight contour dorsal to the forward thrust of the apex typical of the Recent species of *Uria*. Further distinctions lie in the more truncated tip and the more forward-protruding flange along the anterior carinal margin. Only one Recent specimen of murre (*U. aalge californica*, LACM 674) has a suggestion of these characters.

The brachial tuberosity is poorly shown on the right coracoid, and is not visible on the left, which is otherwise better preserved. The glenoid facet is relatively broader than in the modern species of *Uria*. The scapular facet is deeper than in *U. aalge,* being closer to *U. lomvia* in this respect, though more rounded, rather than oval. The length of the procoracoid resembles the condition in Recent *Uria,* but the projection is sharper and more upturned than in most of the specimens examined (see Fig. 2). The small foramen is well below the tip of the procoracoid; the size and position of the foramen is variable in the sample of specimens of the Recent species. Although the sternal facet of the coracoid is not exposed, the shape of the coracoidal sulcus of the sternum suggests that the sternal end of the coracoid is long and narrow as in *Uria,* with the facet possibly even more laterally extensive than in the Recent species. This condition is in contrast to that found in the puffins, or even in *Alca,* in which this articular surface is shorter and deeper.

The left scapula is incompletely revealed in ventral view (Fig. 2). Neither the acromion nor the coracoidal articulation is visible, and the shape of the glenoid facet is not clear.

The broken left humerus (Fig. 4) lies with the proximal end presenting an aspect slightly lateral of anconal, while the distal fragment is turned so as to expose more of the external side. The proximal end of this element shows the most notable differences from the Recent species of *Uria*. As observed in the latex mold (Fig. 4), the pectoral attachment is broad, with a distinct flange extending below the head, narrowing the area between the attachment and the median crest; the head appears to be less sharply undercut. A flange of variable extent occurs in a few specimens of both *U. aalge* and *U. lomvia,* but in none is it as strongly developed or as evenly contoured as in the fossil. The line of the anterior latissimus dorsi muscle in *U. brodkorbi* is as long as in Recent *Uria,* but the slope is more markedly palmad and is emphasized by the more rounded anconal aspect of the shaft. Distally, the external tricipital groove is sharply rimmed; the entepicondyle is incomplete and the width of the internal groove is not clear. However, the slight anconal flare toward the distal end, as shown in the latex mold (see Fig. 3) suggests that the internal groove is broader than the external, thus resembling the condition in *Uria*. This contrasts with *Alca* in which the anconal contour of the shaft bends palmad, and the two grooves are of equal size. The tip of the ectepicondylar process is more prominent than in most specimens of Recent *Uria*. There is, however, considerable variation in the Recent series, and a few specimens approach the same prominence, although only one (of maximum size) is as elevated above the distal end, and the ectepicondylar process is less vertically placed with respect to the shaft.

The ulna and radius are crushed proximally, and provide little information other than approximate length of the radius.

The external side of the complete left carpometacarpus, and the internal side of the distal end of the right carpometacarpus are exposed. In overall length, as well as in the length of the process of metacarpal I, the element falls within the size range of *U. l. arra* (see Table 1). The rounded distal contour of metacarpal III (see Fig. 2) is approached in some specimens of *U. lomvia*.

Comparison with previously recorded fossil Alcidae.—Three extinct species of *Uria* have been previously described, each on the basis of the humerus: *Uria* *antiqua* (Marsh 1870) from the Lower Pliocene of North Carolina; *U. affinis* (Marsh 1872) from the Pleistocene of Maine; and *U. ausonia* Portis 1887 from the Pliocene of Italy. *U. ausonia* is based only on the distal end of a humerus, which I have not examined.

A cast of the holotype of each of the other two species is available. Both are longer than the humerus in the holotype of *Uria brodkorbi* (*U. antiqua* length 96.2 mm, *U. affinis* length 95.0 mm as given by Marsh (1870 and 1872), and closely approximated on the casts), with greater breadth between the pectoral attachment and the median crest. Both also have the line of M. latissimus dorsi anterioris paralleling the shaft as in Recent species of *Uria,* in contrast to *U. brodkorbi* in which the muscle line slopes palmad. *U. affinis* further resembles Recent *Uria,* distally, in the unequal breadth of the tricipital grooves, the internal being wider, as appears also to be true of *U. brodkorbi*. In *U. antiqua* the grooves are of equal breadth. The humerus of *U. antiqua* resembles that of *U. brodkorbi* in the rounding of the shaft toward the proximal end, although the shaft is heavier and the apex more anconal in position in *U. antiqua*.

There is one previous tentative record (Howard 1978) of *Uria* from the Miocene of California. The record is based on an incomplete proximal end of a humerus (LACM 52018) from locality LACM 6902 in the late Miocene Monterey Formation of Orange County. The specimen is slightly smaller than the humerus of the approximately contemporaneous *U. brodkorbi,* lacks the flange from the pectoral attachment to the head, and is more excavated below the head. It resembles the humerus of *U. brodkorbi,* however, in the rounding of the shaft and the palmad trend of the line of M. latissimus dorsi anterioris.

Two extinct genera are worthy of consideration in comparison with *U. brodkorbi*: *Australca* Brodkorb 1955, genotype *A. grandis* from the Middle Pliocene Bone Valley Formation of Florida; and *Miocepphus* Wetmore 1940, genotype *M. mcclungi* from the Middle Miocene Calvert Formation of Maryland. The holotype of *A. grandis* is a coracoid, with humerus, radius, ulna, carpometacarpus and tibiotarsus referred (Brodkorb 1955). The holotype of *M. mcclungi* is a humerus. This and a subsequently referred humerus (Wetmore 1943) from the type locality are the only recorded specimens of *Miocepphus*.

Through the kindness of Dr. Storrs L. Olson, of the National Museum of Natural History, specimens that he considers referable to *Australca* and *Miocepphus* have been made available (see Comparative Material above). The *Australca* material is similar in size to measurements given for *A. grandis* (Brodkorb 1955), but is not from the type locality. The *Miocepphus* humerus, however, comes from the same formation as the holotype of *M. mcclungi,* though in Zone 13 of the Calvert Formation (the type is from Zone 12). The specimen is intermediate in size between the holotype (Wetmore 1940) and the referred specimen (Wetmore 1943) of *M. mcclungi,* both of which are markedly smaller than the humerus of *U. brodkorbi.* As size is not a generic character, the specimens of both *Australca* and *Miocepphus* are analyzed on the basis of their qualitative characters.

The major distinction of the *Australca* coracoid from that of *U. brodkorbi* lies in the more posterior position of the procoracoid (inset from the median edge of the coracoidal shaft). This character is shown clearly in both the referred specimen at hand and in the illustration of the holotype (Brodkorb 1955:50, fig. 24).

Table 1. Measurements (in mm) of holotype of *Uria brodkorbi* and comparable elements of *U. lomvia* and *U. aalge*.*

		U. l. lomvia (2)		*U. l. arra* (10)			*U. a. inornata* (6)			*U. a. californica* (17)		
Element	*U. brodkorbi*	Max.	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.
Skull												
Greatest length	93.6	95.0		108.9	104.7	101.0	107.2	102.2	97.2	110.2	104.6	100.3
Premaxillary symphysis**	25.0	21.7		27.7	25.0	23.3	30.1	28.0	26.2	31.7	28.6	25.5
Greatest height mandible	12.5	11.0		11.8	11.2	10.7	10.4	9.3	8.6	11.0	10.0	9.1
Coracoid												
External length**	42.5	41.8	41.4	47.9	45.9	44.6	42.0	41.7	41.1	43.2	40.4	39.4
Depth to procoracoid**	11.5	11.0	9.7	12.0	11.2	10.5	11.3	10.5	10.0	11.2	10.4	10.0
Breadth glenoid facet	6.5	5.6	3.5	6.4	5.6	5.2	5.7	5.3	4.8	5.6	5.1	4.7
Humerus												
Greatest length	90 approx.	89.9	85.7	99.3	93.4	86.3	88.5	87.6	87.0	91.8	87.6	83.3
Proximal breadth**	18.0	17.4	16.4	18.5	17.7	17.0	17.2	16.8	16.3	17.4	16.5	16.2
Ectepicondylar prominence**	12.3	11.1	11.0	12.3	11.6	11.0	11.5	11.2	11.0	11.3	10.9	10.0
Radius												
Length	66 approx.	65.3	64.0	72.2	68.9	65.8	65.2	62.7	61.8	66.4	63.6	61.0
Carpometacarpus												
External length	47.5	44.3	44.0	49.1	47.6	45.4	45.7	44.4	43.1	46.8	44.4	43.4
Length process metacarpal I	9.3	8.1	7.4	9.4	8.5	8.0	8.6	7.8	7.3	8.8	7.9	7.5

* Numbers in parentheses indicate number of specimens measured (for *U. l. lomvia*, only one skull available).

** See *Measurements* under Systematics for explanation of areas measured.

With respect to this character comparison with *U. brodkorbi* is best observed on the right coracoid of the holotype in which the close proximity of the lower end of the procoracoid to the median edge of the shaft is discernible on the latex mold. In the humerus of *Australca,* the area below the head is broader and the pectoral scar longer and relatively flatter than in *U. brodkorbi*; distally the apex of the ectepicondylar process is more prominent and forms a more acute angle with the shaft. Although the *Australca* carpometacarpus resembles that of *U. brodkorbi* in the long process of metacarpal I, the angle between the process and the external trochlear crest is less acute. *U. brodkorbi* resembles the Recent species of *Uria* in this character.

The humerus of *Miocepphus* is similar to that of *U. brodkorbi* in having a flange from the pectoral attachment narrowing the area below the head. The attachment itself, however, is flatter and less ovoid, and the external tuberosity is less prominent anconally. The line of the M. latissimus dorsi anterioris slopes slightly palmad, as in *U. brodkorbi,* but it is shorter. Distally, the tricipital grooves are equal in size as in *Alca,* as distinguished from the condition in *Uria.* The ectepicondylar process is even more prominent than in *Australca,* and terminates in a distinct papilla.

Summary and Conclusions

The holotype skeletal impression of *Uria brodkorbi,* transformed by latex molds into bones in relief, provides a rare opportunity to study the morphology of the associated elements of one individual fossil bird.

Viewed as a whole, the skeleton resembles that of the murres, genus *Uria.* In relation to Recent species of the genus it appears to have been of sturdier build, with a stronger sternum and a short beak. Although in length the coracoid and humerus are within the size range of *U. aalge californica* (see Table 1), the breadth of these elements equals or surpasses those of the larger *U. lomvia arra.* The carpometacarpus is similar to some specimens of *U. lomvia* in the rounding of the distal end of metacarpal III, and closely resembles *U. l. arra* in size.

Some of the individual elements, if found isolated, might well suggest generic distinction from Recent *Uria.* This is particularly true of the sternum and humerus. However, the large series of modern skeletons studied reveals trends toward one or more of the apparently distinctive characters. Although no single Recent skeleton of *Uria* has a combination of characters matching those of the fossil, there is sufficient similarity within the comparative series to indicate that *U. brodkorbi* is entirely consistent with what would be expected in a Miocene ancestor within the genus.

Therefore, the evidence weighs in favor of the new species being retained in the genus *Uria,* rather than in the erection of a new genus.

Acknowledgments

I am especially indebted to Pierce Brodkorb for the opportunity to study this important specimen from the Sisquoc Formation, and for providing the photograph taken by Robert D. Weigel (Fig. 2). I am also deeply grateful to my husband, Henry Anson Wylde, for preparing the latex molds of the specimen and for photographing Figures 1, 3 and 4. Richard Meier (LACM) assisted by making the excellent print of the photograph for Figure 1.

My thanks are also extended to Storrs L. Olson, Stuart L. Warter, Jean Geary and Diana Matthiesen for providing comparative material. My continuing appreciation is extended to members of the two science divisions of the Natural History Museum of Los Angeles County for their cooperation.

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Reproduction of the Onespot Fringehead, *Neoclinus uninotatus*, in Monterey Harbor, California

David G. Lindquist

Abstract.—Reproduction of the onespot fringehead, *Neoclinus uninotatus* in Monterey Harbor, Monterey, California by David G. Lindquist, *Bull. Southern California Acad. Sci.*, 80(1):12–22, 1981. Males have greater development of the primary ocular cirrus. Nesting males were observed January to March and June to September. Males guarded large egg masses attached to the ceiling and sides

of the inner refuge. Eggs were 1 to 1.3 mm in diameter with one large yellow-orange oil droplet. Larvae hatched at a total length (=notochord length) of 5 mm.

Introduction

Except for the pioneering studies of Carlisle, Turner and Ebert (1964) and Turner, Ebert and Given (1969) on man-made artificial reefs and the work of Stephens and his associates on King Harbor fishes (Terry and Stephens 1976; Stephens and Ellison 1977; Ellison, Terry and Stephens, 1979; Ehrlich et al. 1979; Stephens 1978), little attention has been paid the life histories of the fishes living in and around man-made structures in California's marine environment. Furthermore, these previous studies have been designed primarily to define the effects of man-made alterations of the marine environment on the fish community as a whole. My report is a preliminary analysis of reproduction in a population of *Neoclinus uninotatus* using a man-made wharf habitat.

The natural history of the three California species of the genus *Neoclinus* is poorly known. Only a few minor observations of these fishes in nature have been published (Stephens et al. 1970 on *N. stephensae* and Feder, Turner and Limbaugh 1974 on *N. uninotatus, blanchardi* and *stephensae*). The most detailed studies of the species of this genus were published by Japanese workers (Shiogaki and Dotsu 1972; Fukao 1980).

Methods and Materials

A total of 26 SCUBA dives (30.6 hours) was made under the Monterey Wharf #2 to observe and record populations of the onespot fringehead between June 1969 and June 1971. Most observations (17 hours) were conducted during the last eight months of the study. During various phases of the study, specimens were collected using quinaldine, an anesthetic, mixed with ten parts of 70% isopropanol (Gibson 1967; Stephens et al. 1970).

The study was conducted at the east end of the wharf (Fig. 1). Haderlie and Donat (1978) have prepared a detailed description of the configuration and construction of the wharf.

To facilitate behavioral observations, a square grid was constructed of lines and cinder blocks in the study area (Fig. 1). The grid measured 15 m on a side and was subdivided into nine 5 × 5 m squares. I placed the grid 15 m east of the wharf pilings on a flat, relatively barren sand bottom in 10 m of water during November 1970. The three subsquares closest to the wharf initially contained 30 bottles, three of which housed one each *N. uninotatus*. These three subsquares served as the experimental habitat, whereas the six subsquares furthest from the wharf remained undisturbed during the study. From December 1970, to March 1971, 32 adult (size range = 100–180 mm TL, $\bar{x}$ = 134 mm TL) *N. uninotatus*, within their refuges, and 195 clean bottles and jars (orifice diameter range = 16–28 mm, $\bar{x}$ = 18 mm), were placed randomly within the three experimental subsquares. Care was taken to place the orifices of the refuges level with the substratum to encourage use of them by *N. uninotatus*. The locations of individuals were marked on a prepared map of the grid.

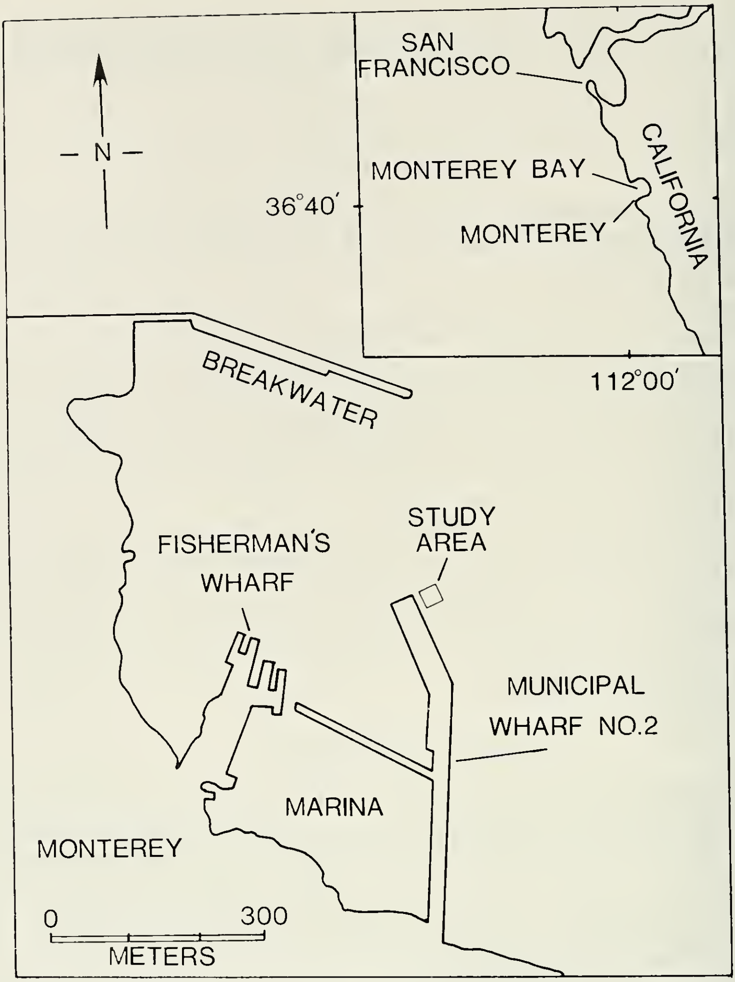

Fig. 1. Configuration of Monterey Harbor in relation to the study area.

Results and Discussion

Sexual dimorphism and function of the ocular cirri.—Although Clark Hubbs (1953) presented six morphometric comparisons of the sexes of *N. uninotatus* that indicated dimorphism, I was unable to use these to determine the sex of specimens in nature. Jordan and Evermann (1896–1900), in their description of *N. uninotatus* (misidentified as *N. blanchardi*), pointed out that males had an ocular cirrus that was twice as long as the female's. Hubbs (1953) did not treat the ocular cirri in his account. However, his illustrations (Figs. 13 and 14) clearly indicate sexual differences in the ocular cirri development. I found the length and amount of branching in the primary ocular cirrus to be a reliable method of sexing individuals in nature.

The male's primary ocular cirrus is not only longer but is also wider with more branching at the cirrus tip (Fig. 2). I devised a cirrus index (product of cirrus length and number of primary and secondary distal cirrus branches) as a measure

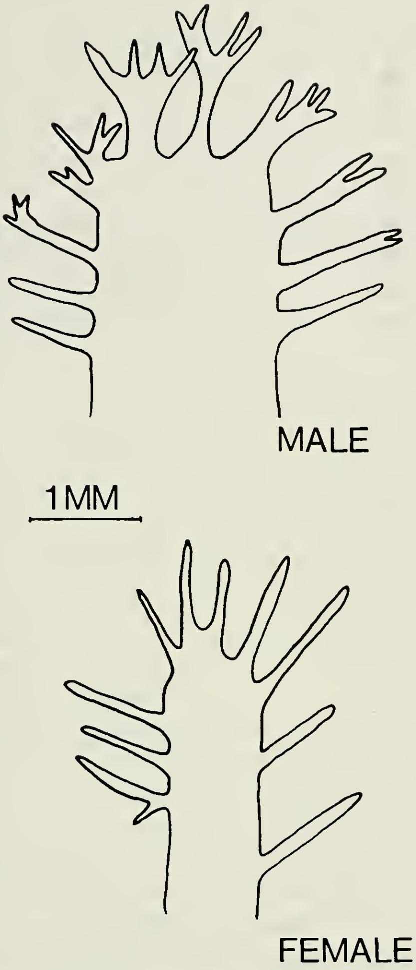

Fig. 2. Tips of the primary ocular cirri for both sexes of *N. uninotatus*. Both male and female measured 120 mm SL: length of male's cirrus is 11 mm and female's is 6 mm. Total branching for male is 27 and for female is 11.

of cirrus development. A plot of the cirrus index on standard length indicates a greater and more rapid development of the male's cirri (Fig. 3). The cirrus index of males appears more closely related to standard length as suggested by the regression coefficient, r. However, additional data are needed for females.

J. S. Stephens, Jr. and H. D. Hickman, Jr. (Occidental College, pers. comm.) found *N. uninotatus* males in southern California with a mean primary orbital cirrus length of 1.7 orbits, never shorter than one orbit and females with a mean of 0.6 orbits, never greater than one orbit. They also found the male's cirrus was stouter and the branching was more palmate, distally. Randall (1966) presented data indicating that the number of ocular cirri of *Hypleurochilus aequipinnis* also increase with size.

The tropical blennioid families Labrisomidae, Clinidae, Blenniidae, and Chaenopsidae, are notable for the various development of cirri over the head (nasal,

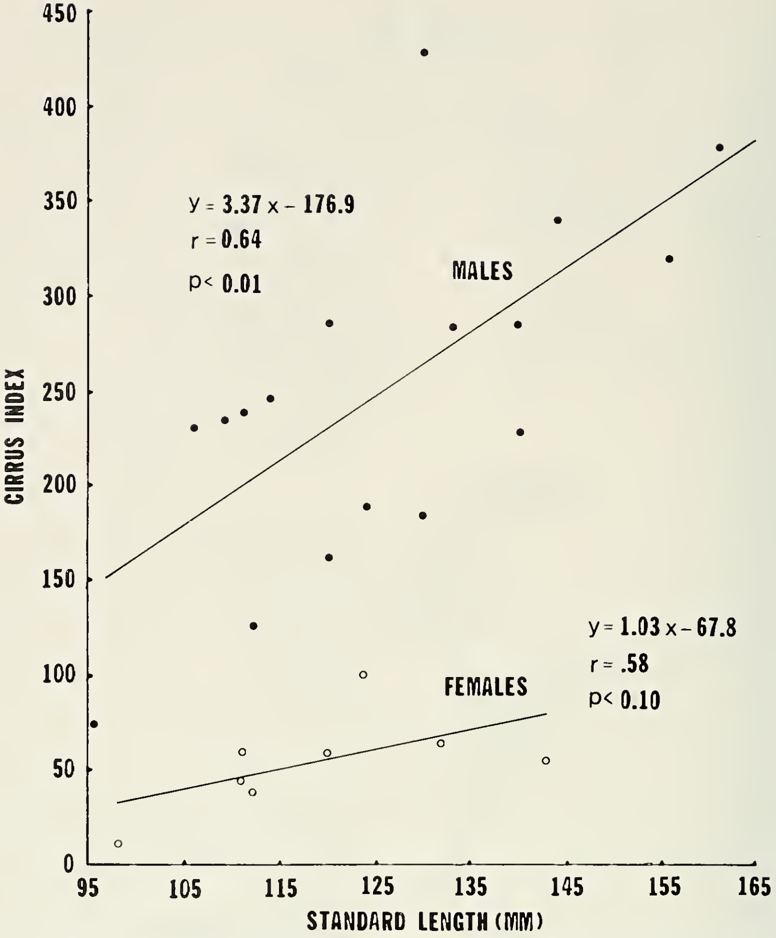

Fig. 3. Least squares regression analysis of cirrus development and SL for both sexes of *N. uninotatus*.

ocular and nape cirri). However, the functional significance of cirri in blennies has been unstudied, by and large, by previous workers. Springer and Gomon (1975) examined the total nape cirri of *Malacoctenus triangulatus* over its entire geographic range and reported an inverse relationship between nape cirri and lateral-line scales. Based on observations of Ford (1959), who reported the cirri of *Malacoctenus hubbsi* to be innervated by at least three cranial nerves, Springer and Gomon (1975) inferred a sensory function for the cirri and suggested that *M. triangulatus* compensates for the reduction in the lateral-line pores by an increase in the nape cirri. Evidence for a sensory function for the cirri is strengthened by the work of Schulte and Holl (1972), who found nerve bundles and sensory organs resembling taste buds in the ocular cirri of *Blennius tentacularis*.

Shiogaki and Dotsu (1972) describe the ocular cirri of *Neoclinus bryope* as "cryptic organs." Their photograph (Fig. 1) of both sexes also suggests that males have a greater development of the ocular cirri. Since male blennies, in general, spend much of their time resting with the head at the entrance of the refuge, it seems advantageous for selection to have favored a greater degree of camouflage (i.e. cirri development) for the male. The male's cirri blend in well with refuge encrusting bryozoans, hydroids, and algae, thus allowing the male a greater degree of crypticity and, thus, protection against predators while stationed at the entrance of the refuge. An alternative but non-exclusive hypothesis has been put forth by Zander (1975). He observed that the male's ocular cirri in four Mediterranean *Blennius* are significantly enlarged, especially during the breeding season. Zander reasoned that the enlarged cirri serve as sign stimuli that aid in attracting females to the spawning refuge. Still another possible function of the cirri is suggested by the fact that the form of the cirri is frequently species specific, such that the shape of the cirri often serve as diagnostic characteristics. Blennies, thus, may also recognize conspecifics at least partially on the basis of the form of the cirri.

Spawning season.—A total of 16 nests, each guarded by a single male, were found in the study area during 12 SCUBA dives as follows: one in January; two in February; one in March; eight in June; one in August; and three in September. Observations at the wharf were made during all months of the year except May. These preliminary observations suggest that the wharf population has either a protracted spawning season from January to September with peak activity in early summer or two separate spawning seasons: January to March; and June to September. At present, I am inclined to favor the latter hypothesis because my observations of 24 mature males in refuges during four SCUBA dives in April revealed none guarding eggs.

Feder et al. (1974) report *N. uninotatus* spawning in April and May. However, the location(s) of these observations is (are) not stated. The observations were made by the late Conrad Limbaugh (J. S. Stephens, Jr., pers. comm.) and could have been made as far north as Monterey Bay but were more likely to have taken place in southern California (i.e. San Diego and Orange Counties), where most of his intensive observations were made (Feder et al. 1974). J. S. Stephens, Jr. and H. D. Hickman, Jr. (pers. comm.) have observed gravid females of *N. uninotatus* from late January through at least September and with males guarding eggs in July off Redondo Beach in Los Angeles County.

Neoclinus blanchardi, the closest relative of *N. uninotatus,* spawns from January through August (Feder et al. 1974). Shiogaki and Dotsu (1972) report intertidal spawning for *N. bryope* during January to April, with peak activity in March and April in Nomozaki, Japan (32°35′N latitude). Feder et al. (1974) report the young of *N. stephensae* in August and September.

Nesting behavior.—In all cases, the 16 nesting males observed in nature were guarding eggs located within glass bottles or, in one case, a glass jar. Although the volume of the containers varied from approximately 0.5 to 2.0 l, most had larger orifices (e.g. 25–30 mm). The outisde of the glass containers were variously encrusted with sessile invertebrates. The refuges were embedded one to two cm into the substratum such that the bottom of the orifice was level with the substratum. Eggs were deposited in large thick masses within the center section of the refuge. The eggs adhered to the ceiling and side walls of the refuge by means of adhesive filaments. The male positioned his body among the eggs with only the head protruding from the refuge. If the refuge was lifted by the diver, the male would depart but would return soon after the refuge was replaced.

In January 1971, I discovered a male and female within a one-half l bottle. Both fish were approximately 140 mm in total length. This was the first evidence of spawning since September 1970. Eggs were present in one small opaque mass and adhered to the ceiling and one side of the bottle. Close inspection revealed the eggs to be in a very early stage of development, indicating that the egg mass had been laid recently. The size of the egg mass was estimated at 60 by 30 mm and 15 mm thick. Shortly after I disturbed the pair, the female was forced from the refuge by the male. One month later I returned and removed the male and his refuge to the laboratory for study. The egg mass now covered the entire ceiling and portions of both sides of the refuge. Three distinct developmental stages were present within the egg mass. The most developed embryos had fully formed eyes and the tail overlapped the head. I estimated the total number of eggs present at 15,350 by the volumetric method (Lagler 1956). The male remained with the egg mass in the aquarium and fanned the eggs with his pectoral fins at a variable rate of 34 to 71 beats per minute ($\bar{x} = 50$, $N = 10$). Many of the eggs were later attacked by fungus and none hatched.

Shiogaki and Dotsu (1972) reported that *Neoclinus bryope* spawned within the dead tubular vermetid gastropod shells of *Serpulorbis imbricatus*. These eggs were deposited in a single layer on the inner walls of the tube and were also guarded by the male. Egg clusters consisted of a maximum of five different developmental stages and eggs ranged in number from 90 to 250.

Within the Blennioidea, the habit of living and spawning within tubular refuges occurs in some of the blenniids (Abel 1962, 1964; Fishelson 1975; Losey 1968, 1976; Wickler 1965), in many of the chaenopsid blennies (Robins, Phillips and Phillips 1959; Böhlke and Chaplin 1968; Kerstitch 1971; Lindquist 1971, 1975; Thomson, Findley and Kerstitch 1979; Longley and Hildebrand 1940, 1941; Stephens, Hobson and Johnson 1966), and in a few labrisomids, namely *Paraclinus marmoratus* (Breder 1939, 1941) and the species of *Neoclinus* (Feder et al. 1974; Fitch and Lavenberg 1975; Lindquist 1971; Shiogaki and Dotsu 1972; Fukao 1980). Although spawning within a refuge of some sort (below a stone or in a cave, etc.) seems to be the general rule for the blenniids (Wirtz 1977), such is not the case for clinids and labrisomids. Most clinids and labrisomids studied are either live bearers or open substrata spawners (Wirtz 1977). The few tripterygiids studied are apparently divided between cavity spawning and open substrata spawning (Wirtz 1977, 1978; Thomson et al. 1979). Unfortunately, because the spawning behavior and general habits of too few species of the five aforementioned blennioid families have been studied, it would be premature to attempt any broad implications of evolutionary relationships based on these characteristics.

However, *Neoclinus* does occupy a unique position among the labrisomids because of its tubiculous habits. (The sponge dwelling habits of *Paraclinus marmoratus* appear to be a special case.) The tube dwelling habits of *Neoclinus* would then seem to align this genus more closely with the blenniids and chaenopsids than with the labrisomids and clinids. Indeed, Hubbs (1952, 1953) placed *Neoclinus* in the subfamily Chaenopsinae and family Blenniidae. Later taxonomic revisions removed *Neoclinus* to the Clinidae (Springer 1955; Böhlke 1957) and elevated the chaenopsins to family level (Stephens 1963). In doing so, *Neoclinus* was considered to be the closest relative of the clinid ancestor that gave rise to the chaenopsids (Stephens 1961, 1963; Stephens and Springer 1971). George and

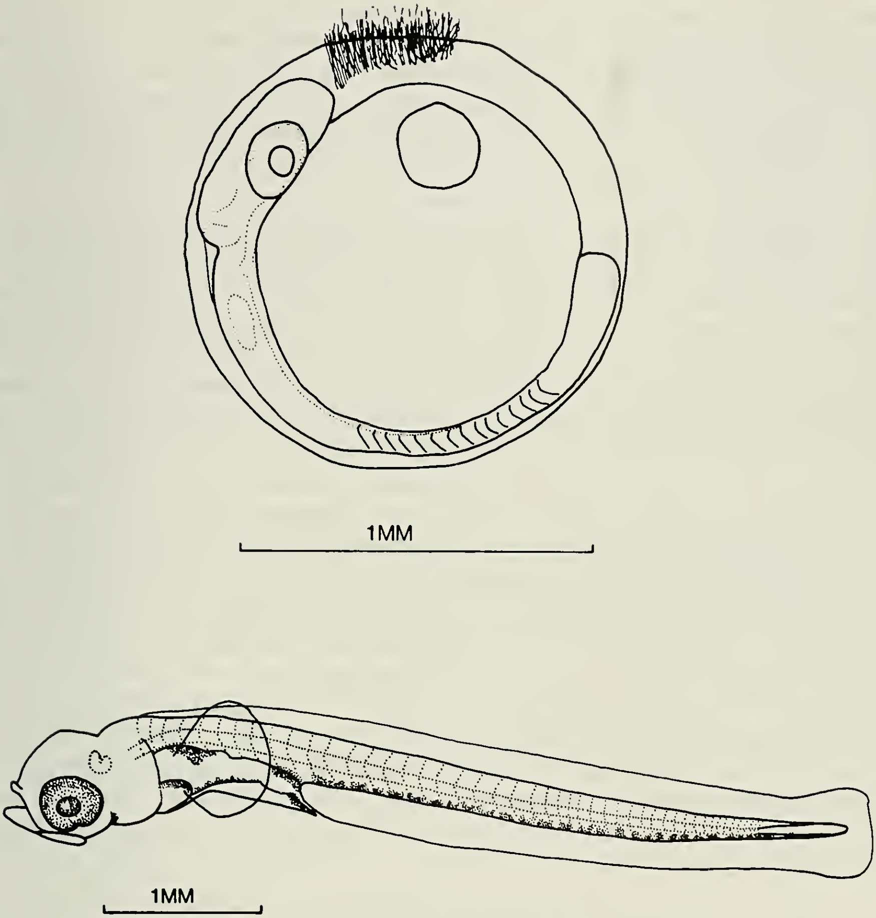

Fig. 4. An intermediate stage egg and preflexion larva of *N. uninotatus*.

Springer (1980) elevated the subfamily Labrisominae, to which *Neoclinus* presumably belongs, to family rank. Although the higher classification of the tropical blennioid groups is still tentative and subject to controversy (Böhlke and Robins 1974; Rosenblatt and Stephens 1978), I believe that the close position of *Neoclinus* to the chaenopsids and blenniids is suggested by their similar tube dwelling habits.

Egg and larval description.—The eggs of *N. uninotatus* range in size from 1 to 1.32 mm in diameter ($\bar{x}$ = 1.19, N = 60). The eggs are spherical and sometimes slightly indented when packed tightly together. Each egg has many adhesive filaments by which it attaches to other eggs or to the substrata. A single large yellow-orange oil droplet is present and ranges in size from 0.25 to 0.33 mm in diameter ($\bar{x}$ = 0.28 mm, N = 30). Other much smaller oil droplets are also present. An intermediate stage egg with a larva having 14 myomeres is illustrated in Figure 4. Melanophores begin to develop ventrally along the post-anal myomeres shortly after passing the 14-myomere stage.

Eggs were hatched in the aquarium shortly after removal from nature. The length of the development period in nature was not determined. The larvae swam near the top of the aquarium, suggesting that they were photopositive. The larvae hatched at an advanced stage of development (Fig. 4). Little yolk remained in the yolk sac at hatching. Dense melanophores are located dorsal to the heart, air bladder, and rectum, as well as ventral to the liver and rectum. A series of 29–32 small melanophores is present along the ventral margin of the myomeres. The myomere count 11 + 34–36 = 45–47.

The 14-myomere stage of *N. uninotatus* and *bryope* (Shiogaki and Dotsu 1972) differ in respect to: 1) the head shape of the embryo; 2) the number of smaller oil droplets in the egg; 3) the presence of Kupfer's vesicles in *N. bryope*; 4) the development of the eyes; and 5) the size of the egg. The dorsal head profile of *N. bryope* is slightly pointed compared to the flat profile of *N. uninotatus*. There are 18 smaller oil droplets in the yolk of *N. bryope* compared to two or three in *N. uninotatus*. Kupfer's vesicle is not developed in the 14-myomere stage of *N. uninotatus*. The eyes are more completely developed in *N. uninotatus*. The eggs of *N. bryope* are slightly larger, 1.28 to 1.49 mm, than those of *N. uninotatus*.

The 5.5 mm larva (Fig. 4) of *N. uninotatus* compares with the 7.5 mm larva of *N. bryope* (Shiogaki and Dotsu 1972) but differs in the following respects: 1) size; 2) placement and number of melanophores; 3) myomere count; and 4) size of the pectoral fins. *Neoclinus bryope* has more myomeres (13 + 35–37 = 48–50), hatches at a larger size (6.6 mm compared to 5.0 mm), has a large melanophore over the yolk in the stomach, has fewer post-anal melanophores (17–20), and has a smaller pectoral fin. Shiogaki and Dotsu (1972) suggested that *N. bryope* spends a longer time in the plankton than other intertidal fishes because the juveniles attained a size of 25 to 29 mm (about one-half the adult size) before entering the benthic mode. The smallest benthic juvenile of *N. uninotatus* was 46 mm SL, suggesting that *N. uninotatus* may also have a lengthy planktonic stage.

Acknowledgments

This study is an expanded portion of my M.A. thesis conducted at the Moss Landing Marine Laboratories of the California State Colleges and Universities. I thank the members of my thesis committee (Nybakken, chairman, Tomlinson, and Yarberry) for their guidance and support. John S. Stephens, Jr., of Occidental College, shared his unpublished observations on *Neoclinus* and has been a source of encouragement and enthusiasm for this study.

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The Fish Population Associated with an Offshore Water Intake Structure

Mark Helvey[1] and Philip Dorn[2]

Abstract.—The fish population associated with an offshore water intake structure by Mark Helvey and Philip Dorn, *Bull. Southern California Acad. Sci.*, 80(1):23–31. This area off Southern California is described from underwater observations. The intake structure was monitored for a year and found to support a diverse population of water column and benthic oriented species. Many fishes resided at the intake year round while others were seasonal visitors. Several water column species including blacksmith, senorita, and jack mackerel interacted with the inwardly flowing water current for short periods of time. The most common response was a positive rheotaxis as they maintained station within the flow. Although the intake water current may be attractive to certain species exhibiting strong rheotactic beahvior it does not influence the composition of the intake fish community.

Introduction

Man-made structures function as artificial reefs when located in areas of the marine environment that lack natural bottom relief (Turner et al. 1969). Artificial reefs provide new sources of food and shelter, thereby concentrating fish in previously unsuitable areas. The majority of man-made structures have been intentionally established for enhancing local sport fisheries, although several studies have shown that industrial structures such as offshore platforms similarly serve this purpose (Carlisle et al. 1964; Treybig 1971; Hastings et al. 1976; Simpson 1977). Other types of industrial structures that may serve as artificial reefs are the cooling water intakes of coastal power generating stations. These intakes normally consist of large vertical concrete conduits which rise several meters above the surrounding sand bottom and are topped with a concrete lid (velocity cap) situated above the conduit opening. Seawater is drawn through the opening between the top of the conduit and velocity cap creating primarily a horizontal water current.

One distinction between cooling water intakes and other artificial reefs is that intakes continuously withdraw seawater which generates a constant water current moving towards the structure. The response to a water current or rheotaxis (Fraenkel and Gunn 1940) plays an important role in the ecology of several fishes (Arnold 1974) such as in the feeding behavior of planktivorous species (Hobson and Chess 1976, 1978; Stevenson 1972). The purpose of this investigation was to evaluate the fish population at an offshore cooling water intake structure and determine what kind of fishes responded to the water current of the intake.

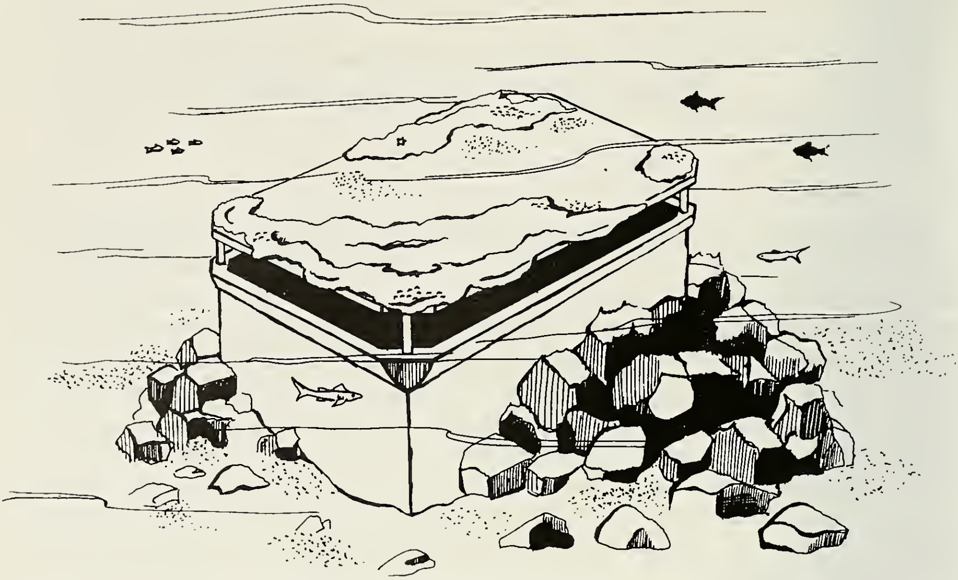

Fig. 1. The offshore cooling water intake structure with its adjacent rock boulder substrate.

Materials and Methods

Study Area

The offshore cooling water intake structure is located 300 m offshore of Redondo Beach, California, bordered by King Harbor on one side and the Redondo Submarine Canyon on the other side. The intake rests in 15 m of water and consists of a concrete conduit or riser bowl that rises 3 m above the ocean floor (Fig. 1). Scattered quarry rock strewn non-uniformly around the base of the riser bowl forms a 15 m radius of rip-rap. A concrete velocity cap is supported by concrete pillars 1.2 m above the top of the riser bowl. Water drawn into the opening has entrance velocities ranging between 48.8–100.6 cm/sec, averaging 73.7 cm/sec (Larson 1978).

Procedures

The fish population at the intake structure was sampled 33 times between September 1976 and August 1977 by SCUBA divers using a Super 8 mm underwater motion picture camera (Kodak XL 360). Each sample (cinetransect) consisted of six 10 m transect stations. Four extended diagonally from each corner of the intake and two extended perpendicularly from its two longer sides. Filming was accomplished between 0830 and 1200 hours by SCUBA divers swimming along each transect course just over the substrate up to the base of the structure. Artificial lighting was not used. The camera was tilted to film individual fish in the transect. When fish schools were encountered on the transect course, the camera was panned to include the entire group. Because cryptic and secretive fishes were not easily photograhed, numbers of such species within the transect course were recorded on a plastic slate by a second diver.

Analysis of movie films included species identification and their abundance as

Table 1. Summary of ANOVA (one-way) for seasonal and daily variation in species diversity.

	ANOVA				
Source of variation	df	SS	MS	F	P
Seasonal (among)	3	17.0	5.7	0.7	0.6
Daily (within)	28	236.8	8.5		
Total	31	253.9			

determined by use of slow motion and stop-action projection. More than 95% of the fish population recorded on film were identifiable. The fish community was analyzed for species diversity using species number (Poole 1974). Community structure was analyzed by combining the log of the proportionate abundance of each species with its frequency of occurrence into a single measure (Mason and Bryant 1974; Alevizon and Brooks 1975). Species were grouped into one of three categories based on frequency of occurrence per season:

A—species occurring in more than 67% of samples;
B—species occurring between 33–67% of samples;
C—species occurring in less than 33% of samples.

The log proportionate abundances were grouped into four categories:

1. relative abundance >100;
2. relative abundance between 10–100;
3. relative abundance between 1–10;
4. relative abundance <1.

The analysis classified each species into any one of 12 categories, ranging from A-1 (dominant species seen frequently) to C-4 (rare species seen infrequently).

The responses of fish to the intake water current were analyzed by divers during 245 minutes of additional observation during the study, between September 1976–January 1977. Individual fish moving into the flow area between the bottom edge of the velocity cap and the top of the riser bowl and extending 1.0 m horizontally out from the intake opening were observed and timed using an underwater watch. The amount of time an individual remained within the study zone was recorded on plastic slates.

Results

A total of 39 species was recorded at the intake structure either in the water column or exposed along the rock substrate surrounding the intake. The number of species encountered seasonally ranged from 26 species in the spring to 29 species during the winter. Results of a one-way ANOVA showed no significant difference ($P > .05$) for species diversity between quarters (Table 1).

Total fish densities varied between seasons with highest densities occurring during the winter and summer seasons (Table 2). This principally reflected the large recruitment of juvenile blacksmith, *Chromis punctipinnis*, in the winter months and the seasonal residence of shiner surfperch, *Cymatogaster aggregata*, during the summer months.

The blacksmith, the senorita, *Oxyjulis californica*, and the blue rockfish, *Se-*

Table 2. Comparative composition of the diurnal fish population at the water intake between September 1976 to August 1977. Species are ranked according to abundance/frequency categories. (See text for definition of categories.) Mean daily abundance per season and percent proportionate abundance (in parentheses) follow each species. Asterisks (*) indicate percentages less than 0.01.

Abundance/ Frequency Category	FALL Sept. - Nov.			WINTER Dec. - Feb.			SPRING March - May			SUMMER June - Aug.		
A-1	*Chromis punctipinnis*	475.0	(56.42)	*Chromis punctipinnis*	1382.9	(65.10)	*Chromis punctipinnis*	365.8	(64.83)	*Cymatogaster aggregata*	2234.7	(73.41)
	Trachurus symmetricus	175.3	(20.82)	*Trachurus symmetricus*	310.7	(14.60)	*Oxyjulis californica*	77.3	(13.70)	*Chromis punctipinnis*	586.1	(19.25)
	Sebastes mystinus	86.8	(10.31)	*Oxyjulis californica*	236.6	(11.14)						
A-2	*Oxyjulis californica*	35.0	(4.16)	*Sebastes mystinus*	127.2	(5.99)	*Sebastes mystinus*	54.5	(9.66)	*Sebastes mystinus*	59.1	(1.94)
	Hypsurus caryi	10.9	(1.29)				*Paralabrax nebulifer*	3.8	(0.68)	*Oxyjulis californica*	49.4	(1.62)
	Phanerodon furcatus	10.7	(1.27)							*Sebastes dallii*	30.7	(1.01)
	Damalichthys vacca	10.2	(1.21)									
A-3	*Sebastes dallii*	6.9	(0.82)	*Paralabrax clathratus*	19.7	(0.93)	*Sebastes dallii*	5.5	(0.97)	*S. serranoides*	23.8	(0.78)
	S. serranoides	4.3	(0.51)	*Sebastes serranoides*	7.3	(0.34)	*Coryphopterus nicholsii*	4.8	(0.86)	*Hypsurus caryi*	16.2	(0.53)
	Coryphopterus nicholsii	1.5	(0.18)	*Paralabrax nebulifer*	5.3	(0.25)	*Paralabrax clathratus*	3.0	(0.53)	*Sebastes paucispinis*	7.3	(0.24)
				Coryphopterus nicholsii	4.3	(0.20)	*Sebastes serranoides*	2.2	(0.38)	*Coryphopterus nicholsii*	7.0	(0.23)
				Caulolatilus princeps	4.1	(0.19)	*Oxylebius pictus*	2.0	(0.35)	*Damalichthys vacca*	6.7	(0.22)
							Damalichthys vacca	1.8	(0.32)	*Phanerodon furcatus*	3.7	(0.12)
										Sebastes auriculatus	3.1	(0.10)
A-4			(0)	*Pimelometopon pulchrum*	2.1	(0.10)			(0)	*Oxylebius pictus*	3.0	(0.09)
				Oxylebius pictus	2.0	(0.09)				*Embiotoca jacksoni*	2.1	(0.07)
				Sebastes caurinus	1.6	(0.07)				*Sebastes caurinus*	2.1	(0.07)
B-1			(0)			(0)			(0)			(0)
B-2			(0)			(0)			(0)			(0)
B-3	*Caulolatilus princeps*	1.7	(0.20)	*Phanerodon furcatus*	7.1	(0.33)	*Sebastes caurinus*	2.2	(0.38)			(0)
	Paralabrax clathratus	1.2	(0.14)	*Damalichthys vacca*	4.1	(0.19)	*Pleuronichthys coenosus*	1.5	(0.27)			
	Sebastes caurinus	1.2	(0.14)				*Scorpaenichthys marmoratus*	0.7	(0.12)			
	Paralabrax nebulifer	1.1	(0.13)									
B-4	*Oxylebius pictus*	0.8	(0.09)	*Sebastes dallii*	2.0	(0.09)	*Pimelometopon pulchrum*	0.5	(0.09)	*Pimelometopon pulchrum*	1.7	(0.05)
	Sebastes auriculatus	0.8	(0.09)	*Pleuronichthys coenosus*	1.0	(0.05)				*Paralabrax clathratus*	1.1	(0.04)
	Scorpaenichthys marmoratus	0.7	(0.08)	*Sebastes auriculatus*	0.9	(0.04)				*P. nebulifer*	1.0	(0.03)
	Pimelometopon pulchrum	0.7	(0.08)							*Scorpaenichthys marmoratus*	0.7	(0.02)
C-1			(0)			(0)			(0)			(0)
C-2	*Hyperprosopon argenteum*	11.0	(1.31)			(0)	*Cymatogaster aggregata*	33.3	(5.91)			(0)
C-3	*Sebastes paucispinis*	2.7	(0.32)	*Sarda chiliensis*	2.6	(0.12)	*Trachurus symmetricus*	2.2	(0.38)			(0)
	Rhacochilus toxotes	2.0	(0.24)				*Lythrypnus dalli*	0.7	(0.12)			
C-4	*Embiotoca jacksoni*	0.6	(0.07)	*Hypsurus caryi*	0.9	(0.04)	*Sebastes auriculatus*	0.5	(0.09)	*Hyperprosopon argenteum*	2.4	(0.08)
	Medialuna californiensis	0.3	(0.04)	*Medialuna californiensis*	0.3	(0.01)	*S. serriceps*	0.3	(0.06)	*Sebastes rastrelliger*	0.4	(0.01)
	Pleuronichthys coenosus	0.2	(0.03)	*Scorpaenichthys marmoratus*	0.3	(0.01)	*Caulolatilus princeps*	0.2	(0.03)	*Girella nigricans*	0.3	(0.01)
	Lythrypnus dalli	0.1	(0.01)	*Cheilotrema saturnum*	0.2	(0.01)	*Neoclinus blanchardi*	0.2	(0.03)	*Pleuronichthys coenosus*	0.3	(0.01)
	Scorpaena guttata	0.1	(0.01)	*Hypsopops rubicunda*	0.2	(0.01)	*Porichthys sp.*	0.2	(0.03)	*Scorpaena guttata*	0.3	(0.01)
	Sebastes serriceps	0.1	(0.01)	*Lythrypnus dalli*	0.2	(0.01)	*Rathbunella hyplopecta*	0.2	(0.03)	*Lythrypnus dalli*	0.2	(0.01)
				Rhacochilus toxotes	0.1	(0.01)	*Rhacochilus toxotes*	0.2	(0.03)	*Caulolatilus princeps*	0.1	(*)
				Scorpaena guttata	0.1	(0.01)	*Scorpaena guttata*	0.2	(0.03)	*Rhinobatos productus*	0.1	(*)
				Cephaloscyllium ventriosum	0.1	(0.01)	*Sebastes rastrelliger*	0.2	(0.03)	*Sebastes serriceps*	0.1	(*)
				Cottidae sp.	0.1	(0.01)						
Total Species		27			29			26			28	
Total Numbers		841.9			2124.2			564			3043	
Samples		9			9			6			9	

Table 3. Fish displaying rheotropic behavior during 245 minutes of observation (n = 21). Species are listed alphabetically.

Species	No. of individuals	% frequency occurrence	Mean time within flow (sec) ± S.E.
Chromis punctipinnis	27	76	10.48 ± 1.98
Damalichthys vacca	9	38	6.78 ± 1.69
Hypsurus caryi	1	5	—
Medialuna californiensis	2	9	3.50 ± 0.5
Oxyjulis californica	23	81	18.82 ± 3.49
Paralabrax clathratus	19	52	9.18 ± 2.15
Phanerodon furcatus	13	33	13.69 ± 3.50
Sebastes mystinus	2	9	20.00 ± 0.0
Sebastes serranoides	1	5	—
Trachurus symmetricus	4	14	69.25 ± 57.26

bastes mystinus, were consistently encountered in the water column throughout the year, accounting for a large proportion of the intake population (Table 2). The blacksmith and senorita regularly swam within the area of high flow for intervals averaging 10 and 19 second intervals, respectively (Table 3). The most typical response of these two species was a positive rheotaxis (Fraenkel and Gunn 1940) against the water being drawn into the intake opening. These fishes occasionally turned upward to meet the curvilinear flow of water being drawn over the edge of the velocity cap (Fig. 2). While maintaining positive rheotaxis, it was not unusual for these species to "switch" back and forth between the rectilinear and curvilinear flows.

Other common residents included the olive rockfish, *Sebastes serranoides*, the kelp bass, *Paralabrax clathratus,* the sheephead, *Pimelometopon pulchrum,* and the pile surfperch, *Damalichthys vacca*. The white perch, *Phanerodon furcatus,* was also a common member except during the spring quarter. The kelp bass, pile and white surfperches frequently responded to the flow (Table 3) normally displaying positive rheotaxis and the "switching" behavior. During late summer, olive rockfish aggregated in groups of up to 15 individuals in a stationary, tail-up attitude immediately adjacent to the riser bowl and just below the intake opening, a low flow area (L. Larson, pers. comm.).

Numerous benthic oriented species including the barred sand bass, *Paralabrax nebulifer*; copper rockfish, *Sebastes caurinus*; brown rockfish, *S. auriculatus*; calico rockfish, *S. dallii*; sculpin, *Scorpaena guttata*; cabezon, *Scorpaenichthys marmoratus*; painted greenling, *Oxylebius pictus*; blackeye goby, *Coryphopterus nicholsii*; and bluebanded goby, *Lythrypnus dalli*, resided at the intake. These species were encountered along the rock boulder substrate that surrounds the intake structure. None of these species swam against the intake water current. Although barred sand bass were occasionally observed on top of the velocity cap, they also were never seen orienting to the intake water current.

Jack mackerel, *Trachurus symmetricus*, were very common during the fall and winter quarters but infrequently seen during the spring and totally absent during the summer. Dense schools of up to 400 jack mackerel frequently maintained station within the horizontal flow zone of the intake for lengthy periods (Fig. 3). They remained within the flow for an average of 69 seconds per visit.

Fig. 2. Positive rheotactic response by a senorita, *Oxyjulis californica,* to the curvilinear water current drawn over the edge of the intake velocity cap. The edge of the velocity cap is in the foreground. An aggregation of jack mackerel, *Trachurus symmetricus,* is pictured in the background.

Some members of the intake fish assemblage included seasonal migrators. Walleye surfperch, *Hyperprosopon argenteum,* moved into the area during late summer and were continually sighted until mid-fall. They were easily disturbed by divers, which biased accurate appraisal of their numbers. They were never observed orienting to the flow. Shiner surfperch, *Cymatogaster aggregata,* initially appeared at the intake towards the end of spring, accounting for 6% of the population, and increased their numbers during the summer to account for 73% of the total population. Shiner surfperch completely encircled the structure during the summer months, with many individuals also orienting to the intake water current.

Discussion

The number of species identified at the intake compares favorably with other artificial reefs in the area (Turner et al. 1969). The species comprising the intake assemblage occur at the adjacent King Harbor breakwater (Stephens and Zerba 1981) and included such residents as blacksmith, senorita, olive and blue rockfish, barred and kelp bass as well as seasonally occurring jack mackerel, walleye and shiner surfperch. In spite of seasonal changeovers in community composition, the intake exhibited a diverse assemblage that remained consistently complex throughout the course of the study.

Undoubtedly, the heterogeneous rock layer surrounding the intake influenced the presence of numerous species. The significance between fish diversity and habitat complexity is well established (Risk 1972; Luckhurst and Luckhurst 1978)

Fig. 3. Positive rheotactic response by a school of jack mackerel, *Trachurus symmetricus,* to the rectilinear water current being drawn to the intake structure shown on the right.

and evolves from the need of many demersal, cryptic and secretive fishes to remain sheltered from predators. The intake rip-rap also permitted successful recruitment as demonstrated by the presence of juvenile blacksmith (<100 mm) close to the cover of rock boulder interspaces during the winter quarter.

Many temperate reef species do not utilize shelter during their inactive periods—perhaps a consequence of low predation pressures (Ebeling and Bray 1976; Stephens and Zerba 1981). Several of these species, including surfperch, are suprabenthic and forage almost exclusively upon epifaunal organisms (Feder et al. 1974; Bray and Ebeling 1975; Ellison et al. 1979). Stephens and Zerba (1981) concluded that food resources along the adjacent King Harbor breakwater were not limiting and actually played a major role in accommodating numerous species within the harbor.

Several intake members were active throughout the day in the water column which indicates a feeding behavior independent of the substrate. Love and Ebeling (1978) found blue and olive rockfish as well as kelp bass to feed primarily on planktonic or nektonic organisms. Senorita are also facultative planktivores (Bray and Ebeling 1975; Hobson and Chess 1976) while blacksmith are obligatory planktivores (Limbaugh 1964; Hobson and Chess 1976; Bray in press). Naturally, fishes active in the water column will passively drift unless they obtain orientation cues such as those perceived by the optomotor response (Lyon 1904; Arnold 1974) which permits maintenance of station (Edmundson et al. 1968). Certainly the high relief of the structure allowed these species to extend their water column activities areally without losing visual contact of the high profiled intake structure.

Some members of the intake community were observed to periodically enter the flow region and remain for short durations. It is noteworthy that many of these species are planktivorous and may utilize the flow as a feeding station. However, this behavior may not pertain to all species. The presence of substrate grazers such as pile and white surfperch may not be related to feeding in the flow but only represent a behavioral response as they contact the flow in transit between the top of the velocity cap and surrounding rip-rap. Both areas were characterized by rich epifaunal invertebrate assemblages. In addition, the presence of jack mackerel schools within the flow suggests that the intake may serve as a schooling companion (Hunter and Mitchell 1967; Klima and Wickham 1971) allowing this species to maintain its normal schooling formation without losing sight of a stationary object.

Conclusions

The species recorded at the intake structure also occur at the adjacent breakwater. This suggests that the intake structure, like other artificial reefs, promotes ocean productivity in an otherwise barren location by providing necessary resource requirements for the associated fish assemblage. Although the additional environmental parameter of a constant water current may offer advantages for some species, it does not appear to influence the structure of the intake fish community.

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A New Coralline Boring Species of *Polydora* (Polychaeta: Spionidae) from Northern California

James A. Blake

Abstract.—A new coralline boring species of *Polydora* (Polychaeta: Spionidae) from Northern California by James A. Blake, *Bull. Southern California Acad. Sci.*, 80(1):32–35. A new species of *Polydora* is described from Tomales Point in northern California. The species is a borer in coralline algae and related to the *P. giardi* group. It differs from its closest relatives in having posterior notopodial spines and a four lobed pygidium.

Nine species of *Polydora* and *Boccardia* (Family Spionidae) were reported to be borers in coralline algae by Blake and Evans (1973). While examining samples of *Lithophyllum pacificum* Foslie collected from Tomales Point (Point Reyes National Seashore) in northern California, a new species of *Polydora* was discovered. This new species shares affinities with *P. giardi* Mesnil, which occurs in the same alga (Day and Blake 1979), but differs in several significant features. A description of this new species is presented herein, along with a discussion of its taxonomic affinities.

The type collection is deposited in the National Museum of Natural History (USNM).

Polydora bifurcata, new species
Figures 1–2

Material examined.—CALIFORNIA, Point Reyes National Seashore, Tomales Point, 38°14′N; 122°59′W, intertidal, boring into the coralline alga, *Lithophyllum pacificum,* March 1970, coll. J. A. Blake, holotype (USNM 58976) and one paratype (USNM 58977).

Description.—Holotype incomplete, measuring 6.7 mm long and 0.5 mm wide for 63 segments; paratype complete, broken into two parts, measuring 4.7 mm long and 0.5 mm wide for 35 segments. Color: light tan in alcohol, no body pigment.

Prostomium strongly bifurcate, forming two prominent lobes (Fig. 1A); caruncle with folds, extending posteriorly into setiger 5; narrow field of nuchal ciliation surrounding caruncle; no occipital tentacle; no eyes. Peristomium narrow; palps short, possibly regenerating on both specimens.

Setiger 1 well developed, with parapodia shifted dorsally; postsetal noto- and neuropodial lamellae prominent; capillary noto- and neurosetae present. Notosetae of setigers 2–4, 6 and subsequent setigers with two-tiered fascicles of unilimbate capillaries, setae of first tier being shorter and thicker than second tier; posterior setigers with five to six long, thin capillaries and three to four thicker curved, pointed acicular spines (Fig. 2D). Neurosetae of setigers 2–4, and 6 sim-

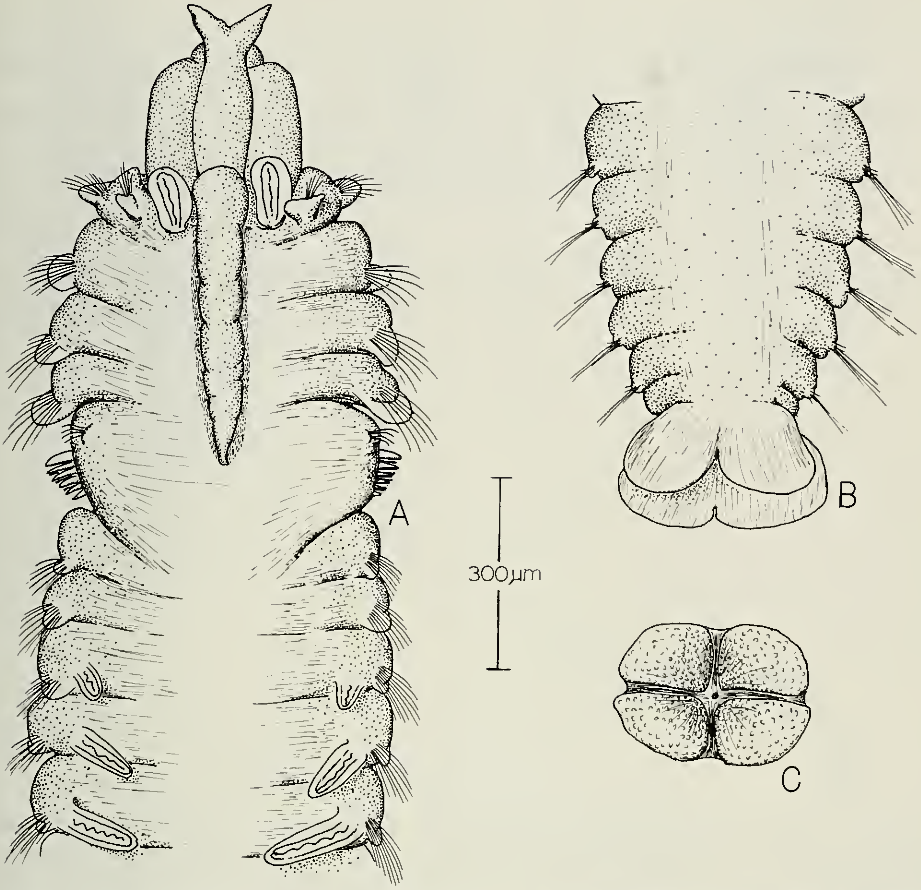

Fig. 1. *Polydora bifurcata* (paratype, USNM 58977): A. Anterior end in dorsal view; B. Posterior end in dorsal view; C. Pygidium in posterior view.

ilar in arrangement and form to notosetae; hooded hooks from setiger 7, numbering three to four hooks per neuropodium throughout most of body, accompanied by two to three inferior capillaries for about 20 segments; capillaries lacking thereafter; hooks lacking constriction on shaft (Fig. 2C), with reduced angle between teeth, but with wide angle between main fang and shaft; fringe of minute bristles present on hood opening.

Setiger 5 strongly modified, overlapping setiger 6 with heavy dorsal musculature (Fig. 1A); setae including a superior dorsal fascicle of broad geniculate bristled setae (Fig. 2B), a curved row of major spines alternating with bristled companion setae (Fig. 2A) and a ventral fascicle of unilimbated capillaries. Major spines falcate, with one large accessory tooth on curved edge and a thin, narrowly adhering spur on convex side.

Branchiae from setiger 8, short at first, reaching to full size by setiger 12, each gill extending maximally one-third of the distance across an individual segment.

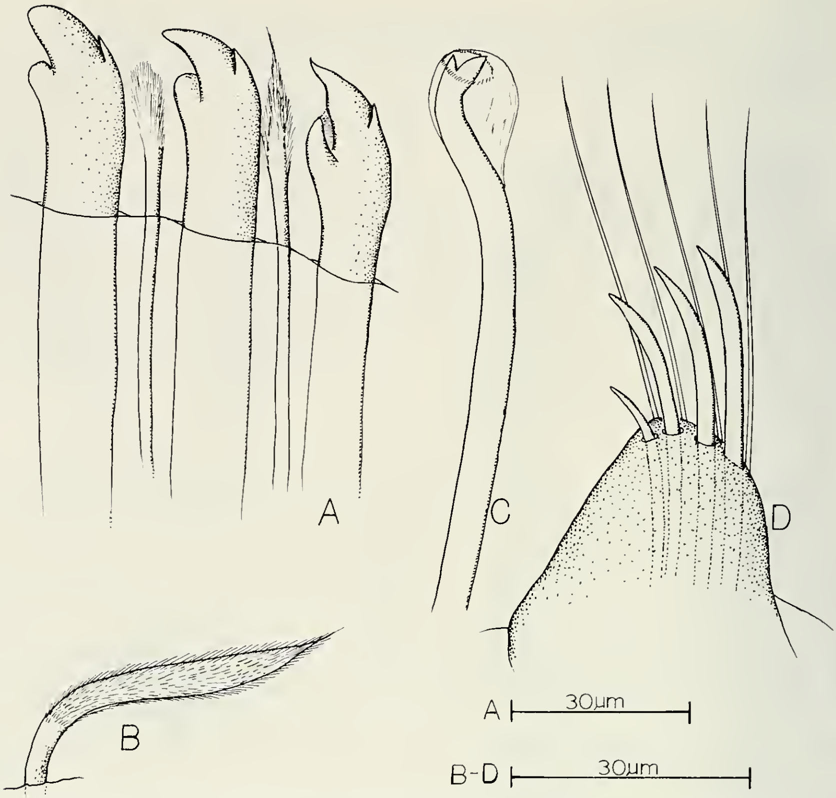

Fig. 2. *Polydora bifurcata* (paratype, USNM 58977): A. Three major spines and two companion setae from setiger 5; B. Geniculate dorsal seta from setiger 5; C. Hooded hook from an anterior neuropodium; D. Posterior notopodium in dorsal view, anterior edge toward the right, indicating position of acicular spines and capillaries.

Pygidium four-lobed (Fig. 1B–C), with dorsal pair being slightly smaller than ventral pair; each pygidial lobe with longitudinal striations composed of separate bacillary glands.

Remarks.—Among approximately 66 species of *Polydora, P. bifurcata* is most similar to the widespread *P. giardi* Mesnil and the central Pacific species, *P. tridenticulata* Woodwick (1964). Each of these species has an accessory tooth on the major spines of setiger 5, hooded hooks without a constriction or manubrium on the shaft and branchiae beginning from setiger 8 or more posteriorly. *P. bifurcata* differs from both of those species in having instead of lacking posterior notopodial spines and in having a pygidium with four lobes instead of a complete disc or cuff.

Polydora bifurcata was associated with two other polydorids, *P. giardi* and *Boccardia columbiana* Berkeley, in the *Lithophyllum* crusts. All three species bore directly into the alga.

Distribution.—Northern California in the vicinity of Tomales Point.

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Research Notes

Observations on the Deep-water Chiton, *Leptochiton rissoi* (Nierstrasz 1905) in the Eastern Pacific

Knowledge of the deep-sea chiton fauna is still fragmentary, even tentative; although some 20 species of chitons are known to be endemic to depths greater than 200 m (Ferreira 1980), in most cases observations have been confined to only a few specimens, often from a single locality. Accordingly, understanding of the anatomical and biological characteristics of such species has been limited.

This paper reports on new data about an eastern Pacific deep-water chiton, *Lepidopleurus rissoi* Nierstrasz 1905, heretofore known only from Nierstrasz' (1905) account based on specimens obtained in the course of the *Siboga* expedition. These observations rest upon the examination of the lectotype in repository at the Zoologisk Museum of Amsterdam (ZMA), and material in the Benthic Collection of the Scripps Institution of Oceanography, La Jolla, California (SIO) and the Department of Invertebrate Zoology of the California Academy of Sciences, San Francisco, California (CASIZ).

Polyplacophora de Blainville 1816
Neoloricata Bergenhayn 1955
Lepidopleuridae Pilsbry 1892
Leptochiton Gray 1847
Leptochiton rissoi (Nierstrasz 1905)
Figures 1–2

Lepidopleurus rissoi Nierstrasz 1905:6–7, figs. 5, 52–55—Ferreira 1979:163, figs. 30–32; 1980:59, tbl. 1.

Type material.—Lectotype, designated by Ferreira (1979), and nine paralectotypes at ZMA.

Type locality.—Eastern Pacific, 3°27.1′N, 125°18.7′W, at 2053 m, *Siboga* station no. 126.

Material examined.—In addition to the lectotype (Ferreira 1979:163, figs. 30–32), six other specimens were studied:

1) SIO M559—5°58.8′N, 81°38.2′W, criss cross dredge, 1190 m, *leg.* T. Chase, 18 March 1963; 1 specimen, in alcohol, 11.8 mm long.

2) SIO M1392—off Arica, Chile, 18°30.0′S, 70°34.5′W, rock dredge, 402–311 m, *R/V T. Washington, leg.* A. Sontar & S. Luke, 7 May 1972; 2 specimens, in alcohol, 14.0 mm and ca. 7 mm long.

3) SIO M1393—off Chile, 21°23.7′S, 70°18.2′W, rock dredge, 450–420 m, *R/V T. Washington, leg.* A. Sontar & S. Luke, 1 May 1972; 1 specimen, in alcohol, ca. 10 mm long.

4) CASIZ 016695—off Oregon, 44°39.1′N, 125°11.0′W, 1420 m, *R/V Ancona,* cruise no. 6304c, 27 April 1963; 1 specimen, in alcohol, ca. 10 mm long.

5) CASIZ016696—Guide Seamount, California, 37°09′40″N, 123°04′40″W,

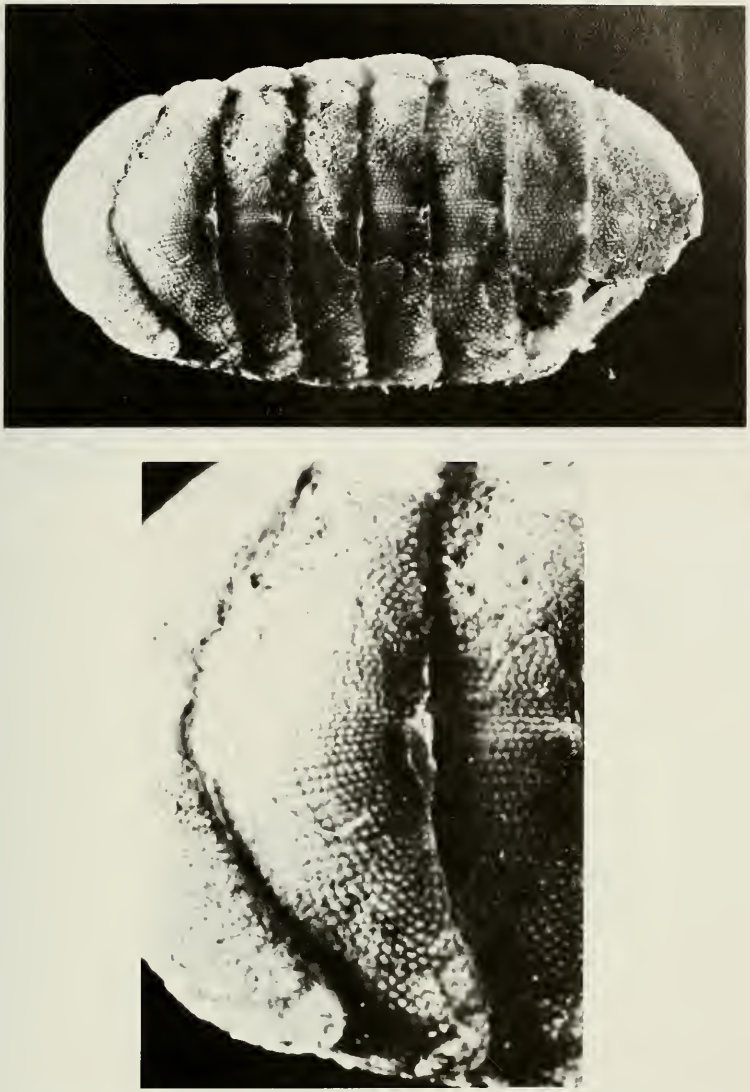


Fig. 1. *Leptochiton rissoi* (Nierstrasz 1905). Specimen 11.8 mm long (SIO M559). A) Dorsal view. B) Close-up of central and lateral areas of anterior valves.

1098–732 m, *R/V Mulberry*, Sta. 45, 15 February 1950; 1 specimen, in alcohol, ca. 15 mm long [CASIZ Color Slides series nos. 727–728].

Description.—The specimens (Fig. 1) conform well to Nierstrasz' (1905) description of *Lepidopleurus rissoi*, and the lectotype (Ferreira 1979). Uniformly white to light cream in color, they vary in length from 7 to 15 mm. A specimen (SIO M1392), 14.0 × 8.5 × 0.8 mm, was disarticulated for close study. The girdle, 0.8 mm wide at the level of valve iv, is covered with spiculoid scales (Figs. 2A-a, and 2B), 60 × 10 μm, sharply pointed, and deeply striated. The underside

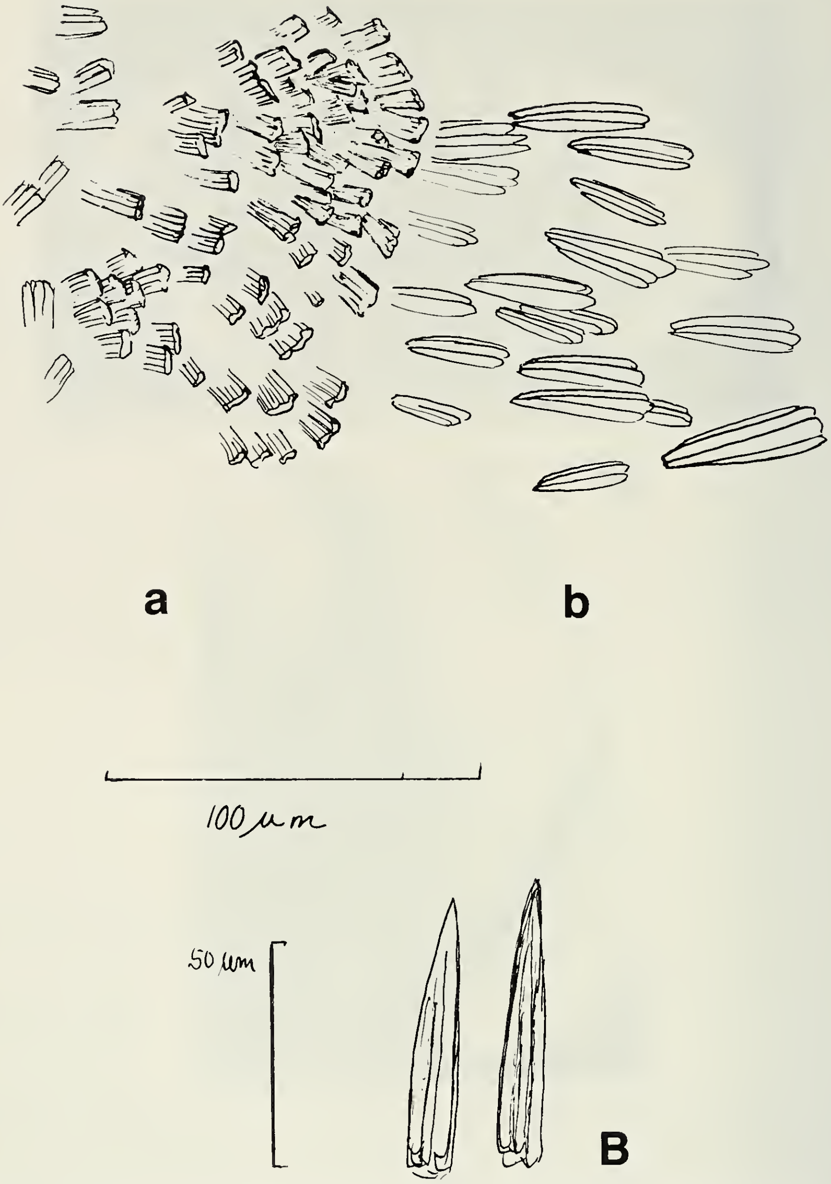
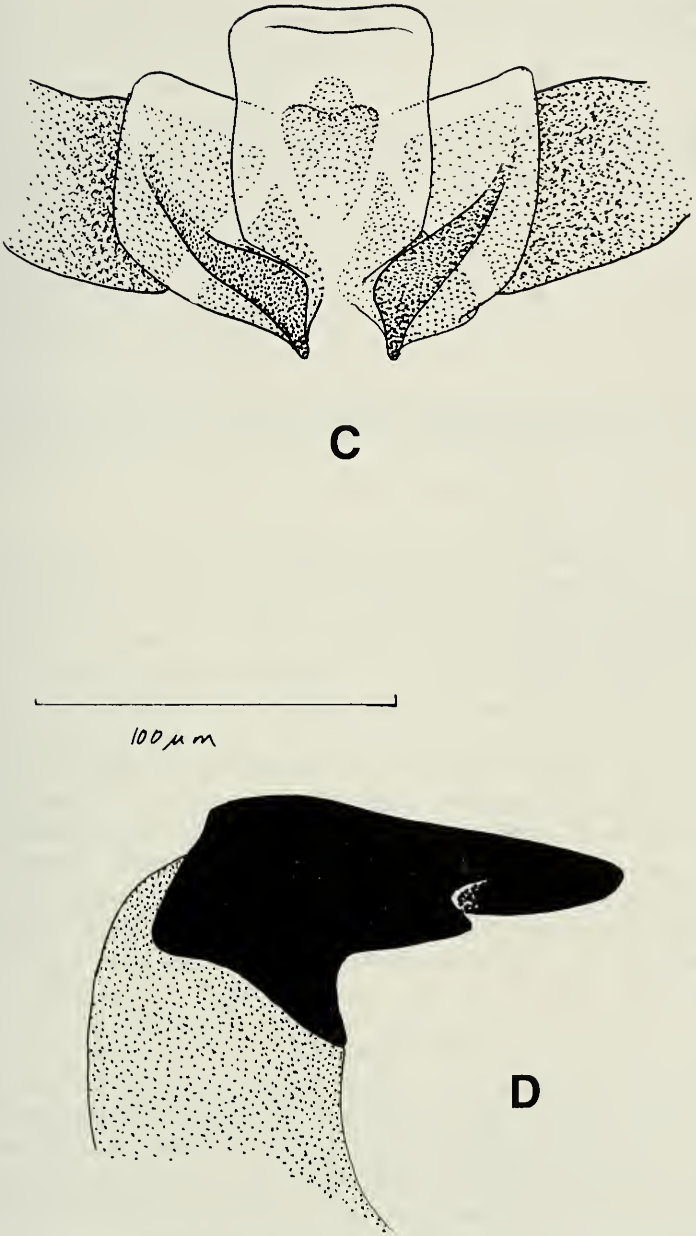


Fig. 2. *Leptochiton rissoi* (Nierstrasz 1905). Specimen 14.0 mm long (SIO M1302). A) Girdle elements of upper surface (a), and undersurface (b). [measured bar = 100 µm]. B) Spiculoid scales

of the girdle is similarly paved with translucid spiculoid scales (Fig. 2A-b), 80 × 15 µm, longitudinally striated. Gills, posterior, abanal, extending about one half of the foot's length, comprise some 15 plumes per side. The posterior valve is absolutely and relatively longer than the others (Table 1): the relative width of its sinus (width of sinus/width of sutural lamina) is 1.5 mm/215 mm = 0.6.

The radula is 5.0 mm long (29% of the specimen's length), and comprises about



of upper surface of girdle [measured bar = 60 μm]. C) Median and first lateral teeth of radula [measured bar = 100 μm]. D) Head of second (major) lateral tooth [measured bar = 100 μm].

35 rows of mature teeth. Median tooth (Fig. 2C), quadrangular, 100 μm long, 75 μm wide at the anterior blade. First lateral teeth (Fig. 2C), somewhat rectangular, about 80 μm long, 60 μm wide. Second lateral teeth with a bicuspid head, the outer cusp much larger than the inner one (Fig. 2D). Spatulate teeth ("Seiten-

Table 1. Length (l) and width (w) of the valves of a 14 mm long specimen of *Leptochiton rissoi* (Nierstrasz 1905).

Valves	l (mm)	w (mm)	l/w
i	1.5	5.0	.30
ii	2.0	5.6	.36
iii	1.6	6.0	.27
iv	1.7	6.8	.25
v	2.0	7.0	.29
vi	1.9	6.8	.28
vii	1.8	6.8	.26
viii	3.3	5.8	.57

plate'') with a very simple spoonlike shape, about 125 μm long. Outer marginal teeth, elongate, 100 × 40 μm.

Distribution.—The range of *Leptochiton rissoi* extends from 44°N to 21°S, and from depths of 216 m to 2053 m.

Remarks.—The assignment of *rissoi* to *Leptochiton* Gray 1847 is in agreement with the current interpretation of the genus (Ferreira 1979). Compared to other congeneric Pacific species, *Leptochiton rissoi* differs in the shape of the valves, tegmental sculpture, girdle elements, and radula (see Ferreira 1979). But the differential diagnosis between *L. rissoi* and the recently described *L. batialis* Sirenko 1979 deserves extended consideration in view of similarities in tegmental sculpture. From the illustrations of *L. batialis* (Sirenko 1979, fig. 2), and measurements thereupon, the two species are seen to differ in significant features: 1) the valves are relatively longer in *L. batialis* than in *L. rissoi* (length/width ratio of valve v is 0.44 in *L. batialis,* 0.29 in *L. rissoi*), 2) the sutural laminae in valve viii are triangular in *L. batialis,* rectangular in *L. rissoi,* 3) the relative width of the sinus [width of sinus/width of sutural lamina] of valve viii is 1.4 in *L. batialis,* 0.6 in *L. rissoi,* and 4) the median tooth of the radula is more elongated in *L. batialis* than in *L. rissoi* (width/length ratio of the tooth, 0.35 and 0.75, respectively).

Acknowledgments

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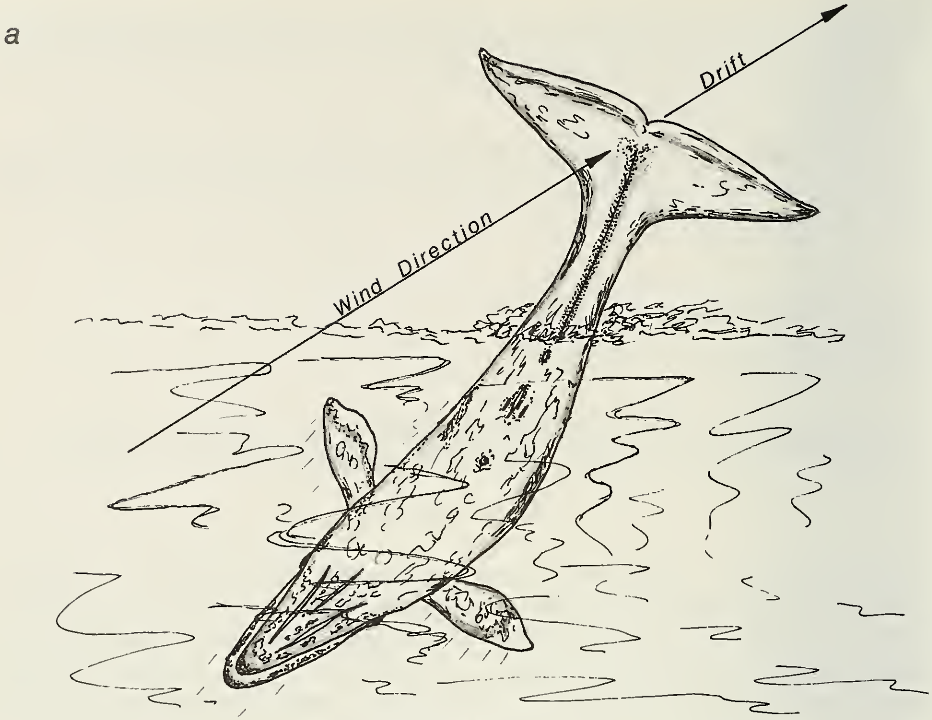
Apparent Wind-oriented Behavior in the Gray Whale (*Eschrichtius robustus*)

In recent years, intensified field observations have been made over large sections of the migratory range of the gray whale (*Eschrichtius robustus* Lilljeborg). These observations have produced a much clearer picture of its behavior and natural history. Since the observations and writings of Captain Charles Scammon (1874), behavioral biologists have been trying to explain repetitive patterns of activities seen in the gray whale along a corridor from Beringia to the lagoons of Baja California, Mexico.

Migration was one of the first behavior patterns to be identified and described. Scammon and others discovered that the gray whales calved and mated primarily in the lagoons of Baja California Sur. Gilmore (1960), Walker (1971), Sauer (1963), Rice and Wolman (1971), Samaras (1974), and others have described the reproduction of these whales and have established some regionally-repetitive, fundamental patterns of socially interactive behavior. Spyhopping, breaching, lobtailing, fluke-stands, and respiratory-swimming patterns may be involved in other activities: feeding, courtship, precopulative interaction, visual orientation and/or navigation, low-frequency audio communication over great distances, shaking off lice-loosened barnacles (Samaras and Durham, in press), and/or recreation.

I would add yet another gray whale activity to the growing list of characteristic forms of behavior—sailing. Roger Payne (1976) has observed, photographed, and described sailing as a characteristic ''recreational'' behavior of the southern right whale, *Eubalaena australis*, in the region of the Valdez Peninsula of Patagonia (Payne 1976). Previously this activity had not been described for any other cetacean. Sailing, or more appropriately, fluke-sailing posture and physical conditions include: the caudal peduncle extended nearly vertically above the sea surface; the ventral surface of the flukes cupped over and facing into the wind (Figs. 1a and 2); and sailing done in an available wind force of at least 10–20 knots (Beaufort Scale 3–5). Because observers have been at low elevation on murky, choppy water, the subsurface posture of a fluke-sailing gray whale can only be conjectured (Fig. 1a).

The apparent sailing activity of adult gray whales was observed in upper Mag-



FLUKE SAILING

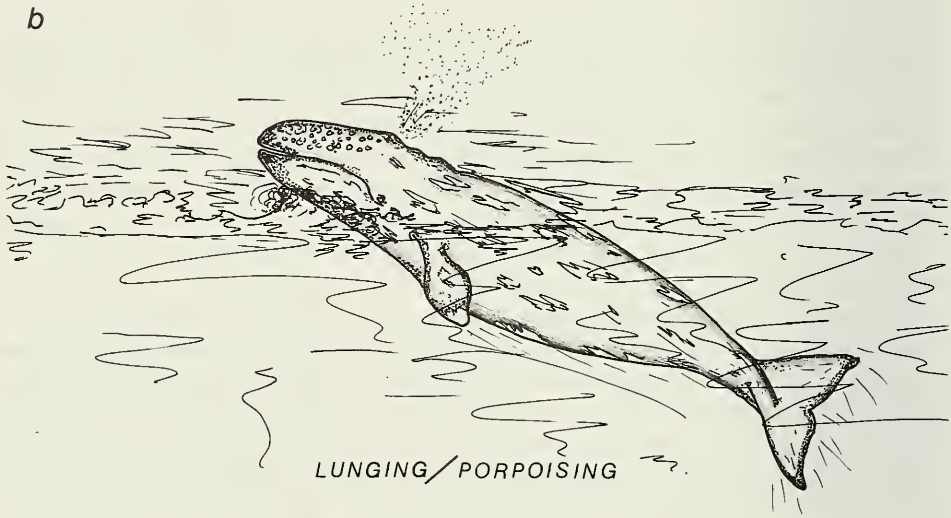
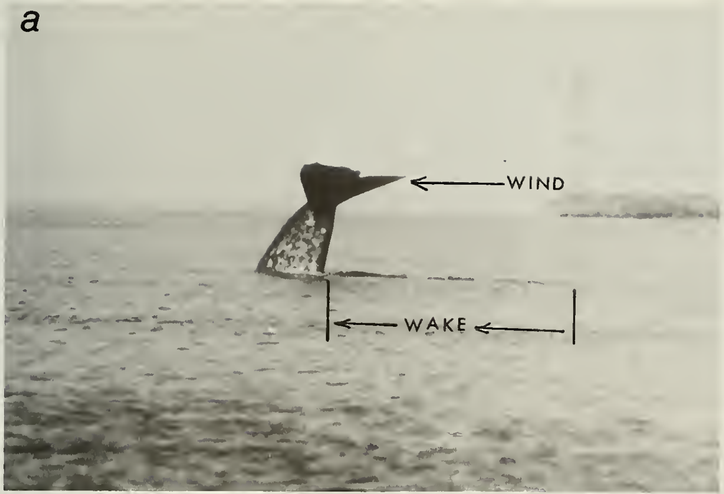


Fig. 1. a. Gray whale fluke-sailing orientation. The subsurface posture of a gray whale involved in fluke-sailing is interpretive. Because of the observed physical orientation of the extended caudal peduncle and cupped flukes, in relation to the wind, the body of the whale is either perpendicular to the surface or bowed slightly with venter up as indicated. The vertical positioning, with flukes maintained high out of the water for prolonged periods of time, is probably facilitated through a sculling action of the pectoral fins. b. Gray whale calf wind-oriented, lunging/porpoising posture as observed in Laguna Guerrero Negro during a moderate gale.



b

c

dalena Bay, Baja California Del Sur on at least three separate occasions between 13 and 16 February 1978. In all cases, large, mature whales engaged in this activity. Fluke-sailing occurred in the afternoon when the prevailing westerlies had freshened sufficiently. The flukes were observed deliberately turning into the wind as they slowly emerged from the water. This activity would last for at least a minute, accompanied by obvious movement or drift of the flukes with the wind (Fig. 2a).

During this mid-February segment of the annual gray whale migration, the whales in upper Magdalena Bay are mostly, if not exclusively, females with calves. Consequently, the whales involved in the apparent fluke-sailing activity were, in all probability, sexually mature females. Similar wind-oriented behavior has not been reported from other traditional calving and mating lagoons, i.e., Laguna San Ignacio, Scammon Lagoon (Laguna Ojo de Liebre) and Laguna Guerrero Negro.

During February 1977, in Laguna Guerrero Negro, Baja California Del Sur, I encountered a different wind-oriented behavior among the lagoon's population of gray whale calves. During this time of year, the prevailing westerlies freshen briskly every afternoon from approximately 1300 hr to well after sunset. On the afternoon of 12 February 1977, the wind force rose to a moderate gale (28–33 knots; Beaufort Scale 7). The water in Laguna Guerrero Negro heaped up, and white foam from the breaking wind-generated waves was blown in streaks along the direction of the wind. Coarse silica sand from Great Dune Island, at least a kilometer to the west, was blown across the lagoon onto our observing site on the abandoned salt-loading pier. The gray whale calves and cows swam around the perimeter of the lagoon in a counterclockwise movement, usually perpendicular to the prevailing wind direction.

As the sea surface approached the spindrift stage, all the visible calves on both sides of the lagoon began lunging out of the water with a low-level porpoising maneuver (Fig. 1b). The cows (female whales) continued to glide slowly through the water, close by their calves, without any apparent change in their normal lagoon swimming-respiratory activity. The calves did not appear to be under stress or in a state of panic, as the observed respiratory interludes were generally regular. But as they lunged or porpoised forward, they would surface head-first at an estimated 30° angle. The lunging motion produced a distinct bow or compression wave ahead and to each side. During each low-level porpoising maneuver, their heads and blowholes (nares) would rise above the spindrift stra-

←

Fig. 2. a. A mature, female gray whale (*Eschrichtius robustus*) fluke-sailing during a gentle breeze with an estimated wind force of 7–10 knots (Beaufort Scale 3). The whale is sailing from right to left as indicated by the wind direction and wake in the photo. In b, the flukes are just emerging and turning into the wind. Sailing has already begun as indicated by the cupped over flukes and a discernible wake stretching to the right of the caudal peduncle. This sailing episode took place in a moderate breeze with an estimated wind force of 11–16 knots (Beaufort Scale 4). In c, the peduncle and flukes of the whale have completely emerged and turned into the wind coming from the direction of the sand dunes in the background. The wind force during this observation was a strong breeze with a velocity of 22–27 knots (Beaufort Scale 6). These fluke-sailings took place in Upper Magdalena Bay, Baja California Del Sur on three separate occasions. The sailings occurred during the afternoon between 13 and 16 February 1978 and were three different whales.

tum at the sea's surface (Fig. 1b). This activity continued into dark. The wind did not moderate until after midnight.

The apparent coordinative and continuous nature of the activity, with a definite relationship to severe wind and sea-surface conditions, suggested a learning and/or conditioning experience. The exposure of the heads and blowholes above most of the spindrift during porpoising could serve to reduce the amount of salty spume inhaled during respiration.

Acknowledgments

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A New Articulate Brachiopod from the Lower Cambrian Latham Shale, Southeastern California

The lower Cambrian Latham Shale of Hazzard (1954) crops out at localities scattered widely throughout the Mojave Desert of southeastern California. Although the formation is highly fossiliferous, descriptive paleontologic documentation of its fauna is limited to a very few reports (Resser 1928; Crickmay 1933; Riccio 1952) dealing mainly with the abundant and diverse assemblage of trilobites. Other notes (Hazzard 1933, 1954; Mount 1974b, 1976) have touched on the stratigraphic allocation of some of the trilobite and non-trilobite taxa.

The purpose of the present report is to provide the description of a new species of *Nisusia,* the only brachiopod of the Class Articulata known to occur in the Latham Shale. *Nisusia* Walcott 1905:247, is the earliest and most primitive articulate brachiopod genus and is recorded from the lower and middle Cambrian of North America, Asia, and Europe. The discovery of the new taxon from the Latham Shale provides one of the oldest known records of the genus from the Cordilleran area.

References to the Department of Earth Sciences, University of California, Riverside, are hereafter abbreviated as UCR.

Order Orthida
Family Nisusiidae
Genus *Nisusia* Walcott, 1905
Nisusia fulleri new species
Figures 1–2

Nisusia n. sp.: Mount 1974c, p. 47, pl. 1, figs. 1, 2; Mount 1976, p. 176, fig. 4.

Diagnosis.—The new species is distinguished from all other species of the genus by having the following combination of characteristics: shell medium in size, transversely subrectangular, greatest width at the hinge; sulcus shallow and wide; ornamentation of numerous, narrow, low costellae of three different strengths, with narrow interspaces.

Description.—Shell medium in size for the genus, apparently thin; outline transversely subrectangular, wider than long with the greatest width at the hinge and maximum length at mid width; cardinal extremities nearly rectangular; lateral margins nearly straight or slightly convex; anterior margin broadly rounded. Sulcus apparently very shallow and wide, originating in anterior third of shell and extending to anterior margin. Umbo short, widely convex, moderately swollen and protruded posterior to the posterior margin; apical angle 112°. Interarea narrow and apparently apsacline. Ornamentation consists of numerous, somewhat regularly arranged, low, narrow, rounded costellae of three different strengths, gauging 4 per mm on the holotype; separated by very narrow interspaces with widths from ⅓ to 1 times the width of the costellae. Surface marked by numerous, fine, slightly raised concentric lines of growth. Interior characteristics unknown.

Holotype.—UCR 10/2031, length 6.5 mm, width 8.0 mm, brachial valve?

Figs. 1–2. *Nisusia fulleri* Mount, new species, holotype UCR 10/2031, brachial? view, ×5. (2) *Nisusia fulleri* Mount, new species, paratype UCR 10/2019, pedicle? view, ×3.

Paratypes.—UCR 10/2019, length 11.3 mm, width 15.0 mm, pedicle valve? UCR 10/2032, eight partial valves on one piece of shale. UCR 10/2037, length 11.0 mm, width 12.3 mm, pedicle valve?

Type locality.—UCR locality 10; at elevation of 1160 ft (305 m), 100 m west of old quarry at the southern end of the Marble Mountains, San Bernardino County; 125 m west and 650 m south of northeast corner of Sec. 11, T.5N., R.14E., Danby 15′ quadrangle (1956 edition); same as locality M-5 of Hazzard (1933).

Stratigraphic position.—The type locality is in the middle one-third of the Latham Shale which is 15 m thick at the site.

Associated fauna.—Anthozoa: *Bergaueria radiata* Alpert

Inarticulata: *Paterina prospectensis* (Walcott), *Mickwitzia occidens* Walcott

Mollusca: *Hyolithes whitei* Resser

Annelida: new genus and species (Mount 1976, fig. 20)

Trilobita: *Olenellus clarki* (Resser), *O. fremonti* Walcott, *O. gilberti* Meek, *O. mohavensis* (Crickmay), *O. nevadensis* (Walcott), *O.* new species (Mount 1976, fig. 11), *Bristolia anteros* Palmer, *B. bristolensis* (Resser), *B. insolens* (Resser), *B.* new species (Mount 1976, fig. 17), *Peachella iddingsi* (Walcott), *Onchocephalus* new species (Mount 1976, fig. 18)

Malacostraca: *Anomalocaris canadensis* Whiteaves

Eocrinoidea: *Gogia ojenai* Durham

Age.—Late Early Cambrian; *Bristolia* Subzone of Mount (1974a, b), *Bonnia-Olenellus* Zone of Rasetti (1951), Waucoban Stage.

Discussion.—*Nisusia fulleri* new species bears similarity in general form and outline to *N. bivia* (Walcott 1912:750) from the lower Cambrian portion of the Carrara Formation in the Resting Springs Range, Inyo County, California, but differs in details of surface sculpture. The latter species has coarser, wider spaced costellae with fine radial lines superimposed on the primary costellae.

Nisusia montanaensis Bell 1941:238, from the middle Cambrian of Montana, has the fine sculpture of *N. fulleri,* however, it is larger, more quadrate, and the hinge line is slightly less than the width of shell at the middle.

Nisusia festinata (Billings 1861:10), the type species for the genus, from the lower Cambrian of eastern North America is closely similar to the new form described here. The former taxon is spino-costellate and appears to have costellae of more even size and a narrower, deeper sulcus.

Nisusia kotujensis Andreeva 1962:87 from the lower Cambrian of the Siberian Platform of eastern Asia is distinguished from the new California species by having coarser costellae and narrower interspaces in proportion to the width of the costellae. Moreover, the hinges are extended into elongated cardinal extremities.

Nisusia mantouensis Resser and Endo 1937:141 and *N. nasuta ramosa* Nikitin 1956:19 from the middle Cambrian of central Asia have some resemblance to *N. fulleri,* however, these Asian species have coarser sculpture, a deeper sulcus and more rounded extremities.

Etymology.—The new brachiopod is named for Mr. James E. Fuller of the University of California, Riverside, who collected the holotype and one of the paratypes.

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Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus.* J. Mamm., 54:452–458.

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Research Notes

COVER: A photograph of a female *Porichthys myriaster,* the specklefin midshipman, taken with its own light produced by photophores on the underside of the animal. Photograph taken off Orange County coast, California, by Tim Salman and Jules Crane of Cerritos College, Norwalk, California, 1981.

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Scymnodon ?ringens a New Addition to the Ichthyofauna of the Late Pleistocene Palos Verdes Sand at Newport Bay Mesa, Orange County, California

Bruce J. Welton

Abstract.—Scymnodon ?ringens, a new addition to the ichthyofauna of the late Pleistocene Palos Verdes Sand at Newport Bay Mesa, Orange County, California. Bruce J. Welton. *Bull. Southern California Acad. Sci.,* 80(2):49–59, 1981. A single lower right anterolateral tooth of *Scymnodon ?ringens* Bocage and Capello (1864) is described from the late Pleistocene Palos Verdes Sand at Newport Bay Mesa, Orange County, California. This occurrence represents the addition of a new taxon to the fauna of the Palos Verdes Sand and the geologically most recent occurrence of *Scymnodon* in the eastern north Pacific basin.

In his publication of "Fish records from the Pleistocene of southern California" Kanakoff (1956) listed eleven species of elasmobranchs from the late Pleistocene Palos Verdes Sand at Newport Bay Mesa, Orange County. Subsequently, Fitch (1970) revised and expanded Kanakoff's list, which now includes the following species:

Carcharhinus spp.
Carcharodon carcharias
Cetorhinus maximus
Dasyatis dipterurus
Galeorhinus zyopterus
Heterodontus francisci
Isurus oxyrinchus
Myliobatis californicus
Prionace glauca
Sphyrna spp.
Triakis semifasciata
Urolophus halleri

Among the fossil fish teeth collected between 1958 and 1963 at LACM vertebrate locality 1066, by Carl and Edward Wiedert of Garden Grove, California, is a tooth of a squaloid shark which has not been previously recorded from this locality. Study of the specimen in comparison with complete dentitions of extant squalomorphs indicates allocation to the genus *Scymnodon* and questionable referral to the extant species *S. ringens* Bocage and Capello (1864).

B. J. Welton *in* Phillips, Welton and Welton (1976:149) reported teeth of *Scymnodon* sp. in the early Miocene Skooner Gulch Formation, Mendocino County, California. The occurrence of a tooth referred to *S. ?ringens* in the Palos Verdes Sand is the second fossil record for the genus and possibly the first occurrence of the species, extant or fossil, in the eastern north Pacific basin.

Locality

The tooth of *Scymnodon* was collected at LACM (Natural History Museum of Los Angeles County, California vertebrate locality), 1066 (=LACMIP 66: Natural History Museum of Los Angeles County, California invertebrate paleontology locality), Newport Bay Mesa, Orange County, California.

LACM 1066 lies approximately ½ mile southeast of the Irvine Company salt reducing plant at the tip of the Newport Estuary, in T.6S., R.10W., at approximately 33°38′37″N and 117°52′37″W, in the Tustin 7.5 minute (1965 ed.) U.S. Geological Survey quadrangle. Approximately two to seventeen feet of fossiliferous Palos Verdes Sand crop out along a 1150 foot long north-south trending dry creek bed. Seven sublocalities, originally designated LACMIP 66-1 through LACMIP 66-7, have been assigned to individual exposures in gullies intersecting this creek bed (all included in LACM vertebrate locality 1066).

This locality (and its sublocalities) were first investigated by museum personnel in February 1945 and were recollected on numerous occasions over the following two decades (Fitch 1970). A housing development now covers the entire mesa south of Newport back-bay, including LACM 1066.

It is clear that the Wiederts collected at LACM 1066; however, their locality data is insufficient to allow for its assignment to one of the seven LACMIP sublocalities.

Geology

The Palos Verdes Sand was defined by Woodring, Bramlette, and Kew (1946) and its usage restricted to the sands and gravels, exclusive of any non-marine cover, which occurred on the lowest emergent terrace along the northern and eastern slopes of the Palos Verdes Hills (Kennedy 1975). The Palos Verdes Sand is equivalent to the Upper San Pedro Series of Arnold and Arnold (1902) and the Palos Verdes Formation of Tieje (1926). Subsequently, the name has been applied to the latest Pleistocene fossiliferous sands on the lowest emergent terrace on the present coastal borders of the Los Angeles Basin, from Pacific Palisades in the north to Newport Beach in the south.

At Newport Bay Mesa, a thin layer of Palos Verdes Sand attains a maximum thickness of between 12 and 20 feet and unconformably overlies the Miocene Monterey and Pliocene Fernando Formations. Fossils occur chiefly in fine to coarse beds of poorly sorted, largely unconsolidated sands resting on basal conglomerates of the truncated underlying sediments (Kanakoff and Emerson 1959).

Age

According to Kanakoff and Emerson (1959), the molluscan fauna at Newport Bay Mesa is correlative with the warm water fauna of the Palos Verdes Sand at its type section at San Pedro, California (Woodring et al. 1946). Most of the thermophilic species from Newport Bay Mesa (LACMIP 66) have been reported from deposits on the lowest emergent terrace elsewhere in the Los Angeles Basin (Kanakoff and Emerson 1959:44).

Carbon-14 age determinations for fossil deposits on the lowest emergent terraces at San Pedro, California indicate an age greater than 30,000 years B.P. (Kulp, Tryon, Eckelman, and Snell 1952). Fanale and Schaeffer (1965) report that uranium-helium ages for Pleistocene mollusks from the 1200-foot terrace in the Palos Verdes Hills ranged from 330,000 to 420,000 years, and from the 70-foot terrace, 95,000 to 130,000 years.

Miller (1971) described the mammalian fauna of the Palos Verdes Sand at LACM 1066 and concluded that it is taxonomically correlative with the late Pleistocene (Rancholabrean) fauna of Rancho La Brea, Los Angeles County, California.

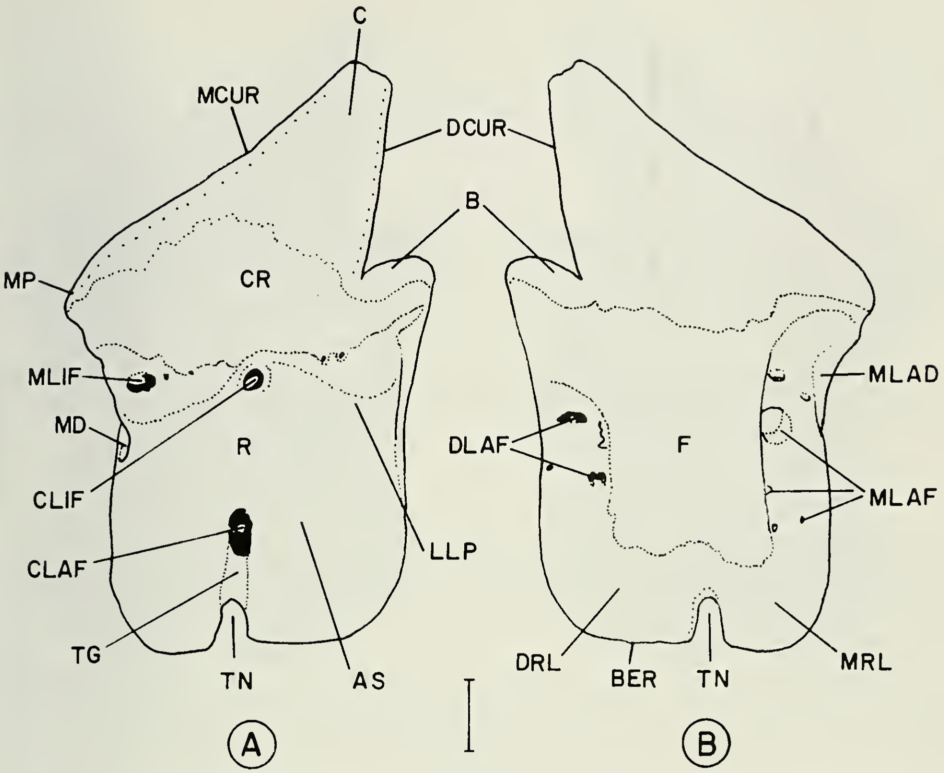

Fig. 1. Tooth terminology as applied to the lower right anterolateral tooth of *Scymnodon ?ringens,* LACM 60613. A, lingual view; B, labial view. Abbreviations: AS, attachment surface of root; B, blade; BER, basal edge of root; C, cusp; CLAF, central labial foramen; CLIF, central lingual foramen; DCUR, distal cutting ridge; DLAF, distal labial foramen; DRL, distal root lobe; LLP, lingual longitudinal protuberance; MCUR, mesial cutting ridge; MD, mesial depression; MLAD, mesiolabial depression; MLAF, mesiolabial foramen; MLIF, mesiolingual foramen; MP, mesial protuberance; MRL, mesial root lobe; TG, transverse groove; TN, transverse notch. Scale line equals 1 mm.

The above data suggest that the fauna at LACM 1066 is probably late Pleistocene.

Dental Terminology

The tooth terminology used throughout this study follows, with slight modification, Casier (1961), Compagno (1970), and Ledoux (1970) and is illustrated in Figure 1. The tooth row-group terminology, as it is applied to the lower dental series in *Scymnodon ringens,* is shown in Figure 2.

Recent Comparative Specimens

A tissue-free tooth set of the lower right functional and first replacement series in *Scymnodon ringens* was prepared from LACM Section of Ichthyology, specimen No. 37974-1; a 1000 mm (total length) female, collected at a depth of 750–800 meters at 56°25′N, 9°15′W, in the North Atlantic, north of Scotland, by Dr.

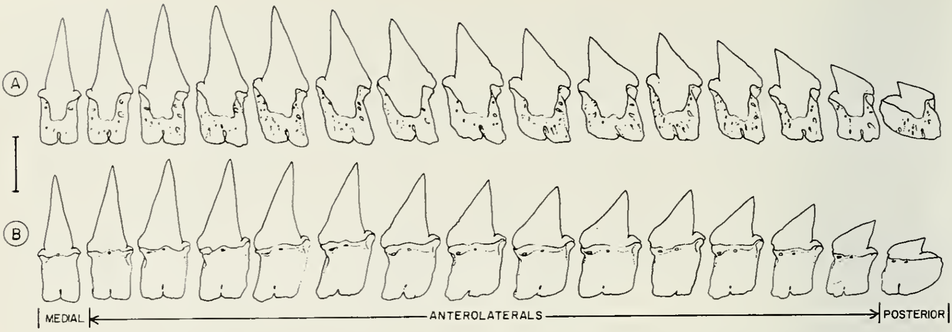

Fig. 2. Tooth row group terminology as applied to the lower right dental series of *Scymnodon ringens* (LACM 37974-1, 1000 mm total length, female). A, labial view of dental series; B, lingual view of dental series. Scale line equals 5 mm.

Jacques Herman, April 4, 1977. A second tooth set of *Scymnodon squamulosus* was prepared from an adult male specimen, Stanford University (SU) 26784 (now in the Ichthyology Department, California Academy of Sciences, San Francisco, California).

Published figures of the dentition of *Scymnodon* are found in Ledoux (1970:349–350: *S. ringens*), Bigelow and Schroeder (1957:98: *S. ringens* and *S. obscurus*), and Bass, d'Aubrey, and Kistnasamy (1976:84: *S. ?obscurus*).

Systematic Paleontology

FAMILY SQUALIDAE Bonaparte 1834
SUBFAMILY SOMNIOSINAE Jordan 1888
GENUS *Scymnodon ?ringens* Bocage and Capello 1864

Text-figs. 1, 3, 4A

Referred Specimen: LACM 60613, one incomplete lower right anterolateral tooth lacking tip of crown.

Description

Large lower right anterolateral tooth; apicobasal height 8.0 mm; mesodistal width of crown 5.30 mm; crown erect, broadly triangular and distally inclined at 40° (as preserved, apex of cusp missing); cusplets absent; distal blade small, apically convex and low crowned; mesial blade absent; mesial cutting ridge of cusp almost straight with very slight concavity; distal cutting ridge of cusp straight and distally inclined; serrations absent from all cutting ridges; crown faces convex, transverse ridges and grooves absent from labial and lingual crown foot; flange well developed, rectangular, not detached, mesodistally very broad and extends basally to a level slightly above the apical rim of the transverse notch and at the level of the basal edge of the central labial foramen; basal edge of flange weakly defined, digitiform and apically convex above the transverse notch; root rectangular, approximately equal to crown height and subdivided by a deep transverse notch into broad mesial and narrow distal root lobes; labial face with well developed, shallow, mesolabial depression high on root below crown foot;

Fig. 3. *Scymnodon ?ringens*; LACM 60613, from the late Pleistocene Palos Verdes Sand, Newport Bay Mesa, Orange County, California. A, lingual view; B, labial view. Scale line equals 1 mm.

mesolabial foramina numerous with one large foramen juxtaposed to mesial edge of flange and opposite basal edge of mesolabial depression; distolabial foramen mesodistally elongate, slit-like and irregular, located next to distal edge of flange on apical half of root; lingual attachment surface broad and extends high on root, almost to the crown foot; lingual longitudinal protuberance well developed, high on root, and divided in the middle by a deep central lingual foramen; distolingual depression broad, shallow, and extends from crown foot of blade to a point slightly below the distal protuberance of the lingual longitudinal protuberance; mesolabial depression visible lingually below the lingual longitudinal protuberance as a rounded depression; mesolingual foramina weakly developed except for one foramen which rests in a depression on the apical surface of the lingual protuberance near the mesial edge of the root, adjacent to the mesolabial depression; apical shelf strongly developed on the apical surface of the distal half of the lingual protuberance, narrowing medially toward the central lingual foramen and terminated distally by the gently rounded mesial edge of the distolingual depression; transverse notch well developed on basal edge of root; transverse groove short and connects transverse notch with central labial foramen; central labial foramen large and lies below lower half of root; crown-root flexure absent.

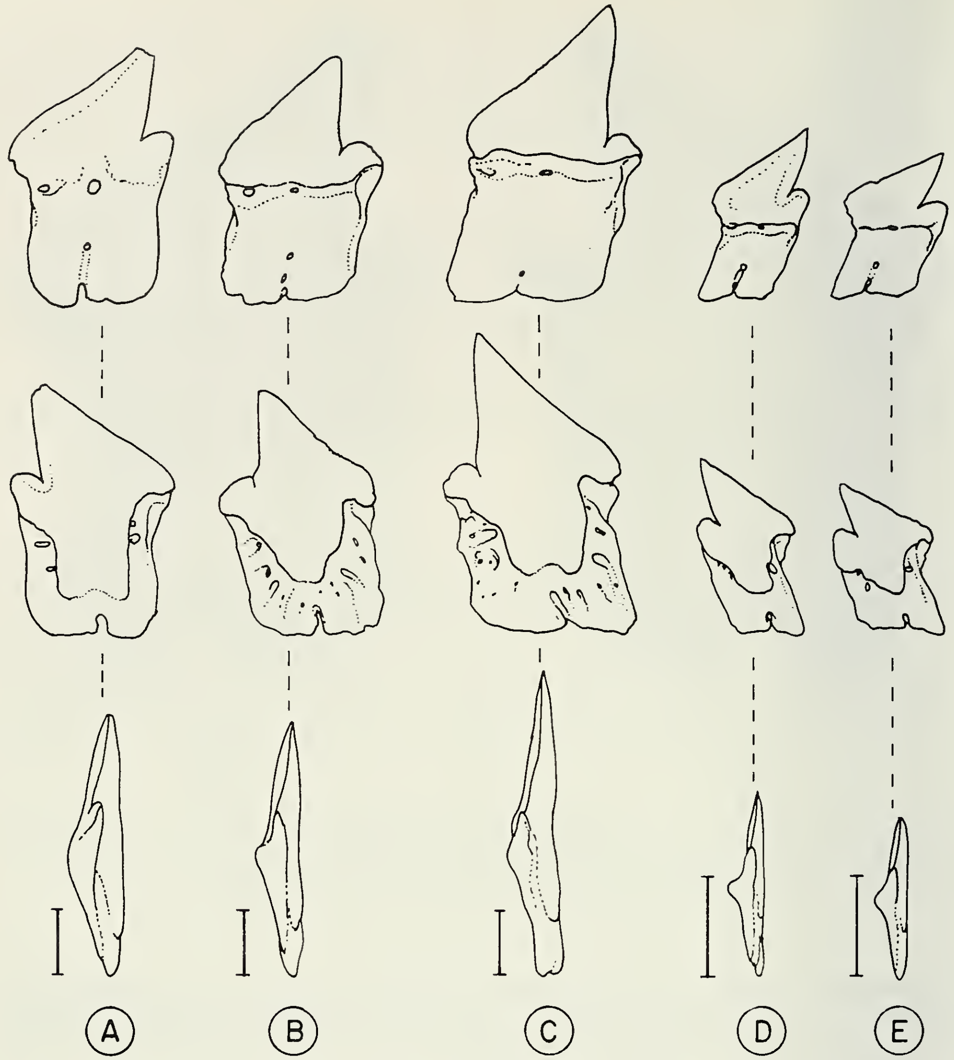

Fig. 4. Comparison of lingual (top row), labial (middle row) and distal (bottom row) views of lower right anterolateral teeth of: A, *Scymnodon ?ringens,* LACM 60613, Palos Verdes Sand, Orange County, California; B, *S. ringens,* LACM 37974-1, AL12; C, *S. ringens,* LACM 37974-1, AL10; D, *S. squamulosus,* SU 26784, AL16; E, *S. squamulosus,* SU26784, AL17. A–C, scale line equals 2 mm. D–E, scale line equals 1 mm.

Predepositional, but postmortum tooth erosion has modified its original morphology, resulting in the elimination or exaggeration of certain features. The labial and lingual crown face shows evidence of strong erosion, particularly at the crown foot. Both mesial and distal cutting edges are smooth, lacking former weak serrations. Foramina, particularly the CLIF, are enlarged and the lingual transverse groove connecting the transverse notch to the CLAF is mesodistally and apically expanded. The lingual longitudinal ridge has been rounded and is not as pronounced. The basal edge of each root lobe has been rounded and shortened. Exposed dental osteons on all root surfaces are further evidence of strong erosion.

Discussion

The high rectangular, tabular, and weakly bilobate root shared by LACM 60613, *Scymnodon,* and *Centroscymnus* readily separates them from lower anterolateral teeth of *Aculeola, Centroscyllium, Centrophorus, Centrophoroides, Centrosqualus, Cretascymnus, Deania, Squalus, Etmopterus, Heteroscymnoides, Somniosus,* and *Isistius.* The above genera and LACM 60613 differ from *Dalatias, Euprotomicrus,* and *Squalious* by lacking a central root aperture on the labial root face, from *Heteroscymnoides* by absence of symmetrical anterolaterals with strong and distinct blades (based upon figures in Fowler 1934), from *Oxynotus* and *Protoxynotus* Herman (1975) by absence of a coarsely serrated crown and very high and narrow root in all anterolaterals, and from *Scymnodalatias* by less attenuated crowns. However, the teeth of *Scymnodalatias* are very similar to those of high crowned species of *Scymnodon* (such as *S. ringens*), and the systematic relationships of this taxon to the somniosinae (in the sense of Compagno 1973) need to be reconsidered.

Bocage and Capello (1864:263 and 1866:19–20, 24, 29) separated *Centroscymnus* from *Scymnodon* on the basis of superficial characteristics of the crown morphology in the lower dental series. *Centroscymnus* was characterized as possessing low oblique crowns, as in *Centrophorus,* but lacking a symmetrical median tooth, whereas, *Scymnodon* possesses a symmetrical median tooth which is flanked by very high crowned symmetrical anteroposteriors with well developed gradient monognathic heterodonty. Subsequently, Rey (1928:486, fig. 152) notes that the "upper teeth along the central sector of the mouth are nearly as long as those midway out along each side of the jaw in *Centroscymnus,* they are much shorter than those midway along the jaw in *Scymnodon*" (Bigelow and Schroeder 1957:86).

The chief difficulty in separating *Centroscymnus* from *Scymnodon* stems from the traditional usage of the shape of the dermal denticles as a primary generic character. In particular, the presence of entire margined denticles with a concave outer surface has been regarded as a hallmark of *Centroscymnus* (and remains so), while sharks in all other respects similar, but having tridentate denticles, have been assigned to *Scymnodon* (Garrick 1959:75–76).

As pointed out by Tortonese (1952:386) and confirmed by Bigelow and Schroeder (1957:86), juvenile specimens of the genotype *Centroscymnus* and *Coelolepis* have tridentate denticles, and *C. crepidater* has tridentate denticles in the adult stage. These findings have led to a more cautious approach in dealing with dermal denticles as a primary generic characters.

More recently, Garrick (1959:76) has shown that superficial dental characteristics such as those outlined by Bocage and Capello (1864), Rey (1928), and Bigelow and Schroeder (1957) are not absolute. Garrick (1959:76) describes a New Zealand specimen of *C. crepidater* with a well developed symmetrical median tooth and erect anteroposteriors as in *Scymnodon.* In the same study, Garrick also notes that one New Zealand specimen of *C. plunketi* has the lower dentition of *Centroscymnus* and the upper dental pattern of *Scymnodon.*

The validity of one or both of the above genera must be resolved through careful comparative studies of external and internal anatomy. It is obvious from the above that dermal denticles and tooth characters vary continuously between presently recognized species (Garrick 1956, 1959, and L. J. V. Compagno, personal communication 1976). Unfortunately, illustrations of the dentitions of species in either *Centroscymnus* or *Scymnodon* given by any of the neoichthyologists writing on this subject are usually stylized or so generalized as to be useless for paleontological purposes. Neoichthyologists usually rely only upon characters of crown shape and gross dental formulae for separation of these genera. However, details of the root morphology, arrangement of formina, and basal crown structures (i.e., flange, peg, etc.) are critical characters which must be used for determining both generic and specific differences in fossil squalomorph teeth. The latter has been abundantly demonstrated in the works of Casier (1961) and Ledoux (1970), the only two existing studies on squaloid dentitions that provide adequately illustrated teeth.

Ledoux (1970) illustrated and described the dentition of *Centroscymnus* and *Scymnodon* and noted that the two genera possess numerous characters in common. When one carefully analyses the teeth of these two genera, one finds that there are no consistent characters which may be used for diagnosing one or the other genus from isolated teeth. This is abundantly demonstrated by observation of morphological data summarized for five species of *Centroscymnus* and two species of *Scymnodon* in Table 1.

If the lower anterolateral teeth of all species of *Centroscymnus* and *Scymnodon* were arranged in a morphological series according to cusp height and distal inclination, the two contrasting extremes of this morphocline would represent the characters which most ichthyologists recognize as the diagnostic difference separating the two genera. When the center of this morphocline is examined at the point where *Centroscymnus* ends and *Scymnodon* begins, it becomes very difficult, if not impossible, to define a unique set of characters which will serve to separate the genera from one another. It is at this point in neoichthyological studies that generic separation is based upon soft part morphology and not dentition.

Characters which, when taken in combination, separate LACM 60613 from *Centroscymnus coelolepis, C. cryptacanthus* and *C. owstoni* are a moderately erect crown (40°), smooth cutting ridges, rectangular flange which extends basally below the center of the root, a well developed transverse notch, high root, and a central labial foramen which lies well below the center of the root and is connected to the transverse notch by a short transverse groove. *Centroscymnus crepidater, C. plunketi, Scymnodon ringens* and *S. squamulosus* are all similar to LACM 60613 in possessing moderately erect to erect crowns, illustrating a gradation in this morphology from *Centroscymnus coelolepis* to *S. ringens*. *Centroscymnus crepidater* differs from LACM 60613 by having a short, triangular labial flange lying above the center of the root, a weak transverse notch (sometimes absent) and a central labial foramen which lies lower on the root. *Centroscymnus plunketi* resembles LACM 60613 in most aspects of its gross morphology but differs in having a narrower flange and less erect crown with a convex mesial cutting ridge of the cusp. LACM 60613 is similar to the more distal anterolaterals of *Scymnodon squamulosus* but possesses a longer and mesodistally broader flange and attains a much larger adult size.

In the absence of either comparative material or good dental illustrations of *Scymnodon obscurus,* it is not possible to characterize the latter or provide a discussion of its similarities and differences to LACM 60613.

Table 1. Checklist of morphological characters found in the lower anterolateral teeth of *Centroscymnus coelolepis*, *C. crepidater*, *C. owstoni*, *C. plunketi*, *Scymnodon ringens*, *S. squamulosus* and in *Scymnodon* from the Palos Verdes Sand (LACM 60613).

		Centroscymnus coelolepis	*Centroscymnus cryptacanthus*	*Centroscymnus crepidater*	*Centroscymnus owstoni*	*Centroscymnus plunketi*	*Scymnodon ringens*	*Scymnodon squamulosus*	*LACM 60613*
General Characters of tooth									
Crown:	Erect		X	X			X	X	
	Oblique	X	X						
	Serrated					X	X		
	Smooth	X	X	X			X	X	
	Blade	X	X	X	X	X	X	X	
	TG & TR								
Flange:	Rectangular	X	1		2	X	X	X	3
	Triangular			X					3
	In basal half of root	X	4		X	X	4		X
	At half root height							X	
Characters of the labial face									
	TN	X	X	5	X	X	X	X	X
	MLAD	X	X	X	X	X	X	X	X
	MLAF Large	X	X	X	X	X	6	X	X
	MLAF Small	X	7	7	X	7	8	8	X
	Root High	X	X	X	X	X	9	X	X
Characters of the lingual face									
	CLIF High	X	X	X	X	X	X	X	X
	CLAF almost reaches CLIF	X	X		X				
	CLAF below half root height			X			X		
	CLAF at half root height					X		X	
	TG very long	X	X		X				
	TG short			X		X	X	X	X
	One large MLIF on LLP	X	X	X	X	X	X	X	X

* Key: 1. Rounded and short. 2. Rectangular and narrow. 3. Intermediate, rectangular to triangular. 4. Slightly below half root height. 5. Weak or absent. 6. Large and low on root. 7. Large DLAF. 8. Intermediate DLAF. 9. Root height intermediate. X indicates presence of character.

LACM 60613 compares favorably with the dentition of *S. ringens* in possessing a large tooth with a broad and basally elongate labial flange and erect crown. Differences in root shape, size of foramina, and absence of cusp serrations can all be the result of poor preservation.

LACM 60613 most closely resembles the dentition of *S. ringens*; however, it is only questionably referred to this species because of the differences described above.

Conclusions

According to Bigelow and Schroeder (1957), nominal extant species referable to *Scymnodon* include *S. ringens* (Portugal and eastern north Atlantic); *S. squamulosus* (Gunther 1877) (Japan); and *S. obscurus* (Vaillant 1888)(northwestern Africa) and perhaps South Africa (Bass et al. 1976). There are no extant northeastern Pacific *Scymnodon* known at this time.

Teeth of the genus *Scymnodon* have been described from the early Miocene of northern California (Welton, B. J. *in* Phillips et al. 1976) and the genus is now known from the Late Pleistocene Palos Verdes Sand at Newport Bay Mesa, Orange County, California. The occurrence of *Scymnodon* at LACM 1066 represents the addition of a new taxon to the fauna of this locality and to the Palos Verdes Sand. On the basis of comparison with the dentitions of extant species of *Scymnodon,* LACM 60613 is referred to *S. ?ringens.*

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I am particularly grateful to Dr. Jacques Herman of Brussels, Belgium for donating the modern jaws of *Scymnodon ringens* to the Ichthyology Section of the LACM, and to the curators of this section, Dr. Robert Lavenberg and Dr. Camm Swift for making the specimen available for study.

The excellent illustration of the tooth in Figure 3 was drawn by Miss Mary Butler, Staff Artist of the LACM.

I would also like to thank Chevron Oil Field Research Company for support of this study and Mr. David Ward, Mr. Richard Huddleston and Dr. Leonard J. V. Compagno for reviewing and making suggestions toward improving this investigation.

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Relationships between Ecogeographic and Morphologic Variation of the Agile Kangaroo Rat (*Dipodomys agilis*) in Baja California, Mexico

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Abstract.—Relationships between ecogeographic and morphologic variation of the agile kangaroo rat (*Dipodomys agilis*) in Baja California, Mexico by Troy L. Best, *Bull. Southern California Acad. Sci.,* 80(2):60–69, 1981. Interlocality variation in temperature and precipitation were analyzed for 11 localities in Baja California where kangaroo rats (*Dipodomys agilis*) were collected. Correlations between these data and kangaroo rat morphologic variation were determined. Principal component I (size) of the morphologic data was significantly correlated with latitude and longitude for both sexes. The female component II (nasal width, ulna length, and hind foot length) was correlated with July mean temperature and January mean precipitation.

Previously I examined external, skeletal, bacular, and burrow variation in populations of kangaroo rats (genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico (Best 1978, 1981, 1982). The present study examines intraspecific morphologic variation and its covariation with ecogeographic parameters for one species of the group, *Dipodomys agilis*.

In their review of geographic variation studies, Gould and Johnston (1972) emphasized the importance of examining environmental correlates of geographic variation in populations. Since vertebrate populations are influenced by numerous environmental attributes simultaneously, analyses of general morphologic variation should include comparisons with generalized ecogeographic variation, rather than only to variables measured at each collecting site. Principal components analyses have been used herein to reveal general trends in the multi-character data sets for morphology, temperature, and precipitation. I have examined interlocality variation, and have determined the covariation of ecogeographic variables with morphologic variation. In addition, characters measured at each collection site have been compared to morphologic variation.

Methods

The 216 *D. agilis* collected for this study were from 11 localities in Baja California (Fig. 1). Table 1 lists the 19 morphologic characters examined; sample sizes and descriptions of these characters were given previously (Best 1978). The character numbers and mean values were taken from Best (1976, Appendix I). No female data were obtained for populations 2 and 8. The environmental phenograms and three-dimensional models utilize matrices and phenograms with all 11 localities represented; comparisons involving female matrices were based on 9.

For each locality, altitude, latitude, longitude, temperature, and precipitation were taken from the nearest weather station as determined from the maps in

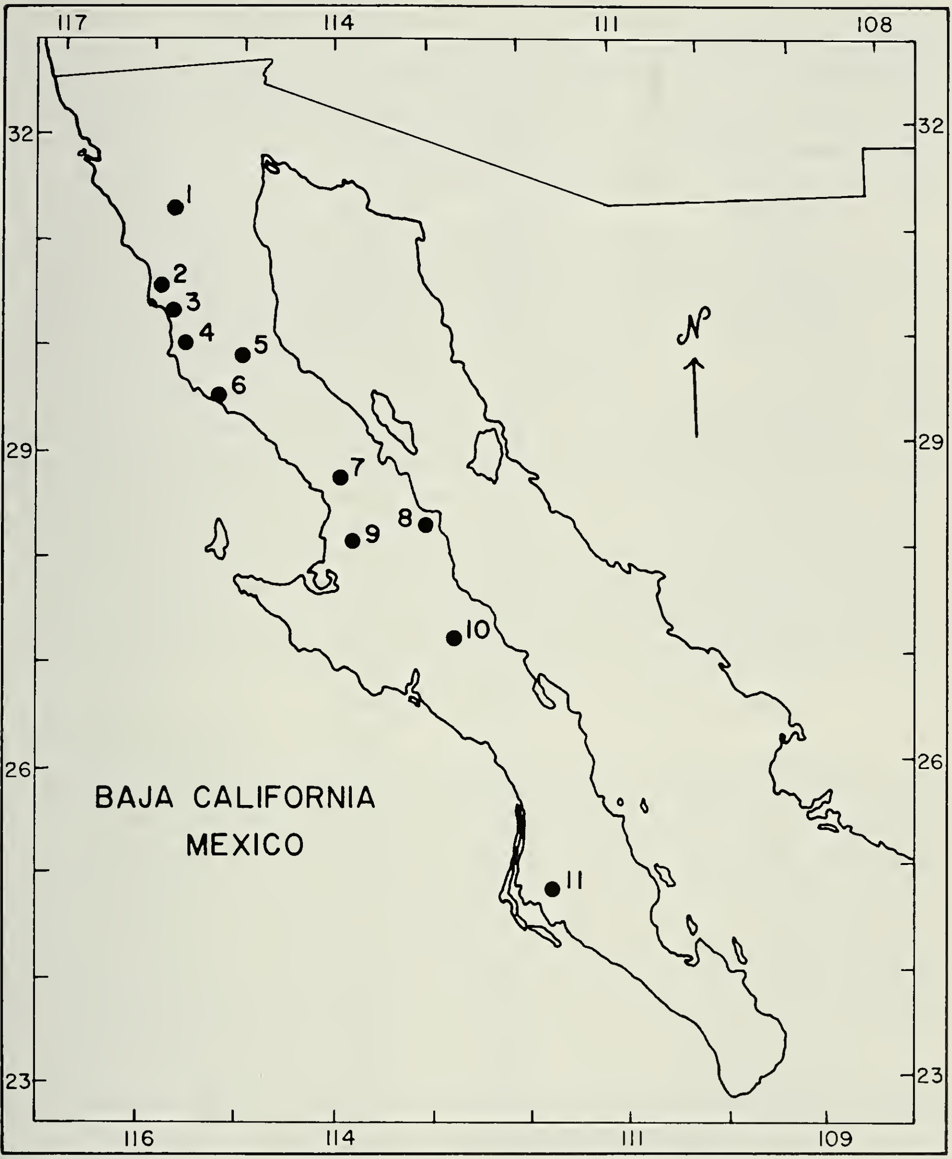

Fig. 1. Map of the 11 localities in Baja California, Mexico, where kangaroo rats (*Dipodomys agilis*) used in this study were collected. Numeral identifications, code names, nearest weather station (from Hastings and Humphrey, 1969), elevations, latitudes, and longitudes are: 1) TRINIDAD Valle de la Trinidad, 900 m, 31°10'30"N, 115°46'30"W; 2) ESCOAGIL Las Escobas, 24 m, 30°20'30", 115°53'30"; 3) SOCORRO El Socorro, 10 m, 30°20'00", 115°49'00"; 4) ROSAAGIL El Rosario, 15 m, 30°00'30", 115°43'30"; 5) AGUSTINE San Agustine, 580 m, 29°50'30", 115°00'00"; 6) CATARINA Santa Catarina (Sur), 450 m, 29°40'30", 115°09'30"; 7) SANBORJA San Borja, 375 m, 28°40'00", 113°56'00"; 8) EL-BARRIL El Barril, 100 m, 28°10'30", 112°54'00"; 9) R.ALEGRE Rancho Alegre, 500 m, 28°10'00", 113°53'00"; 10) IGNACIO San Ignacio, 105 m, 27°10'30", 112°54'00"; and 11) REFUGIO El Refugio, 29 m, 24°40'30", 111°45'30".

Table 1. Character loadings of the first three principal components of interlocality morphologic variation.

Char. No.[1]	Character	Sex	Principal Components I	II	III
Skin					
3	Tail length	♂♂	.548	−.685	.218
		♀♀	.863	−.096	.274
4	Hind foot length	♂♂	.691	.333	.191
		♀♀	.538	−.681	.262
5	Ear length	♂♂	.725	−.167	.391
		♀♀	.803	−.224	.003
Skull					
7	Greatest length	♂♂	.954	.202	−.080
		♀♀	.924	−.161	−.243
9	Interorbital width	♂♂	.702	−.077	−.503
		♀♀	.676	.214	−.570
10	Nasal length	♂♂	.844	.360	−.052
		♀♀	.781	−.541	−.112
11	Intermaxillary width	♂♂	.817	−.032	−.009
		♀♀	.849	−.161	−.469
12	Alveolar length	♂♂	.538	−.316	−.303
		♀♀	.389	.501	−.585
15	Basioccipital length	♂♂	.558	.340	−.684
		♀♀	.653	.212	−.258
16	Greatest depth	♂♂	.950	.108	−.027
		♀♀	.831	−.057	−.289
17	Greatest width	♂♂	.881	−.103	.136
		♀♀	.973	−.114	−.143
19	Nasal width	♂♂	.720	.493	.304
		♀♀	.574	.623	.063
Post-cranial skeleton					
23	Ulna length	♂♂	.784	.277	.250
		♀♀	.531	.754	.211
28	Scapula width	♂♂	.839	−.249	.373
		♀♀	.599	.577	.461
30	Scapula depth	♂♂	.891	−.081	−.022
		♀♀	.637	.094	.309
36	Femur proximal width	♂♂	.894	−.203	.075
		♀♀	.916	.023	.315
38	Pelvis depth	♂♂	.941	−.118	.040
		♀♀	.890	.195	.125
40	Pelvic foramen length	♂♂	.740	−.266	−.563
		♀♀	.728	−.514	.284
42	Number fused vertebrae	♂♂	−.021	−.832	−.053
		♀♀	−.315	−.106	−.833
Percent of total variation explained		♂♂	59.1	11.7	9.0
		♀♀	53.5	14.9	13.3

[1] Character numbers correspond to the 19 selected characters used by Best (1978).

Hastings and Humphrey's (1969) report on the climate of Baja California (see Best 1976, Appendices II and III, for temperature and precipitation means used in this study). For both temperature and precipitation I used 12 monthly and 4 seasonal means (Table 2). With one exception, collecting localities were within 20 km of a weather station. For Santa Catarina Landing, which is located on the west coast, the nearest weather station is approximately 35 km inland at an elevation of 450 m.

Product-moment correlation and average distance matrices (Sneath and Sokal 1973) were calculated from the standardized locality means of the morphologic, temperature, and precipitation data for each site. Clusters of localities from these original matrices were obtained with the unweighted pair-group method using arithmetic averages (UPGMA). Principal components were calculated from a matrix of correlations among characters and locality means. Projections of the localities were plotted on the first three principal components. A shortest minimally connected network computed from the original matrix of distance coefficients has been superimposed on these three-dimensional plots to indicate where possible distortion may be present.

Analyses were performed using the IBM 370 computer at the University of Oklahoma Computation Center. Bivariate correlations were determined with a program (BIVAR) written by Power (1967), and multivariate analyses were conducted using the NT-SYS series of programs (Rohlf, Kishpaugh, and Kirk 1972).

Results and Discussion

Interlocality Variation

Figure 2 shows phenograms for male and female morphologic variation constructed from correlation and distance matrices. Male (Fig. 1A) and female (Fig. 2C) correlation phenograms are very different, and do not reflect geographic groupings. In the male distance phenogram (Fig. 2B) populations 9 and 11 form a cluster distinct from the other populations, and for females (Fig. 2D) 5, 7, 9, and 11 are separate from the other populations. These results are in close agreement with my previous study that included measurements for *D. gravipes* (Best 1978), indicating that the inclusion of the second species does not greatly change the results of the analyses.

The temperature correlation phenogram (Fig. 2E) shows two very distinct clusters. This represents a separation of the northern-inland and Gulf of California side of the peninsula (localities 1, 5, 6, 8) from the southern and Pacific side of the peninsula. Temperature data for locality 6 were taken about 35 km inland from the actual collecting site, accounting for its inclusion in the Gulf of California-northern-inland cluster. The distance phenogram (Fig. 2F) shows localities 8, 10, and 11 clustered together and well separated from the other localities. These are in the southern half of the peninsula and have the warmest mean annual temperatures.

Two major clusters comprise the precipitation correlation phenogram (Fig. 2G). Localities in the upper cluster are all of the northern localities, except locality 5. The two major clusters in the distance phenogram (Fig. 2H) reflect the difference in mean annual precipitation of the localities. The cluster containing localities 1 and 9 represents the two sites with the greatest mean annual precipitation. Be-

Table 2. Character loadings of the first three principal components of interlocality temperature and precipitation variation.

Char. No.	Character	Temperature			Precipitation		
		I	II	III	I	II	III
1	January mean	.853	−.516	−.004	.658	−.446	.503
2	February mean	.893	−.435	−.080	.973	−.113	.067
3	March mean	.951	−.302	−.002	.931	−.036	.105
4	April mean	.993	−.054	−.061	.729	−.380	−.366
5	May mean	.983	.108	−.122	.527	−.353	−.257
6	June mean	.871	.465	−.150	.728	.177	.338
7	July mean	.808	.584	−.004	.511	.817	.006
8	August mean	.818	.565	.082	.202	.835	−.442
9	September mean	.924	.347	.134	−.334	.864	.104
10	October mean	.994	.057	.063	.227	.747	.167
11	November mean	.933	−.327	.066	.912	.240	.304
12	December mean	.908	−.407	.070	.667	−.038	−.371
13	Winter mean	.892	−.452	−.004	.936	−.161	−.030
14	Spring mean	.994	−.081	−.062	.806	−.102	−.295
15	Summer mean	.839	.543	−.024	.228	.869	−.230
16	Fall mean	.993	.050	.099	.169	.865	.201
Percent of total variation explained		84.2	14.6	0.6	43.3	29.9	7.7

cause of its extreme aridity, locality 8 is quite divergent from the others in the lower cluster.

Principal Components

The loadings of morphologic characters on the first three component axes are presented in Table 1 and three-dimensional projections are depicted in figures 3A and 3B. The character correlations with principal component I for males are high for all characters except 3 (tail length), 12 (alveolar length), 15 (basioccipital length), and 42 (number of fused vertebrae). For females the only low loadings were for characters 4 (hind foot length), 12 (alveolar length), 19 (nasal width), 23 (ulna length), and 42 (number of fused vertebrae). This component is taken to represent overall size in both sexes, since it accounts for most of the variation among characters. On principal component II, characters 3 (tail length) and 42 (number of fused vertebrae) have highest loadings for males. Characters 4 (hind foot length), 19 (nasal width), and 23 (ulna length) are highest for females. Component III has highest loadings for character 15 (basioccipital length) for males and 42 (number of fused vertebrae) for females. The three components explain about 80% of the total character variance for each sex (see bottom of Table 1).

Principal component I separates populations in figures 3A and 3B by size. For males, populations 1, 3, and 6 are the smallest and 9 and 11 are the largest. The same is true for females; however, the central populations in the figure are not as distinct as for males. This is due to the missing data for female populations 2 and 8, and to the separation along principal component II. This second component in males generally places the longer tailed forms toward the back of the model.

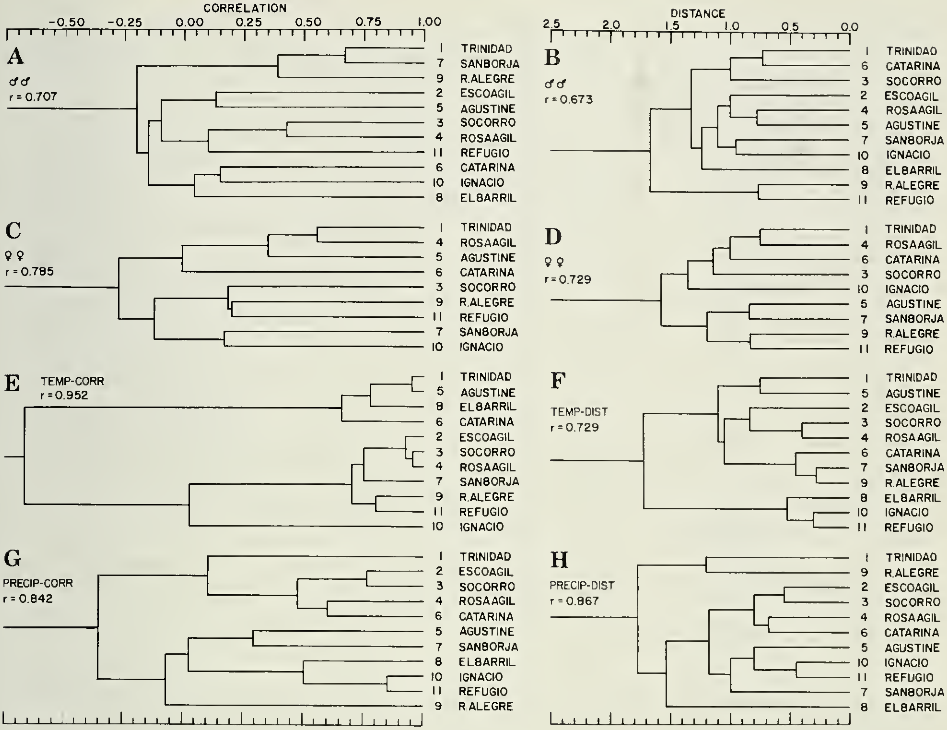

Fig. 2. Phenograms constructed from correlation and distance matrices for: (A and B) male kangaroo rats; (C and D) female kangaroo rats; (E and F) temperature; and (G and H) precipitation in Baja California. Cophenetic correlation coefficients (r) are given; accuracy of the diagrams in depicting interlocality relationships increases from left to right.

For females, populations with shorter hind feet and longer ulnas are in the front of the model. Component III for males separates populations with longer basioccipital lengths from population 2. For females the populations close to the base of the model generally have more fused vertebrae.

Plots of the first three principal components of temperature and precipitation are also presented in Figure 3. All 16 temperature characters for both sexes have high loadings on principal component I (Table 2), which represents 84.2% of the total variance. A listing of the localities from lowest to highest mean annual temperature is as follows: 2, 1, 3, 4, 5, 6, 9, 7, 10, 11, 8 (Best 1976, Appendix II). A similar order appears across the axis representing the first principal component in the 3-D model of temperature variation (Fig. 3C). Principal component II has highest loadings for January, July, August, and summer means. This component represents 14.6% of the total variation, and separates the northern localities into distinct Pacific coastal (2, 3, 4) and inland (1, 5, 6) groupings. As expected, the weather data for locality 5 has placed it more with the inland than coastal sites. Of the southern localities, number 11, representing a Pacific coastal site, is also displaced slightly by this component from the two Gulf of California localities (8 and 10). The third principal component has low loadings for all characters and represents less than one percent of the variation.

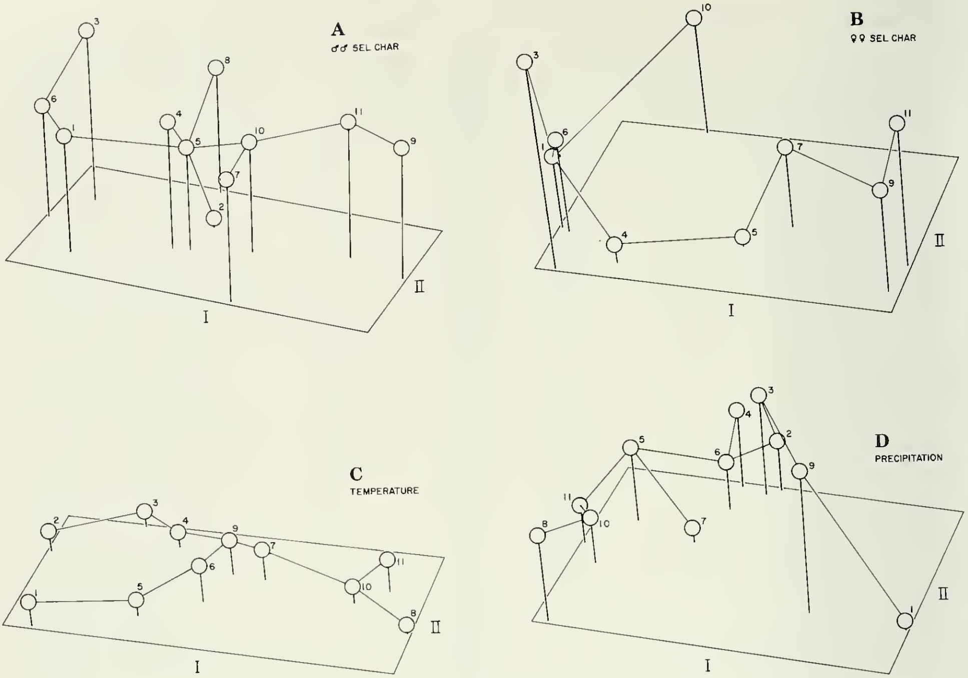

Fig. 3. Projections of localities onto the first three principal component axes of variation based on the matrix of correlations of 19 skin and skeletal characters of (A) male and (B) female *Dipodomys*, (C) 16 temperature characters, and (D) 16 precipitation characters for Baja California. The shortest simply-connected network is superimposed on the principal component space to indicate where possible distortion may be present. Numeral identifications are the same as listed below Figure 1.

Also listed in Table 2 are the results of a principal components analysis of the precipitation data. Figure 3D depicts a plot of these first three components. Principal component I accounts for 43.3% of the variation in the precipitation data. Highest loadings on this component were for the November through May, winter, and spring means. The high character loadings for winter means on component I is shown in the separation of localities along the first axis. Localities on the left have the least winter rainfall and those on the right the greatest. The second component of precipitation variation represents a relatively high percentage of the variation in the data (29.9%). Highest loadings are for July through October, summer, and fall means. Along principal component II the placement of localities 2 through 7 toward the back of the plot, 9, 10, and 11 in the middle, and 1 and 8 at the front appears to be primarily attributable to the summer mean data although the same general grouping of the localities is shown in the fall means (Best 1976, Appendix III).

Hastings and Turner (1965) found the Pacific side of the peninsula received its maximum precipitation in winter, and the Gulf of California side received most of its annual moisture during late summer and fall. These data closely agree with my principal components I and II, representing winter–spring and summer–fall precipitation means, respectively. The third component represents 7.7% of the

Table 3. Product-moment correlation coefficients calculated between the first three principal components of morphologic variation and 11 ecogeographic variables.[1]

Variable	Sex	Principal Components I	II	III
Latitude	♂♂	−.698*	.238	−.232
	♀♀	−.729*	.392	−.314
Longitude	♂♂	−.655*	.250	−.255
	♀♀	−.731*	.530	−.268
Altitude	♂♂	−.137	.586	.026
	♀♀	−.110	.063	−.429
Temperature—January mean	♂♂	.475	−.353	.453
	♀♀	.484	−.282	.441
Temperature—July mean	♂♂	.201	−.133	.247
	♀♀	.326	−.715*	−.154
Temperature—Principal Component I	♂♂	.453	−.325	.374
	♀♀	.594	−.589	.242
Temperature—Principal Component II	♂♂	−.219	.203	−.181
	♀♀	−.179	−.258	−.393
Precipitation—January mean	♂♂	−.109	.052	.086
	♀♀	−.113	.715*	.346
Precipitation—July mean	♂♂	.357	.146	.155
	♀♀	.218	−.190	.055
Precipitation—Principal Component I	♂♂	−.198	.401	−.066
	♀♀	−.283	.421	−.029
Precipitation—Principal Component II	♂♂	.358	−.133	.246
	♀♀	.409	−.431	.015

[1] For values marked (*) r is significant at $P \leq 0.05$.

variation with the highest loading for the January mean. No general relationship can be detected concerning the distribution of localities along component III.

Environmental-Morphologic Covariation

Results of analyses of covariation of the first three principal components of 19 morphologic characters of Baja California *D. agilis* with 11 ecogeographic variables are presented in Table 3. The first principal component of male and female *Dipodomys* variation is correlated significantly with latitude and longitude. In Kennedy and Schnell's (1978) analyses of 16 cranial characters for *D. ordii*, latitude, mean annual and January temperatures, and mean annual precipitation were significantly correlated with their males' principal component I (size). Latitude, annual, and January mean temperatures were significantly correlated with their female component I (size). Similar results were expected for *D. agilis* in Baja California, since species of *Dipodomys* are morphologically quite similar (Schnell et al. 1978). My data show that body size increases as latitude and longitude decrease (larger animals are in the southern populations). Geographically Baja California juts irregularly from near the United States border, near

32°31′N latitude, southeast across the Tropic of Cancer to Cabo San Lucas, near 22°50′N. This southeastward projection accounts not only for the latitudinal variation, but also for the longitudinal variation. Latitude is very significantly correlated with longitude ($r = 0.950, P < 0.01$) in Baja California. It is clear that the high correlation with longitude does not represent east-west variation across the peninsula, but simply is a result of changing latitude.

Male component II is not correlated with any of the ecogeographic variables, but principal component II for females is significantly correlated with July mean temperature and January mean precipitation (Table 3). These data for females show that southern populations, i.e., those with wider nasal bones, longer ulnas, and shorter hind feet, occur in association with high mean July temperatures and low January mean precipitation.

Principal component III of *Dipodomys* morphologic variation is not significantly correlated with any of the ecogeographic variables. For males, the only character with a high loading for this component was basioccipital length, and for females, number of fused vertebrae in the pelvic girdle (Table 1).

Conclusions

The analyses of environmental variables reported herein elucidate general trends in temperature and precipitation variation in Baja California. The northern region of the peninsula is cooler and receives most of its precipitation during the winter and spring. The warmer southern area has most of its rainfall occurring during the summer and fall. Both sexes of kangaroo rats are generally larger in the southern region of the peninsula; the males have longer tails and more fused vertebrae, and the females have wider nasal bones, longer ulnas, and shorter hind feet. The statistically significant relationships I found cannot be interpreted as cause-and-effect, but they do give an indication of the complex interrelationships of variables that likely interact with vertebrate populations in desert environments.

Acknowledgments

Many persons have contributed significantly to one or more aspects of this study. Most of them have been acknowledged previously (Best 1978, 1981), but again I wish to express my sincere thanks for their assistance. J. J. Hellack provided valuable assistance in data analyses. This project was partially supported by grants from the National Science Foundation to G. D. Schnell (GB-33062, GB-30814) and a Grant-in-Aid of Research award from The Society of the Sigma Xi.

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Color Pattern Morphs of the Kingsnake (*Lampropeltis getulus*) in Southern California: Distribution and Evolutionary Status

Richard G. Zweifel

Abstract.—Color pattern morphs of the kingsnake (*Lampropeltis getulus*) in southern California: distribution and evolutionary status by Richard G. Zweifel, *Bull. Southern California Acad. Sci.*, 80(2):70–81, 1981. Four basic color pattern morphs occur in southern California and northern Baja California: ringed, striped, Long Beach, and Whittier. Ringed is found throughout the wide range of *L. g. californiae,* whereas the other morphs apparently are confined almost wholly to coastal drainages from Los Angeles County to the vicinity of Ensenada, Baja California, though none but ringed occupies the whole area. Pattern intermediates between ringed (genetically recessive) and striped (dominant) occur infrequently within the range of striped and evidently more commonly than striped in peripheral regions. An hypothesis concerned with genes that modify the dominance of striped is advanced to explain this phenomenon. The two most abundant patterns, ringed and striped, are thought to function in different ways to confound sight-hunting predators. The various nonringed morphs in the study area and others known from central California and southern Baja California may have originated as independent mutations from ringed ancestors. If so, dispersal over improbably long distances is not required to explain their scattered distributions.

Snakes of the species *Lampropeltis getulus* in southern California exhibit striking color pattern polymorphism. The two commonest pattern morphs are so distinct that herpetologists for many years recognized two sympatric species, but following Klauber's (1936, 1939) demonstration that both "species" could occur within a single brood, most herpetologists adopted Klauber's view that the pattern variants represent morphs of a single subspecies, *Lampropeltis getulus californiae* (Blainville). Exceptionally, Smith (1943) felt that two hybridizing species were involved. His view was countered by Klauber (1944) and Mayr (1944), and the single species and subspecies concept has been generally accepted.

Despite the intrinsic interest of the situation, the problems of genetics, distribution, and evolution of the polymorphic populations remained unstudied for decades after the brief flurry of publication in the 1930's and 1940's. In 1977 Blaney, in a systematic revision of the species, gave information on distribution of pattern types and speculated on their evolution. I have recently (Zweifel 1981) presented breeding data and hypotheses to explain the genetic bases of the several pattern types. The purposes of the present contribution are to provide more detailed information on the geographic distribution of the pattern types than was appropriate to my 1981 paper and to consider explanations for the evolution and maintenance of polymorphism. Polymorphic populations in central California and

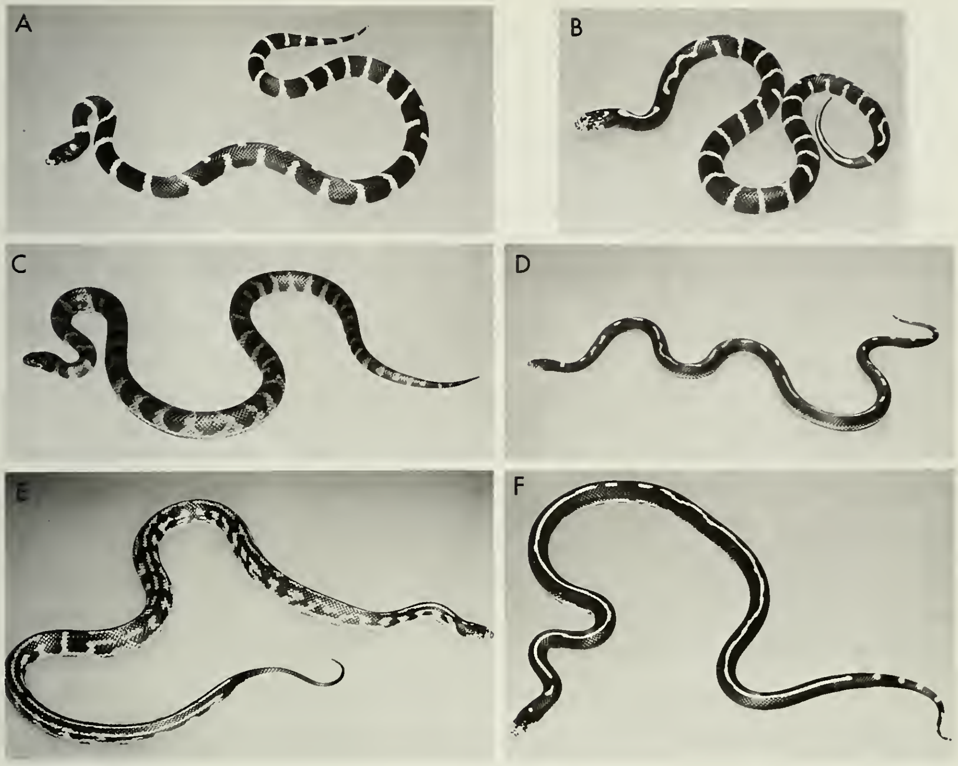

Fig. 1. Color pattern variation in *Lampropeltis getulus californiae*. A. Ringed, AMNH-LB 1125C, captive bred. B. Mixed, AMNH-LB 1223C, captive bred. C. Whittier, AMNH-LB 1176, Whittier, Los Angeles Co. D. Broken stripe, AMNH 114506, captive bred. E. Long Beach, AMNH 114505, Long Beach, Los Angeles Co. F. Striped, AMNH 111622, captive bred. Specimens in figures A, D, and F are siblings.

in the Cape region of Baja California, about which little is known, are dealt with only briefly.

Color Pattern Classes

Lampropeltis getulus californiae in southern California has four basic morphs of the dorsal color pattern: ringed, striped, Long Beach, and Whittier. In addition, patterns intermediate between ringed and striped, referred to as broken stripe and mixed, occur. The patterns are described by Zweifel (1981), so will be characterized only briefly here. Figure 1 illustrates the major variants.

Ringed.—Dorsum with narrow yellow to white rings on a brown to black background. Ventral surfaces (body and tail) with dark and light areas more nearly equal in width than on the dorsum and less regularly arranged.

Striped.—A yellow vertebral stripe on a dark brown background, scales of one or more lower dorsal rows each with a pale central spot. Underside of tail always dark, rest of ventral surface pale or dark.

Broken stripe.—As in striped, but arbitrarily defined as having six or more breaks in the vertebral stripe; short broken segments may be rotated at an angle to the vertebral axis, but do not form true rings. Underside of tail dark, rest of ventral surfaces usually pale.

Mixed.—Variable, but typically with striped patterns anteriorly and posteriorly and a more or less well-developed ringed area at midbody. Underside of tail dark, other ventral surfaces typically pale or as in ringed, rarely dark.

Long Beach.—Vertebral stripe present but generally broken and irregular; lateral markings resemble interrupted crossbands and stripes. Tail dark above, yellow on sides and largely dark below; other ventral surfaces pale to completely dark.

Whittier.—Dorsal pattern as in ringed, but obscured by a general melanic suffusion. Ventral surfaces wholly black.

The nomenclature for patterns used here is much the same as that of Klauber (1939). He did not recognize Long Beach as distinct type, considering it along with broken stripe and mixed as an ''aberrant'' pattern. Klauber recognized striped snakes with black venters as a separate class, but I have presented evidence that these are the homozygous individuals of the striped morph (Zweifel 1981).[1] Evidently Klauber saw no specimens of the Whittier morph. Blaney (1977) did not recognize Long Beach as an entity, but pooled it with the broken stripe and mixed pattern types. He examined a specimen of the Whittier morph and equated it with a black-bellied form of central California (see below).

Geographic Distribution of Pattern Classes

Information presented in this section derives largely from specimens I examined. Other authors have sometimes used the term ''striped'' to include snakes that I distribute among four categories, so published references are often not adequate for mapping purposes.

Ringed.—Snakes with this pattern occur throughout the distribution of *Lampropeltis getulus californiae,* from southern Oregon to the southern tip of Baja California and from the Pacific Coast to western Colorado and Arizona. Only ringed snakes occur in most of this area, and where other patterns are found, ringed is always in the majority.

Striped.—This pattern occurs from the vicinity of Ensenada in northern Baja California Norte northward to Riverside County, California (Fig. 2A). Because of inadequate sampling, the southern part of the range is not well documented, so striped snakes may occur south of the limits presently known. The northernmost striped snake that I examined is from San Jacinto, Riverside County (CAS 1216). I found no striped specimens from Orange, Los Angeles, or San Bernardino counties. Striped or possibly broken stripe snakes occur in the desert foothills of southeastern San Diego County (open circle in Fig. 1A; Klauber 1939), but it is not clear whether one or both forms are there. Except for this single record of Klauber's (I could not locate a specimen), nonringed snakes are known only from west of the drainage divide (dashed line in Figs. 2A–D).

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[1] Meager evidence from breeding experiments is bolstered by data obtained after Zweifel (1981) went to press. The cross of two heterozygous snakes produced the following seven offspring (genotypes and expected frequencies in parentheses): striped with dark venter, 2 (homozygous dominant, 1.75); striped with pale venter, 3 (heterozygous, 3.5); ringed, 2 (homozygous recessive, 1.75).

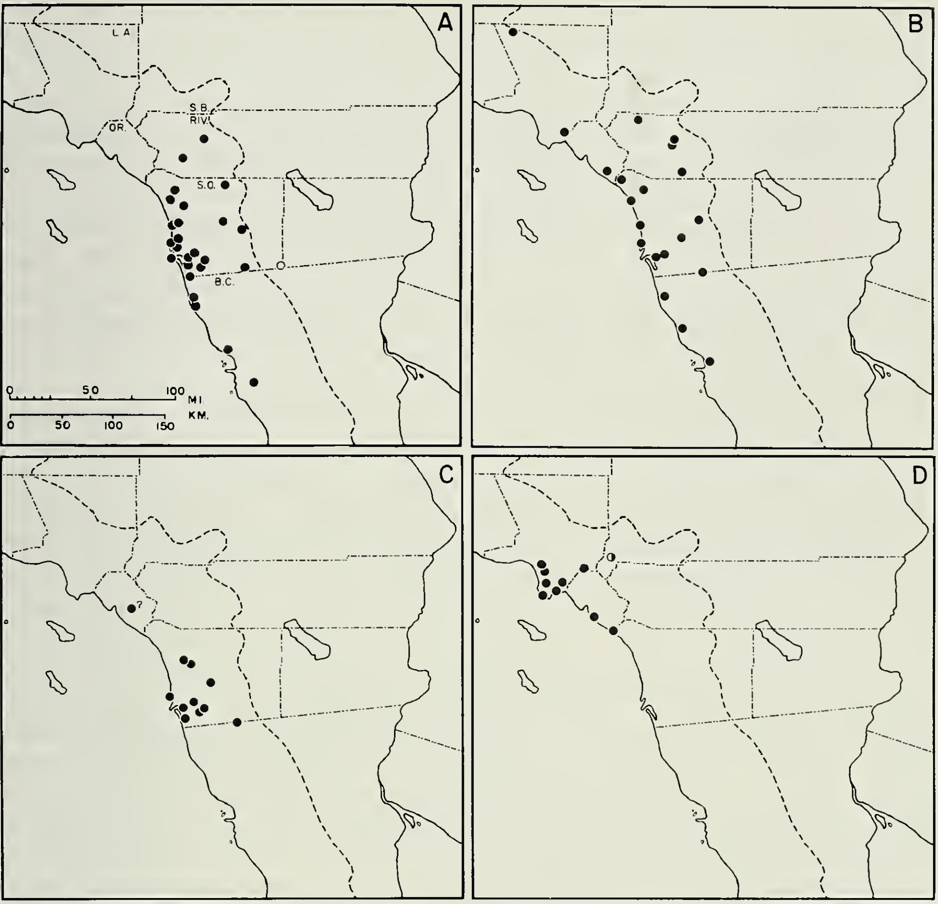

Fig. 2. Distribution of four pattern classes of *Lampropeltis getulus californiae* in southern Cali-ornia and northern Baja California, Mexico. Abbreviations: L.A., Los Angeles Co.; S.B., San ernardino Co.: OR., Orange Co.; RIV., Riverside Co.: S.D., San Diego Co.; B.C., Baja California. ashed line marks the watershed between coastal and interior drainages—essentially, the western edge f the desert region. A, striped (see text for open symbol); B, broken stripe; C, mixed (questioned ocality may be striped X Long Beach—see text); D, Long Beach (half closed circle indicates an typical specimen—see text).

In mapping the distribution of striped snakes, Blaney (1977, fig. 35) pooled ecords for my striped, broken stripe, mixed, and Long Beach categories (pers. omm.). He also mapped a record (UMMZ 70499) which he thought was from an Luis Obispo County (pers. comm.), from well to the north of the area in outhern California from which striped snakes have been known. However, the ata accompanying the specimen, which I have examined and which the Uni-ersity of Michigan received from L. M. Klauber, indicate only that the specimen as collected by Klauber at San Miguel Mountain, California, in the summer of 930. There are San Miguel Mountains in San Diego County within 15 miles of entral San Diego City. I think the specimen in question did not come from San uis Obispo County, as it is most unlikely that Klauber would have exchanged a unique specimen collected far to the north of the known range of its phenotype. It is much more likely that Klauber provided a local snake from the San Diego area.

Broken stripe.—Snakes with this pattern are found throughout the area occupied by striped snakes, and appear northward sporadically as far as Sandbergs in northwestern Los Angeles County (SDNHM 5562) (Fig. 2B). See comments under *Striped* for possible distribution in eastern San Diego County.

Mixed.—All specimens I have examined with mixed patterns are from San Diego County, except for one from barely across the border at Tecate, Baja California Norte (Fig. 2C). A specimen from Mission Viejo High School, Orange County (LACM 102515, the questioned locality in Fig. 2C) has a somewhat peculiar pattern and may not represent a true mixed type; it could have resulted from the crossing of Long Beach and striped snakes.

Long Beach.—Fifteen specimens of typical Long Beach pattern with specific locality data are from the coastal regions of Los Angeles and Orange counties, and one is from slightly inland (Friendly Hills, Los Angeles County, LACM 108302) (Fig. 2D). A specimen from farther inland (Chino, San Bernardino County, SDNHM 29084) is atypical, with a pattern that relates to the Long Beach pattern as the mixed pattern does to striped; it has several complete or nearly complete cross rings, and only traces of a vertebral stripe. A specimen cataloged from "San Diego Co." (S. R. Telford 1784, Univ. Florida collection) may have been obtained from a commercial dealer in the Los Angeles area, so the locality data cannot be verified (P. Meylan and H. Campbell, *in litt.*). Klauber (1939) described what seems to be the Long Beach phenotype, and stated: "These specimens are few in number, some 5 or 6 out of three or four hundred . . . they are of frequent occurrence in the vicinity of Laguna Beach, Orange County." I infer from the apposition of "frequent occurrence" and "5 or 6" that the latter were from San Diego County, but one wishes Klauber had been more specific as to their provenance. Dr. Howard Campbell (*in litt.*) reports having seen a snake of the Long Beach type in coastal San Diego County, but no specimen is available. I examined 139 nonringed snakes from San Diego County (127 in the SDNHM collection) without finding any of the Long Beach morph.

Whittier.—The four specimens of this pattern class are all from Los Angeles County. Three with the most precise locality data are from the coastal side of the mountains, within the area also inhabited by the Long Beach morph (Fig. 1D), and the fourth ("Los Angeles") probably is too: LACM 102493, Long Beach; LACM 58903, Los Angeles; AMNH 64365, Inglewood; AMNH-LB 1176, Whittier. Blaney (1977, fig. 35) mapped one of these specimens as his "pattern 28," equating it (incorrectly in my opinion) with another morph found in central California.

Other Polymorphic Populations of Western Kingsnakes

This paper concerns polymorphism in southern California and northern Baja California, but two other areas in which polymorphism occurs need brief mention. In the central valley of California, 150 miles or more from the nearest locality for a variant snake in southern California, occasional snakes are found that have the ventral surfaces totally black or almost so. The dorsal pattern may duplicate that of normal ringed snakes, but more often it is a confused mixture of irregular rings and stripe segments.[2] Snakes with black ventral surfaces and ringed dorsa superficially resemble the Whittier morph, but lack the overall dusky suffusion that tends to obscure the light rings of that form. There are no data relating to the incidence of variant snakes in the central California area, and their geographic distribution is only sketchily known. I have examined three specimens from Fresno County (CAS 41668, Jameson; CAS 41700, Firebaugh; USNM 11747, Fresno) and five from Merced County (all MVZ: 5434, Gadwall; 13847, 2 mi N Los Banos Duck Refuge; 78021, Dos Palos; 78022, 1 mi E Dos Palos; 78023, 4 mi S Dos Palos).

A striped pattern type of *Lampropeltis* distinct from the striped morph of southern California occurs in the Cape region of Baja California, some 700 miles from the nearest known locality for the northern striped form. Evidently it is uncommon—only five specimens have been reported since it was described as *Lampropeltis nitida* by Van Denburgh in 1895. By analogy with the situation in southern California, recent authors have not accorded it status as a species (or subspecies) distinct from the sympatric ringed *californiae*. Drewes and Leviton (1978), however, give credence to the idea that *nitida* represents a distinct species, though they present no evidence other than an additional specimen of this pattern type and speculation on biogeographic parallels.

Genetics

A brief exposition of the inferred and hypothesized genetics of the pattern classes is needed to support further discussion; for details, see Zweifel (1981). The ringed, striped, and Long Beach patterns evidently are mediated by three alleles at a single locus. Ringed is recessive to striped, and snakes with the striped dorsal pattern may be homozygous dominant or heterozygous. The broken stripe and mixed patterns occur in heterozygous snakes and may be the result of the breakdown of a modifer system that normally enhances the dominance of the gene for striping. Long Beach breeds true and is not a "hybrid" pattern (a Long Beach female had both Long Beach and ringed young), but the dominance relationship to ringed and striped has not been worked out. Whittier appears to be a melanistic version of ringed, but the genetics have been worked out only to the point that the melanistic condition is known not to be dominant.

Discussion

Geographic variation in color pattern is the norm among species of snakes with wide geographic distributions, but polymorphism is also common. Neill (1963) presented an excellent survey of polychromatism, and although other examples of color and pattern polymorphism among snakes have come to light since his summary, they add little to what Neill wrote. Evidently the appearance of striped

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[2] A snake of the latter sort serves as the holotype of Yarrow's (1882) *Ophibolus getulus eiseni*, type locality "Fresno," and currently considered a junior synonym of *L. g. californiae* (Blainville). Schmidt (1953) restricted the type locality of *californiae*, originally given as "Californie" (Blainville, 1835), to "the vicinity of Fresno." Because Blainville's snake had bright yellow undersides, it cannot represent the central California variant. If restriction of the type locality should prove necessary in the future, the type specimen should be restudied in light of information on the various pattern morphs now available.

snakes in typically blotched or ringed populations is not an uncommon phenomenon. I reiterate that polymorphism in *L. getulus* is not unique to southern California and northern Baja California; besides the other areas of polymorphism in *L. g. californiae* in central California and southern Baja California, striped or otherwise variant individuals of *L. getulus* occur in the eastern United States as well (Neill, 1963). The situation in southern California differs in that one of the alternate morphs—striped—is locally nearly as abundant as is the typical morph, whereas in other areas the variant morphs appear to be much less common. Aside from questions concerning the variety and geographic distribution of the polymorphic phenotypes treated in foregoing sections, there remain fundamental questions relating to the function, incidence, and evolution of the morphs.

Function.—I assume that the polymorphism seen in *Lampropeltis getulus californiae* results ultimately from mutation, and that even the rarest of these morphs is too common to be maintained by recurrent mutation alone. Why is the polymorphism maintained?

Endler (1978) attributed three main functions to animal color patterns: thermoregulation, intraspecific communication, and evasion of predators. Differences in relative amounts of dark and light pigment in the different morphs of kingsnakes could conceivably influence the rates at which radiant heat is absorbed and so have a thermoregulatory function. But if such an effect is operative, one might expect to find different proportions of the principal morphs in different habitats, and Klauber (1939) found no significant differences in proportions of ringed and striped snakes from coast to mountains in San Diego County.

Sexual dimorphism in snake color patterns is rare and does not occur in *L. getulus*. Therefore, it seems reasonable to dismiss any intraspecific communication function for the color patterns under consideration.

One possible protective aspect of color pattern—mimicry of a venomous species—can be eliminated, as there is no similar, sympatric venomous species to serve as a model. Two protective aspects of color pattern remain to be considered.

Patterns that contrast light stripes with a dark background are common to a great many species of snakes. Almost everyone who has observed such snakes in the field must be aware of the effect such a pattern of a rapidly moving snake has on human visual perception and, presumably, that of other predators. Rather than moving to follow the animal, the observer's attention tends to become fixed in one place. Suddenly the snake has left, and if the vegetation is adequately dense, or other cover is near, it may well be out of sight by the time the viewer becomes reoriented. In a relatively slowly moving snake such as a kingsnake, quick concealment would be especially vital. Striped kingsnakes do not live in desert regions, where sparse cover would render momentary confusion of a predator relatively ineffective.

The ringed pattern presumably conveys protection largely in a more static way. In the broken shade of a shrub or in tall grass, this pattern tends to conceal the snake from predators. In desert regions, where light-shade contrasts are likely to be more pronounced, the contrast between light rings and dark ground color in *L. g. californiae* is accentuated. When a snake with a ringed or blotched pattern moves, the concealing effect is lost, but the pattern can blend into a uniform blur, producing an effect not unlike that of a moving striped snake. Pough (1976) and

Jackson, Ingram, and Campbell (1976) discussed this visual blending illusion in terms of critical flicker fusion, and the latter authors discussed the visual effects of striped, unicolor, and other patterns as well.

The two extremes in *Lampropeltis* color pattern morphs—striped and ringed—can thus be considered as adaptive peaks in protective coloration, working in largely different ways to confound sight-hunting predators. The intermediate mixed pattern lies between the adaptive peaks and therefore might protect its bearers less well than would either extreme. The scarcity of intermediate patterns in the San Diego County population (see below) probably reflects strong selection for modifier genes that intensify the dominance of the gene for striped, thus polarizing the pattern types. A broken stripe pattern with the stripe not greatly disrupted should be scarcely less effective than striped, considering that the visual blending effect should compensate for small breaks in the light stripe when the snake moves.

The Long Beach pattern combines elements of both striped and ringed patterns but may, in contrast to the mixed pattern, convey benefits of both extreme patterns. Continuous segments of dorsal striping and shorter broken segments would, as suggested above for broken stripe, blend to give an effect similar to that of a complete stripe. At the same time, the broken aspects of the lateral pattern should blend in the same fashion as would a ringed pattern in a moving snake. With the snake at rest, the pattern should act as does the ringed pattern to conceal the snake. The critical difference from mixed is that mixed does not present a continuity of either pattern: striped segments are generally anterior and posterior, with the intermediate area ringed. The pattern has neither the advantage of full-body disruptive coloration, nor continuous striping.

I offer no explanation of the function of the pattern of the rare Whittier morph, nor any for the variation seen in ventral coloration. Ventral surfaces would normally be concealed from predators, and even if exposed to view (as could happen if a snake foraged above the ground, or were overturned by a predator) no particular advantage of one pattern—black, crudely ringed, or pale—over another is apparent to me.

Incidence.—The only good information on the incidence of morphs is Klauber's (1939) data for 1739 snakes recorded over a 16-year span in San Diego County. In this sample, the yearly incidence of "striped" (i.e., striped, mixed, and broken stripe) snakes varied from 27.6% to 50%, with a mean of 41.4%. Another tabulation separated the sample into snakes from the coastal region, inland valleys, foothills, and mountains. Klauber could detect statistically significant variation in neither temporal (yearly) nor geographic aspects of these data. Utilizing a group of 140 specimens that he assumed was free of sampling bias, Klauber derived proportions of ringed, striped, and aberrant morphs. He included "black ventrums" among his aberrant snakes. Because I consider his black ventrum class to be merely the homozygous dominant striped, I have adjusted his figures to the following: ringed, 76 (54.3%); striped, 56 (40.0%); broken stripe, 5 (3.6%); mixed, 3 (2.1%).

No comparable data for morphs in other regions exist. Blaney (1977) stated: "In Orange, Riverside and Los Angeles counties, however, only 6% of the population show any tendency toward striping and the mixed pattern [largely individuals of the Long Beach morph] is five times more abundant than the striped pattern.'' Blaney's figure of six percent presumably is based on specimens he examined and no doubt overstates the true abundance of these patterns, for collectors are much more inclined to save and preserve ''aberrant'' specimens of this common species. Among the nonringed morphs, Long Beach is clearly the more abundant in the northern coastal part of the region. I examined 13 specimens of this morph from Los Angeles County, compared with four Whittier and two Broken Stripe. Orange County yielded four Long Beach and one possible mixed (discussed previously), San Bernardino County had one ''mixed'' Long Beach, and Riverside County gave two striped and five broken stripe. If six percent of the museum specimens from these counties are nonringed (*fide* Blaney), the true proportion of any one of them in nature may well be under one percent.

Reasons for the geographic restriction of the nonringed morphs are not readily evident to me. A possible explanation of the selective disadvantage of the striped morph in desert regions where the ringed morph alone occurs, has been suggested above, but there is no similar explanation for the concentration of striped snakes on the coastal slope of San Diego County, where Klauber's data collected over 16 years suggest that a balanced polymorphism may exist, with striped snakes comprising about 41 percent of the population. Klauber showed that the relative proportion of ringed and striped snakes remains constant through diverse habitats from mountains to coast in San Diego County, and habitats of the sort in which striped snakes live extend well north of the range of that morph.

If color pattern is primarily adapted to minimizing predation, one might look to differences in predators in various regions for an explanation of differences in morph distribution. These snakes are active by day and night, depending on season and temperature, and are exposed to a variety of potential predators among both mammals and birds. The most significant sight-hunting predators are likely to be birds of prey. There are many records in the literature of raptors preying on snakes, some of the literature emphasizing snakes in the diet (e.g. Knight and Erickson 1976). However, I have found no published record of predation on *Lampropeltis getulus* and cannot even cite known predators! Moreover, the broad geographic and ecologic distributions of most mammalian and avian predators make it unlikely that the distribution of any of them offers the explanation sought.

One might suppose that the striped morph became established only relatively recently and is still enlarging its range. Any attempt to test this hypothesis by long-term monitoring of morph frequencies would be frustrated by the increasingly rapid alteration of natural environments in coastal southern California.

Evolution of polymorphism.—Three authors (Blanchard 1921; Blaney 1977; Smith 1943) have offered scenarios for the evolution of the varied color patterns seen among populations now referred to *Lampropeltis getulus californiae*. Briefly, the scenarios may be characterized by two common themes: (1) the differences in color pattern between striped and ringed forms imply considerable genetic differentiation, with the forms thought by two of the authors (Blanchard and Smith) to have achieved a specific level of differentiation; (2) the broad distribution and sympatry of ringed and nonringed pattern types reflect extensive dispersal of one form through the range of the other. Both Blaney and Smith devised allopatric speciation models for ringed and striped forms, Blaney considering the southern California and southern Baja California striped forms as monophyletic, whereas Smith thought the two to be parallel developments. Blanchard merely suggested that the striped form arose by mutation in central California and spread southward.

Evidence newly available casts doubt on the first of the two themes, as the ringed, striped, and Long Beach patterns appear to be mediated by three main alleles at a single locus (Zweifel 1981). The absence of detectable differences among the forms in any characters except color pattern also argues against much genetic differentiation. The second theme is similarly weak. The hypothesis of extensive dispersal through areas occupied by closely related forms, not too appealing a concept even if the populations had virtually attained species status, grows even less attractive when the forms are seen to be so little differentiated genetically.

Striped or partly striped individuals of *Lampropeltis getulus* appear occasionally in populations of the eastern United States (Neill 1963), and similarly variant individuals of other species of *Lampropeltis* are known as well (Ashton 1973; Gehlbach 1962). If these variations are due to heritable mutations and are not just individual developmental anomalies (I know of no breeding experiments to test this), they show how polymorphism may have originated in *L. g. californiae.* I suggest that the nonringed morphs of *californiae* scattered between central California and southern Baja California have arisen as several independent mutations that have prospered differentially. If this is the case, there is no need to invoke improbable long distance dispersal to explain their widely disjunct distributions.

Earlier investigators considered that the scarcity of pure striped snakes in the counties north of San Diego County was due to intergradation with the adjacent largely ringed population, but this required postulating a high degree of isolation between sympatric ringed and striped populations in San Diego County, where "intergrades" are relatively scarce (Klauber 1939). An explanation may better be sought in the relationship between the gene for striping and the modifiers postulated to enhance the dominance of that gene.

If the striped gene became established through mutation and subsequent selection somewhere in the region of greatest incidence, coastal San Diego County, its increase and spread would be favored by parallel selection for the modifiers. These would come to be present both in the genotypes of striped snakes and of ringed, though unexpressed in the latter, leading to purity of the two morphs in the presence of free interbreeding. In peripheral areas, a large proportion of the population would consist of snakes lacking the modifiers, so that offspring heterozygous for the striped gene would in most instances show an imperfect striped phenotype. This agrees with the observed condition. A corollary of this argument is that the modifiers cannot be closely linked with the gene for striping, or else the two would act as a single selective unit. In laboratory crosses (Zweifel 1981) a much higher proportion of broken stripe and mixed snakes appears than is seen in the San Diego County population. This suggests that modifier and striping genes are assorting independently.

I had hoped that a survey of nonringed specimens from San Diego County would show whether the proportion of striped to other nonringed (broken stripe and mixed) snakes varied in a regular fashion away from the obvious concentration of striped in the area of San Diego City. Though there are proportionately fewer striped specimens from localities to the north and east of the City, the number of specimens from peripheral areas is too few to inspire confidence, and the collections are almost certainly biased in favor of the "odd" specimens.

Acknowledgments

This study entailed examination of specimens held in several museums. A list of the museums, responsible curators, and abbreviations used in the text follows: American Museum of Natural History, New York (AMNH for preserved specimens, AMNH-LB for those still alive at this writing); California Academy of Sciences, San Francisco (Alan Leviton, CAS); Natural History Museum of Los Angeles County, Los Angeles (John Wright, LACM); Museum of Vertebrate Zoology, University of California, Berkeley (Harry Greene, MVZ); San Diego Natural History Museum, San Diego (Crawford Jackson, SDNHM); University of Michigan Museum of Zoology, Ann Arbor (Arnold Kluge, UMMZ); Museum of Southwestern Biology, University of New Mexico, Albuquerque (William Degenhardt, UNM); National Museum of Natural History, Washington (W. Ronald Heyer, USNM). I express my thanks to the curators listed, to Richard M. Blaney for generously sharing information on which his study was based, and to Howard Campbell and Peter Meylan for solving problems concerning specimens in the Florida State Museum.

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The Spring–Summer Ichthyofauna of Surfgrass (*Phyllospadix*) Meadows Near San Diego, California

Edward E. DeMartini

Abstract.—The spring–summer ichthyofauna of surfgrass (*Phyllospadix*) meadows near San Diego, California by E. E. DeMartini, *Bull. Southern California Acad. Sci.*, 80(2):81–90, 1981. Daytime underwater observations were made of the noncryptic fishes that inhabited shallow subtidal (0–3 m below MLLW) surfgrass meadows near San Diego, California, during the spring–summer periods of 1977 and 1978. The juveniles and adults of an atherinid fish (*Atherinops affinis*) were most ubiquitous and numerically abundant. Other common rocky, inshore and kelp (*Macrocystis*) bed fishes (e.g., *Oxyjulis californica, Girella nigricans, Embiotoca jacksoni*) also were commonly encountered. Although juveniles–subadults were present, adults predominated for many species.

Shallow subtidal beds of marine flowering plants are generally recognized as important feeding and sheltering habitats for many fishes, especially their juvenile stages, both in the temperate zone and the tropics (Kikuchi and Pérès 1977; Weinstein and Heck 1979; and references therein). Detailed studies have been made of the ichthyofaunas of wave-sheltered seagrass meadows in several areas of the world (e.g., see Adams 1976; Weinstein and Heck 1979; Robertson 1980; Horn 1980). Only fragmentary information, however, exists on the natural history (Feder, Turner, and Limbaugh 1974) and synecology (Ebeling, Larson, and Alevizon 1980) of the fishes inhabiting surfgrass (*Phyllospadix*) meadows of the western coast of North America. This lack of knowledge exists despite the fact that surfgrass habitat prevails in the shallow subtidal zone along much of the wave-exposed, rocky shorelines between Alaska and Baja California (Ricketts and Calvin 1968).

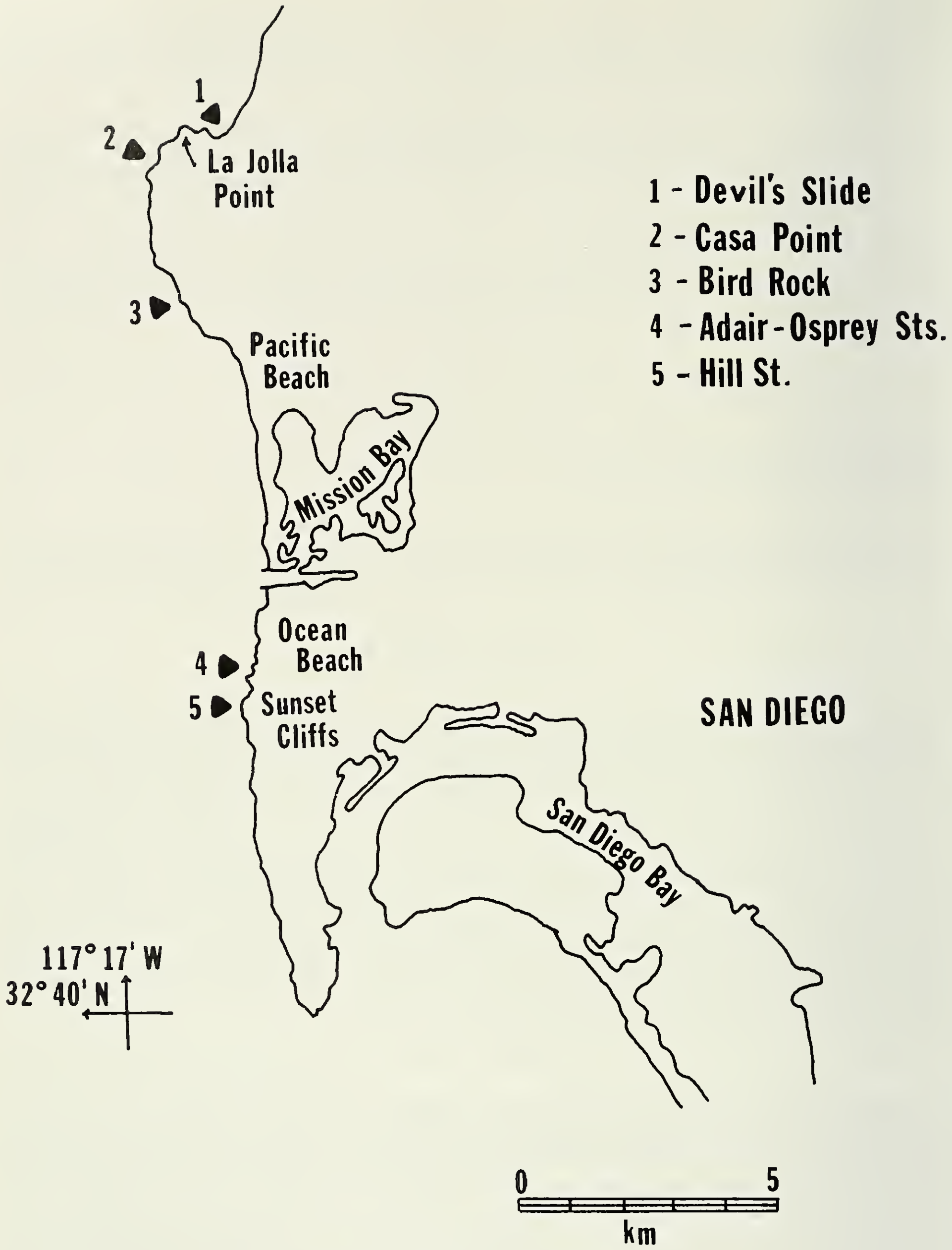

Fig. 1. Map of the study sites.

In this paper I characterize the noncryptic, diurnal, spring–summer ichthyofauna within *Phyllospadix*-dominated areas of the shallow subtidal zone (0–3 m below MLLW) at San Diego, California. The rocky substrate and extreme turbulence of this habitat precluded the use of nets and other indirect censusing methods such as ichthyocides. Hence fishes had to be surveyed by direct diver-observation. Sea conditions permit diving in this habitat only 25% of all days during the year, and water clarities are adequate (⩾3 m) for observations during only one-fourth of these calms. For this reason, I restricted surveys to April–August periods (1977, 1978), when mild sea conditions were most predictable.

Study Areas

Eleven of a total of 16 surveys were conducted at two La Jolla sites, Casa Point (seven surveys) and Devil's Slide (four surveys). I made another five surveys at three other sites within the Pacific Beach-Sunset Cliffs area of San Diego (Fig. 1). All sites are partially protected by offshore kelp beds (Sunset Cliffs) or coastline topography as well as kelp beds (La Jolla, Bird Rock). Surface water temperatures during the study varied from 17–24°C.

All of the surfgrass habitats surveyed were low relief (<1 m) sandstone bench rock with >90% *Phyllospadix* cover. Study sites included surge channels whose substrates of shell gravel, sandstone rubble, or cobble supported a diverse flora of bushy red (mainly *Gelidium* spp.) and brown (*Dictyopteris undulata*) algae. The large perennial kelp *Eisenia arborea* occurred at depths >3 m, seaward of the average lower bound of *Phyllospadix* dominance. The feather boa kelp *Egregia menziesii* also prevailed at shallow depths seaward of the surfgrass regions. Extensive rocky substrates occurred subtidally in all areas; and giant kelp (*Macrocystis*) beds, well developed at the time of study, dominated at 12–20 m depths from one to four km offshore of the various sites.

The physical characteristics, flora, and invertebrate fauna of intertidal regions at Casa Point and at Sunset Cliffs are described by Stewart and Myers (1980). Gunnill (1980) provides analogous data for the Devil's Slide and Bird Rock areas.

Methods

Observations.—I completed all surveys within one hour of high tide during mid-morning to early afternoon periods of gentle winds. Data were recorded on plastic slates and later transcribed to permanent records. Surveys were modified species-time random counts (see Jones and Thompson 1978), based on haphazard swims throughout roughly circular, 25-m radius (~2000 m^2) areas. Each one-hour survey was subdivided into 12 successive five-minute recording intervals. In addition to information on order of encounter (Jones and Thompson 1978), I tabulated data on frequency of occurrence (per five-minute interval) and estimated the numerical abundance of each noncryptic fish species. Cryptic forms (e.g., *Clinocottus analis, Gibbonsia* spp., *Gymnothorax mordax*) were inadequately censused and excluded from consideration. Fishes seen were classified as either juveniles, subadults, or adults, based on published length-maturity relations (Fitch and Lavenberg 1971, 1975; Feder et al. 1974). The proportion of fish in each maturity class was then calculated for most species, and summed over all surveys.

Analysis.—Surveys were too few and the choice of sampling dates and locations too haphazard to warrant rigorous analyses of numerical abundance data. Jones and Thompson (1978) scores, i.e., relative abundance indices based on order of encounter alone, are inadequate for characterizing the relative abundance patterns and community structure of southern California reef fishes (E. DeMartini

Table 1. List of the 27 taxa of noncryptic fishes observed. Source of names is Miller and Lea (1972).

Elasmobranchs

- Family Carcharhinidae
  - *Mustelus* sp.
  - *Triakis semifasciata*
- Family Rhinobatidae
  - *Zapteryx exasperata*
- Family Dasyatididae
  - *Urolophus halleri*

Teleosts

- Family Osmeridae
  - osmerid sp.
- Family Atherinidae
  - *Atherinops affinis*
- Family Scorpaenidae
  - *Sebastes serranoides*
- Family Serranidae
  - *Paralabrax clathratus*
  - *Paralabrax nebulifer*

Teleosts cont.

- Family Pristipomatidae
  - *Anisotremus davidsonii*
  - *Xenistius californiensis*
- Family Girellidae
  - *Girella nigricans*
- Family Kyphosidae
  - *Hermosilla azurea*
- Family Scorpididae
  - *Medialuna californiensis*
- Family Embiotocidae
  - *Cymatogaster aggregata*
  - *Damalichthys vacca*
  - *Embiotoca jacksoni*
  - *Hyperprosopon argenteum*
  - *Micrometrus minimus*
  - *Phanerodon furcatus*

Teleosts cont.

- Family Pomacentridae
  - *Chromis punctipinnis*
  - *Hypsypops rubicundus*
- Family Labridae
  - *Halichoeres semicinctus*
  - *Oxyjulis californica*
  - *Pimelometopon pulchrum*
- Family Clinidae
  - *Heterostichus rostratus*
- Family Pleuronectidae
  - pleuronectid sp.

and D. Roberts, ms.). For this reason, I evaluated the data using an alternative index of relative abundance. Numerical abundance and frequency of occurrence data were combined to form the integrated index of Alevizon and Brooks (1975). Three letter designations were used to code for three equal frequency classes:

A. species occurring in >67% of samples
B. species occurring in 33–67% of samples
C. species occurring in <33% of samples.

Four number designations were used to code for four levels of numerical abundance:

1. proportionate abundance >10%
2. proportionate abundance 1–10%
3. proportionate abundance 0.1–1%
4. proportionate abundance <0.1%.

Results

Species composition.—A total of 27 taxa representing 16 families of noncryptic elasmobranch and teleost fishes were observed at the various study sites on 16 surveys during the spring–summer periods of 1977 and 1978 (Table 1). A mean and mode of 15 (range 12–18) taxa were seen each survey.

Perciform fishes dominated in number of species (Table 1). The best represented perciform families were the viviparous surfperches (Embiotocidae), with six species; wrasses (Labridae), with three species; grunts (Pristipomatidae), with two species; damselfishes (Pomacentridae), with two species; and sea basses

Table 2. The abundance and frequency (a/f) characteristics and summary a/f categories for each of the 27 fish taxa encountered during the surveys. Categories based on log proportionate abundance and relative frequency of occurrence (Alevizon and Brooks 1975), summed over all 192 five-minute observation intervals of the 16 one-hour surveys.

		Numerical Abundance				Frequency of Occurrence	
Category	Taxon	Estimated Number Observed	% Total Fishes	Rank Total Fishes	Median No. Per Survey	% Total Intervals	Rank
A1	*Atherinops affinis*	24,032	56	1	500	83.8	1
A2	*Oxyjulis californica*	2261	5	4	100	68.8	3.5
	Micrometrus minimus	457	1	9	17	68.2	5
A3	*Hypsypops rubicundus*	399	<1	12	25	79.2	2
	Embiotoca jacksoni	329	<1	13	16	68.8	3.5
A4							
B1	*Hyperprosopon argenteum*	4820	11	3	61	52.6	8
B2	*Girella nigricans*	1225	3	5	30	53.6	7
	Medialuna californiensis	708	2	8	34	64.1	6
	Halichoeres semicinctus	437	1	10	15	50.5	9
B3	*Paralabrax clathratus*	159	<1	15	8	39.1	10
B4							
C1	*Chromis punctipinnis*	5031	12	2	0	5.2	19
C2	*Xenistius californiensis*	795	2	7	0	10.9	16.5
	osmerid sp.	1000	2	6	0	1.0	24
C3	*Anisotremus davidsonii*	403	<1	11	4	26.6	11
	Sebastes serranoides	99	<1	17	0	17.7	12
	Hermosilla azurea	118	<1	16	4	15.6	13
	Cymatogaster aggregata	283	<1	14	0	10.9	16.5
	Phanerodon furcatus	52	0.1	18	0	7.8	18
C4	*Damalichthys vacca*	33	<0.1	19	1	14.1	14
	Heterostichus rostratus	27	<0.1	20	0	13.0	15
	Urolophus halleri	5	0.01	21	0	2.6	20
	Pimelometopon pulchrum	4	<0.01	22	0	1.6	22
	Triakis semifasciata	3	<0.01	23	0	2.1	21
	Paralabrax nebulifer	2	<0.01	24	0	1.0	24
	Zapteryx exasperata	1	<0.01	25	0	1.0	24
	Mustelus sp.	1	<0.01	26	0	0.5	26.5
	pleuronectid sp.	1	<0.01	27	0	0.5	26.5
	Total Fishes	42,685					

(Serranidae), with two species. I also observed two species of small, suprabenthic sharks (Carcharhinidae). All other fishes seen were single representatives of various families (Table 1).

The 27 taxa were classified according to the abundance/frequency categories of Alevizon and Brooks (1975) (Table 2). *Atherinops affinis*, a nonperciform te-

Table 3. Proportion of juveniles, subadults, and adults of each of the 19 fish species seen during more than one survey and represented by 25 or more individuals sighted during the 16 surveys. Percentages expressed on the basis of the estimated total number of individuals sighted, summed over all surveys (see Table 2).

	% Total Individuals Sighted		
Species	Juvenile	Subadult	Adult
Atherinops affinis	P[a]	P[a]	P[a]
Sebastes serranoides	100	0	0
Paralabrax clathratus	39	40	21
Anisotremus davidsonii	34	62	4
Xenistius californiensis	20	25	55
Girella nigricans	21	11	68
Hermosilla azurea	0	1	99
Medialuna californiensis	0	100[b]	
Cymatogaster aggregata	23	36	41
Embiotoca jacksoni	11	3	86
Hyperprosopon argenteum	2	0	98
Micrometrus minimus	55[c]	45[c]	
Phanerodon furcatus	4	0	96
Damalichthys vacca	21	15	64
Chromis punctipinnis	>99	<1	<1
Hypsypops rubicundus	19	21	60
Halichoeres semicinctus	39	3	58
Oxyjulis californica	P[a]	P[a]	P[a]
Heterostichus rostratus	11	22	67

[a] Juveniles, subadults, and adults well represented, but proportions inestimable due to dense aggregations of mixed-sized individuals.

[b] Subadults and adults present, but mainly adults.

[c] Only young-of-the-year *M. minimus* recognizable as juveniles; larger, older fish classified as subadults-adults (see Terry and Stephens 1976).

leost, clearly dominated the fish assemblages as the most numerically abundant and the most ubiquitous species encountered (Table 2). *Oxyjulis californica* and *Micrometrus minimus* also were ubiquitous and abundant (Table 2). Another embiotocid (*Embiotoca jacksoni*) and *Hypsypops rubicundus,* a brilliantly colored, territorial pomacentrid, were ubiquitous and moderately abundant. A third embiotocid (*Hyperprosopon argenteum*) was occasionally encountered in very dense schools. *Girella nigricans, Medialuna californiensis,* and *Halichoeres semicinctus* were fairly ubiquitous and moderately abundant. *Paralabrax clathratus* was fairly ubiquitous but relatively rare. A second pomacentrid (*Chromis punctipinnis*) was infrequently encountered but sometimes very abundant. *Xenistius californiensis* was abundant on occasion. All of the remaining 15 taxa were rare to uncommon and rarely encountered (Table 2).

Proportion of immature to adult fish.—Table 3 provides a summary of the proportion of observed individuals of each species that were either juveniles, subadults, or adults. Nineteen of the 27 taxa were encountered in sufficient numbers (>25 fish) to allow a breakdown by maturity stage. Juveniles and(or) subadults clearly predominated, with adults absent or nearly so, for three of the 19 species (*Sebastes serranoides, Anisotremus davidsonii, Chromis punctipinnis*). I observed varying but nontrivial proportions of both the immatures and adult stages of eleven species (Table 3). Two other species (*Hermosilla azurea* and *Medialuna californiensis*) were represented by subadults and adults only. Adults predominated for three embiotocids (*Embiotoca jacksoni, Hyperprosopon argenteum,* and *Phanerodon furcatus*) (Table 3).

Discussion and Conclusions

Species composition.—Daytime observations of the more conspicuous fishes inhabiting surfgrass meadows near San Diego during spring–summer indicate that the most abundant and frequently encountered species are not endemic to surfgrass habitat. Rather, the major fishes observed in *Phyllospadix* beds are common inhabitants of giant kelp (*Macrocystis*) beds and other rocky, inshore habitats off southern California (see Carlisle, Turner, and Ebert 1964; Quast 1968; Turner, Ebert, and Given 1968, 1969; Feder et al. 1974; Ebeling et al. 1980). The fishes observed in surfgrass meadows near San Diego seem to have generalized habitat requirements (see Feder et al. 1974; also see discussion in Stephens and Zerba 1981). Most of these species are eurythermal (Quast 1968) and have broad bathymetric ranges. Only *Micrometrus* (Terry and Stephens 1976) and *Hermosilla azurea* and *Hyperprosopon argenteum* (Feder et al. 1974) have relatively narrow depth distributions. In general, shallow subtidal surfgrass meadows appear to be one of a wide variety of bathymetric regions and structured (rocky, vegetated) habitats occupied by these fishes (Quast 1968; Feder et al. 1974; Ebeling et al. 1980).

In particular, the more abundant species in surfgrass meadows near San Diego represent a large fraction of the fishes that are common at greater (to 30 m) depths on rocky bottoms at La Jolla (Quast 1968; Clarke 1970; Hobson 1971). Hobson (1971) noted the prevalence of *Atherinops, Oxyjulis, Hypsypops,* and *Phanerodon furcatus* relative to the lower abundances of *Chromis, Medialuna,* and *Damalichthys* at his 3–10 m station off La Jolla Point (Fig. 1). With the exception of *P. furcatus,* whose abundance increases in deeper subtidal regions at La Jolla (E. DeMartini, pers. obs.), Hobson's (1971) observations and those of this study are in agreement.

Many of the similarities between the fish faunas of shallow subtidal surfgrass meadows and the faunas of deeper rocky areas surely reflect the geographical proximity of rock reefs and kelp beds offshore of the study sites. Tagging studies would be needed to determine whether these offshore areas significantly influence shoreline fish composition, or vice versa.

Comparison with other surfgrass ichthyofaunas.—Burge and Schultz (1973) provide data on the fish fauna of a shallow (3 m) *Phyllospadix*-dominated area within Diablo Cove, about 90 km north of Point Conception (34.5°N). Juvenile rockfishes (*Sebastes* spp.) numerically dominated their censuses during summer–fall 1970 and 1971. Little is known about the surfgrass ichthyofaunas of southern California waters. Two of the commoner fishes (*Micrometrus minimus, Hyperprosopon argenteum*) observed in *Phyllospadix* beds during this study were included among the four embiotocids that comprised the "inner-marginal" group of Ebeling et al. (1980). These surfperches prevailed during the day in regions where surfgrass was plentiful shoreward of kelp beds along the mainland near Santa Barbara, California (Ebeling et al. 1980), although *Hyperprosopon* dispersed offshore at night (Ebeling and Bray 1976). The data of Ebeling and coworkers and Hobson (1971) suggest that my characterization of some of these major species is applicable to other surfgrass habitats in southern California.

However, factors such as the varying abundances of certain species throughout the Southern California Bight, and seasonal and annual variability, make the results of the present study less applicable to some other species. For example, *Halichoeres semicinctus* is rare within shallow subtidal *Phyllospadix* beds in the northern part of the Bight, as it is at other mainland habitats near Santa Barbara (Ebeling et al. 1980). *Hypsypops rubicundus* likewise is less common along the mainland in the northern Bight. Certain other fishes (e.g., juvenile *Sebastes serranoides*) occur seasonally in southern California inner coastal waters (Feder et al. 1974). My study probably overestimates the average, year-long representation of seasonal species in surfgrass meadows, since observations were made only when summertime seasonals are present in nearshore waters. Adams (1976) and others have noted major seasonal fluctuations in the abundance and composition of other seagrass ichthyofaunas. Some species (*S. serranoides*) also recruit sporadically near San Diego (E. DeMartini, pers. obs.). The data for species like these are influenced by fluctuations in year-class strength, which may or may not reflect an ''average'' situation at the time of study.

The observational nature of my data excluded cryptic species from consideration. Observations also were biased for daytime inhabitants of surfgrass and biased against fishes that might utilize surfgrass as feeding or sheltering areas only during the night. Distinct diel differences have been noted in the ichthyofaunas of diverse seagrass beds (e.g., Ogden and Zieman 1977; Horn 1980).

Surfgrass meadows as juvenile nursery habitats.—Many prior studies of seagrass fish communities have emphasized the role that these habitats play as nursery areas for juvenile fishes (e.g., Adams 1976; Kikuchi 1974). Seagrass meadows within bays and other protected (e.g., coral reef) habitats are highly productive (Zieman and Wetzel 1980) and provide both forage and shelter (the two key resources: Kikuchi 1980) for juvenile fishes. My observations suggest that *Phyllospadix* beds, unlike seagrass meadows in general, do not constitute major nursery habitat for fishes. Perhaps the surf-swept nature of *Phyllospadix* habitat provides little shelter and effects the transport of much surfgrass production to other habitats. At present, further speculation regarding the possible nursery function(s) of surfgrass meadows seems unwarranted. I stress that my observations should be considered preliminary because the study was limited to the April–August period, nighttime observations were not made, and the cryptic ichthyofauna was not censused.

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Hesperocimex Reared in Permanent and Electromagnets (Hemiptera: Cimicidae)[1]

Raymond E. Ryckman and Robert D. Sjogren

Abstract.—*Hesperocimex* reared in permanent and electromagnets (Hemiptera: Cimicidae) by Raymond E. Ryckman and Robert D. Sjogren, *Bull. Southern California Acad. Sci.*, 80(2):90–93, 1981. The continuous culture of 3 generations of *Hesperocimex* bugs in a permanent magnet at 4000 gauss and in an electromagnet at 14,000 gauss did not result in any identifiable mutations. Control and experimental colonies were prolific; fecundity and fertility were not impaired by the experimental conditions.

There is, and has been for many years, concern regarding the effects of magnetic and electromagnetic fields on biological organisms (Johnson and Shore 1976). Consequently a number of papers have been published describing the effects of magnetic and electromagnetic fields on vertebrates and invertebrates. Diebolt (1978) has reported on the negative influence of electrostatic and magnetic fields on *Drosophila melanogaster*; in addition he has reviewed the literature concerned with *Drosophila* in magnetic fields. Ondracek, Zdarek, and Landa (1976) have reported that the bug *Pyrrhocoris apterus* L. can detect and orient away from non-uniform microwave electromagnetic fields.

For this research it was necessary for the experimental animals to be small enough to pass through their life cycles between the poles of the magnets, to possess a rather short life cycle, and to be available. For the above reasons, cimicids of the genus *Hesperocimex* were chosen. *Hesperocimex* spp. are ectoparasites of birds, i.e., Purple Martins in the United States and Mexico. This study was conducted to determine the possible effects of permanent and electro-

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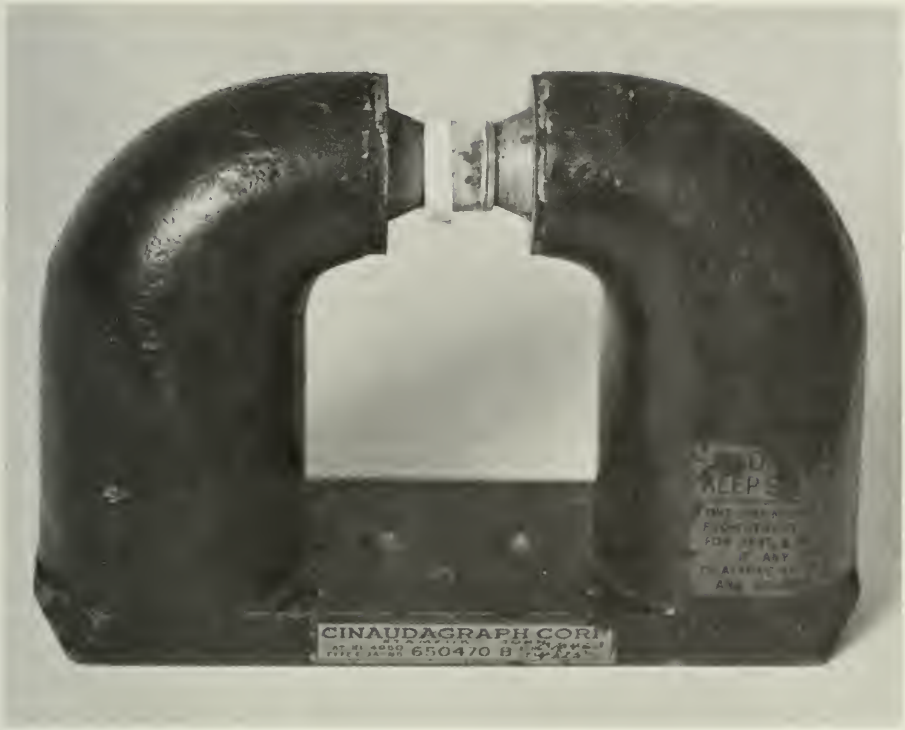

Fig. 1. Permanent magnet with rearing unit in place between the poles of the magnet.

magnetic forces on cimicids of the genus *Hesperocimex*. Preliminary studies were conducted with *Hesperocimex sonorensis* Ryckman 1958. Subsequent and more detailed studies were completed using a population of *Hesperocimex cochimiensis* Ryckman & Ueshima 1963.

In our opinion this is the first report of cimicid bugs having been reared for a complete generation, egg to egg, in permanent and electromagnetic fields. Experimental colonies of *H. cochimiensis* were reared in small circular plastic containers (diameter 1.9 cm × depth 1.5 cm) fitted between the pole pieces of a Cinaudagraph fixed magnet Type 6.3A485, as shown in Figure 1. This magnet produced a force of 4000 gauss between the poles. The control colonies were placed in a dummy or simulated magnet, i.e., between two circular iron pieces 2.5 × 6 cm. The water-cooled electromagnet was made by Precision Scientific Co., Electromagnet R-3, #76246; this electromagnet developed 14,000 gauss between the poles under the condition of its use. The power supply used 110–120 volts at 5 amps. In this case the experimental colonies were reared in blotter paper wafers held in place between the poles of the electromagnet. (The blotter paper wafers were made by cutting 2.5 cm circular holes in laminated layers of paper built up to 3 mm in thickness.) The bugs were held inside the wafers by fine mesh cloth glued on both sides of the blotter paper. A second set of control colonies was placed in a simulated magnet consisting of two circular pieces of iron as mentioned above.

All eggs used in this study came from a common pool, and were less than 16 hours old. Thirty-eight eggs of *H. cochimiensis* were placed in the permanent magnet and 38 in the control unit; the eggs began to hatch in both units by the 5th day and were all hatched in both units by the 6th day after oviposition. The nymphs in both these units were fed on the 7th day, one day after the last nymphs had emerged. Both colonies contained adult males and females on the 38th day post-oviposition, i.e., 31 days from their first blood meal. By the 41st day eggs were laid in the F_1 control colony and on the 42nd day in the F_1 magnetic unit. The last F_1 bugs became adults on the 61st day in the control colony and on the 80th day in the magnetic unit. From the first blood meal until the last adult was 54 days in the control and 73 days in the experimental colony.

F_2 eggs began to hatch on the 7th and 8th days respectively. From their initial blood meal to the first F_2 adults was 36 days in both the control and experimental colonies. The F_2 generation began laying eggs in the control unit at 7 days of age and in the magnetic unit at 8 days of age. Eggs laid by the F_2 colonies began to hatch by the 7th day. Large numbers of normal-appearing F_3 nymphs were produced by the F_2 colonies. The experiment was terminated with the third generation; all experimental colonies were continuously reared in electromagnetic fields.

A careful examination of all eggs, nymphs, and adults revealed normal specimens in the control and experimental colonies. At no time was there any indication of mutations or mortality due to the magnetic fields in which the bugs were reared. The F_1 control colony reached the adult stage in 31–61 days, and the experimental colony continuously reared in 4000 gauss reached the adult in 31–80 days. The developmental time is calculated from the first blood meal. The F_2 control colony attained the adult stage in 36–57 days and the F_2 experimental colony in 36–60 plus days. At the time the F_2 experimental colony was terminated there were still 5 nymphs that had not reached the adult.

Conclusions

The continuous culture of *Hesperocimex* bugs in a permanent fixed magnet to the 3rd generation did not produce any identifiable mutations; however, developmental time in the colonies reared in magnets was longer in the F_1 and F_2 generations than in the control colonies. The control and experimental colonies in the F_1 and F_2 generations were quite prolific in fecundity and fertility.

The continuous culture of *Hesperocimex* bugs in electromagnets of 14,000 gauss did not produce any identifiable mutations; the F_1 developmental time in the electromagnet was 38–67 days and in the control colony was 34–59 days.

In the electromagnet studies at 14,000 gauss, eggs began to hatch on the 6th day in the control colony and on the 5th day in the electromagnet. The F_1 nymphs reached the 2nd instar on the 12th day in the control colony and on the 11th day in the electromagnet. The first F_1 adults appeared in the control colony on the 34th day and on the 38th day in the electromagnet. Fifty percent of the bugs in the control colony became adults by the 40th day, and 50% reached the adult in the electromagnet colony by the 40th day. The last bug in the control colony became an adult on the 59th day, and on the 67th day in the electromagnet. The first generation bugs (F_1) in the control colony produced eggs by the 44th day and in the electromagnet by the 43rd day; i.e., from egg to egg in the control and electromagnet colonies was 44 and 43 days respectively. The first F_2 1st instar nymphs were produced on the 51st day in the control colony and on the 49th day in the electromagnet.

Acknowledgments

The power supply unit for the electromagnet was built by Dr. Roland C. E. Zimmermann. The manuscript was critically read by Donna G. Bentley.

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Bull. Southern California Acad. Sci.
80(2), 1981, pp. 94–95

Research Notes

Batrachoseps major (Amphibia: Caudata: Plethodontidae) from the Colorado Desert

On 26 January 1979, a small salamander was encountered on a cement walkway at the Palm Springs Desert Museum (DM). It was early morning (0855 hours) of an overcast day, and a slight rain had been falling for several hours. The specimen was identified as *Batrachoseps major,* the garden salamander, by Arden H. Brame, Jr., and archived in the museum (DM5-79-OA). On 9 April 1979, a second *B. major* was found in a backyard swimming pool in Palm Springs (DM6-79-OA). A search of collections in southern California revealed that another specimen had been collected on 20 March 1964 by S. B. Murphy in Andreas Canyon (5.5 mi S of Palm Springs post office), which is deposited at the Natural History Museum of Los Angeles County (LACM 85755).

These three specimens, along with two other observations not verified by individuals, lead me to believe that a resident population of *Batrachoseps major* is established within the city limits of Palm Springs (Riverside County, California). Palm Springs lies along the western margin of the subdivision of the Sonoran Desert, known as the Colorado Desert, where the mean annual precipitation in the vicinity of the collection sites is 13.7 cm with a mean annual temperature of 22°C.

These records and sightings have their origins along the eastern base of the San Jacinto Mountains that rise abruptly from the desert floor at 147 m. Homes and apartments now occupy the flatlands immediately adjacent to the steep hillside. Ornamental trees, shrubs and lawns are the dominant vegetation around most homes but plants typical of the creosote scrub community (*Larrea tridentata, Ambrosia dumosa, Encelia farinosa*) dominate the hillsides. Prior to the suburban development of the past few decades, the flatlands were covered with plant species of the creosote scrub community, interrupted occasionally by quasi-permanent streams, which drained the mountains to the west. An anonymously-collected, and doubted (Dunn 1926), series of individuals was deposited in the National Museum of Natural History (USNM 31638–41) in 1897 as from Palm Springs. My confirmation of the species in Palm Springs along with these older records suggest that *B. major* occupied this region prior to any made-made alterations of the environment. However, it is possible that the present salamander population is increasing in size because of the increase in moist habitats resulting from artificial landscape projects.

These records extend the known range of *Batrachoseps major* 19 km ESE, from the San Gorgonio Pass into the Colorado Desert. In addition, this species is only the third salamander definitely known to occupy a desert region, all of the genus *Batrachoseps. B. aridus,* the desert slender salamander, is the first (Brame 1970), *B. campi,* the Inyo Mountains salamander, the second (Marlow, Brode and Wake 1979). With these authenicated *B. major* records I should note that they are in close proximity to those of the remotely related *B. aridus,* which is south of Palm Desert.

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Protochrysomyia howardae from Rancho La Brea, California, Pleistocene, New Junior Synonym of *Cochliomyia macellaria* (Diptera: Calliphoridae)

W. D. Pierce (1945) described *Protochrysomyia howardae* from a series of puparia (Nat. Sci. Mus. Los Angeles Co., Invert. Paleo. [LACMIP] syntypes 3073-3083, 6439-6440) found in the end of a bone fragment of a Pleistocene bird (*Teratornis merriami* Miller) from the Rancho La Brea asphalt deposits, Los Angeles, California. Pierce asserted that he named the new taxon because ". . . little good work [had] been done in describing the puparia of modern flies." His frustration at not having a comprehensive identification guide is evident, but he did not indicate whether he had consulted specialists with knowledge of calliphorids. That the name *P. howardae* has stood until now is testimony to the fact that the taxonomy of fossil and recent insects have generally been considered separate disciplines; catalogs of modern insects typically ignore names of fossils, even those based on Pleistocene forms.

The *Teratornis* fragment (LACM B2309) was collected at 6.5 m (21.5 feet) deep in grid E-3 of Pit 3 at Rancho La Brea (Miller and Peck 1979). Although no direct age data exist for the types of *Protochrysomyia howardae* or the bird with which they were associated, radiocarbon dates of *Smilodon californicus* Bovard bone collagen at the 6.7 m (22 foot) level elsewhere in Pit 3 suggest an age of some 21,000 C^{14} years (Berger and Libby 1968).

A syntype of *Protochrysomyia howardae* that we studied (LACMIP syntype 3075) belongs to *Cochliomyia macellaria* (Fabricius). We are designating that specimen as lectotype of *P. howardae,* thus reducing the name *Protochrysomyia* to an objective synonym of *Cochliomyia.* LACMIP syntypes 3073–3074, 3076–3083, 6439–6440 become paralectotypes. Pierce (1945) correctly noted that the hind spiracles had open peritremes, placing his new species in the same group as *C. macellaria* and *Phormia regina* (Meigen). The walls of the spiracular slits have lateral swellings that distinguish this species from *P. regina*. The posterior tubercles of the puparia are as for *C. macellaria* as well shown in Hall (1948). A row of spines on segment 10 is interrupted dorsally and is absent on the entire dorsum of segments 11 and 12. Besides examining the exterior shell of the puparium, we broke off the anterior portion to free the last instar mouth-parts that generally adhere to the inside of the exoskeleton; the asphalt around the mouth-parts was dissolved in xylol and the tissue surrounding the cephalopharyngeal skeleton softened in a sodium hydroxide solution. The mouth-parts lack an accessory sclerite and their shape is also as shown in Hall (1948).

Cochliomyia macellaria ranges from southern Canada to southern South America, and is still common in southern California. It feeds on decaying animal matter, so it can be found in situations similar to the La Brea record. Additional calliphorid puparia have been found elsewhere in asphalt deposits at La Brea, but have not been critically studied.

We thank E. C. Wilson (LACMIP) for loaning us the syntypes that Pierce (1945) designated.

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The BULLETIN is published three times each year (April, August, and November) and includes articles in English n any field of science with an emphasis on the southern California area. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data n a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, achieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous reference of pronouns, and logically placed modifiers.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

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COVER: Ringed pattern variation in the kingsnake *Lampropeltis getulus californiae* found from southern Oregon to the southern tip of Baja California, and from the Pacific coast to western Colorado and Arizona. Photograph by Richard G. Zweifel.

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Date of this issue 16 August 1982

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The Taxonomy and Distribution of Some North American *Pogonomyrmex* and Descriptions of Two New Species (Hymenoptera: Formicidae)

Roy R. Snelling

Abstract.—The taxonomy and distribution of some North American *Pogonomyrmex* and descriptions of two new species (Hymenoptera: Formicidae) by Roy R. Snelling, *Bull. Southern California Acad. Sci.* 80(3):97–112, 1981. In the nominate subgenus, the new species, *Pogonomyrmex colei,* is described from females and males; it is a workerless social parasite in nests of *P. rugosus* Emery. The previously unknown sexual forms of *P. wheeleri* Olsen are described, and new data on the distribution of *P. tenuispinus* Forel are presented. Of indeterminate status when Cole revised *Pogonomyrmex, P. hindleyi* Forel is synonymized with *P. californicus* (Buckley).

In the subgenus *Ephebomyrmex,* a new key for workers is presented, correcting errors in that of Cole; two species are added: *P. guatemaltecus* Wheeler and *P. laevinodis,* new species. New distribution data are cited for *P. guatemaltecus,* extending the range from Guatemala to Mexico. *P. laevinodis* is described from workers from Baja California Sur, Mexico.

Introduction

The North American species of *Pogonomyrmex* Mayr, 1868, were revised by Cole (1968), who recognized 22 species in two subgenera: *Pogonomyrmex,* sensu stricto, and *Ephebomyrmex* Wheeler, 1902. One name, *P. californicus* var. *hindleyi* Forel, 1914, was of indeterminate status. The present contribution provides new taxonomic and distributional data on some of these species, corrects a few errors, disposes of *P. hindleyi,* and describes two new species.

Terminology

The descriptions below are patterned after those of Cole (1968) to facilitate comparison with his descriptions. A few comments on terminology are necessary.

I prefer to use propodeum rather than "epinotum" as Cole has it. Although the latter is traditional to ant systematics, it is at variance with terminology used throughout the remainder of the aculeate Hymenoptera.

Cole uses "gena" for the area usually designated the "malar" or "oculomandibular" area; his "postgena" is the true gena. I have not followed his terminology.

The following abbreviations are used in the descriptions that follow, consistent with those of Cole.

CI (Cephalic index)—(HW)(100/HL).

EL (Eye length)—Maximum length of compound eye in lateral view.

EW (Eye width)—Maximum width of compound eye in lateral view.

HL (Head length)—Length of head, in full face view, from anteriormost portion of clypeus to top of occiput.

HW (Head width)—Maximum width of head, excluding the eyes, in full face view.

OI (Ocular index)—(EL)(100/HL). Francoeur (1973) defined OI as (EL) (100/HW). I have made no effort to determine which of these indices has "priority" but am following Cole to be consistent with his work on this genus and because I prefer it. In any event, authors should be aware of this confusion and be careful to specify which formula they are employing.

PNL (Petiolar node length)—Length of only the node of the petiole as measured in profile.

PNW (Petiolar node width)—Maximum width of the node of the petiole in dorsal view.

PPL (Postpetiolar length)—Maximum length of the postpetiole in either profile or dorsal view.

PPW (Postpetiolar width)—Maximum width of postpetiole in dorsal view.

SI (Scape index)—(SL)(100/HW). Cole incorrectly cites this as (SL) (110/HW).

SL (Scape length)—Maximum length of the scape, exclusive of the basal condyle.

WL (Weber's length)—Length of the thorax (including the propodeum) in profile view, measured diagonally from the anterior declivity of the pronotum (excluding the pronotal neck) to the tip of the metasternal lobe.

Institutional Abbreviations

The materials examined are in the collections of the following institutions: American Museum of Natural History (AMNH), Museum of Comparative Zoology, Harvard University (MCZ), National Museum of Natural History (USNM), Natural History Museum of Los Angeles County (LACM), University of California, Berkeley (UCB), University of California, Davis (UCD).

Systematics

Subgenus *Pogonomyrmex*

Pogonomyrmex (*P.*) *californicus* (Buckley, 1867)

Forel (1914) described *P. californicus* var. *hindleyi* from a single worker from Escondido, California. Later authors were unable to do much with the name. Cole (1968) rightly equated Creighton's (1950) interpretation of *P. hindleyi* with the spinose variant of *P. maricopa* Wheeler, 1914. Since Cole had not seen the type of var. *hindleyi*, he treated it as a "species indeterminata."

Forel's type is in the collections of the Museum d'Histoire Naturelle, Geneva and was made available to me. The specimen is in good condition but is heavily encrusted with dirt. I cleaned enough dirt from the specimen to determine that the juncture of the dorsal and posterior propodeal faces is weakly angulate and that the thoracic integument, between the fine rugulae, is shiny. In all respects, *P. californicus* var. *hindleyi* agrees with a common variant form of *P. californicus*; it is clear that this form may be safely relegated to the synonymy of *P. californicus* (NEW SYNONYMY).

Pogonomyrmex (*P.*) *colei* New species
Figures 1–11

Diagnosis.—Separable from other members of rugosus group by the following combination of characters. Female: HW less than 1.80 mm; face, between eye and frontal lobe, contiguously punctulate, with scattered piligerous punctures; dorsum of petiolar node with broad, shallow longitudinal impression. Male: HW less than 1.55 mm; body hairs short, stiff, blunt; basal face of propodeum finely rugulose; color blackish brown.

Description.—Female: HL 1.60–1.68 mm; HW 1.67–1.77 mm; CI 100–106; SL 1.17–1.23 mm; SI 67–72; EL 0.37–0.40 mm; EW 0.28–0.32 mm; OI 22–24; WL 2.23–2.43 mm; PNL 0.50–0.57 mm; PNW 0.47–0.50 mm; PPL 0.40–0.43 mm; PPW 0.73–0.83 mm.

Mandible (Fig. 3) with six teeth along strongly oblique masticatory margin; subapical tooth about half as long as apical tooth, closely appressed to it; first and second basals approximately equal in length, well separated from each other; penultimate basal a little shorter, subequal to basal tooth, which makes a nearly straight angle with upper mandibular margin; all teeth, except sometimes basal, moderately sharp.

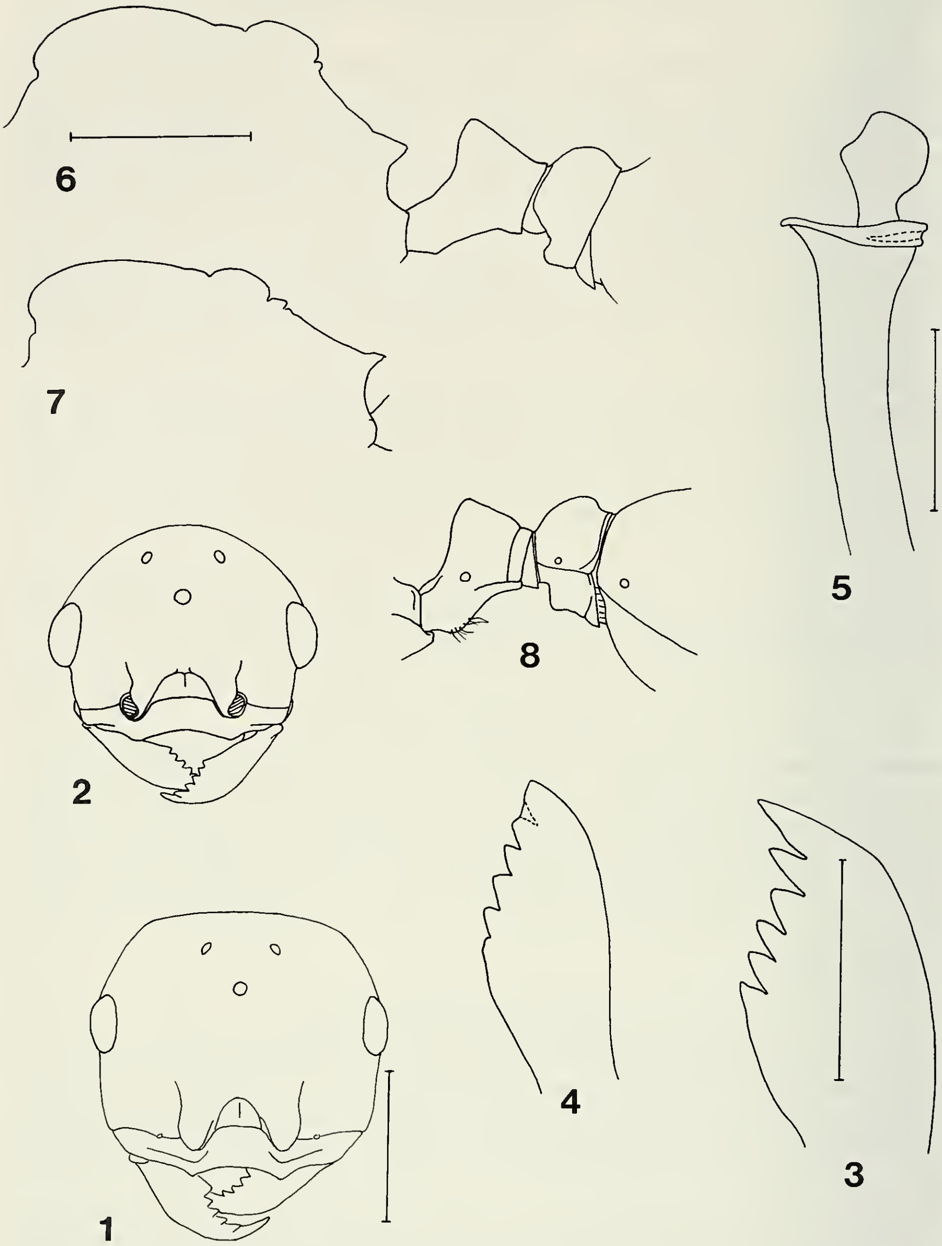
Basal enlargement of antennal scape (Fig. 5) flared, declivity of superior lobe meeting shaft in a nearly straight line; basal flange thin, reaching apex of superior lobe; lip weak, only slightly curved distad; point weak or absent.

Longitudinal rugulae extending from frontal lobes to occiput, fine and dense on frontal lobes, becoming a little coarser and less close toward occiput; weak, irregular rugulae between eye and mandible and on lower gena; no rugulae surrounding antennal fossa. Side of head, between eye and median band of rugulae, dull, irregularly microrugulose, contiguously punctulate and with scattered minute piligerous punctures, a few obscure rugulae near eye margin; upper gena weakly reticulose, interspaces microrugulose. Frontal area sharply depressed. Lateral lobe of clypeus weakly compressed, not projecting shelflike below antennal fossa. Disc of middle lobe of clypeus roughened, preapical area coarsely reticulopunctate.

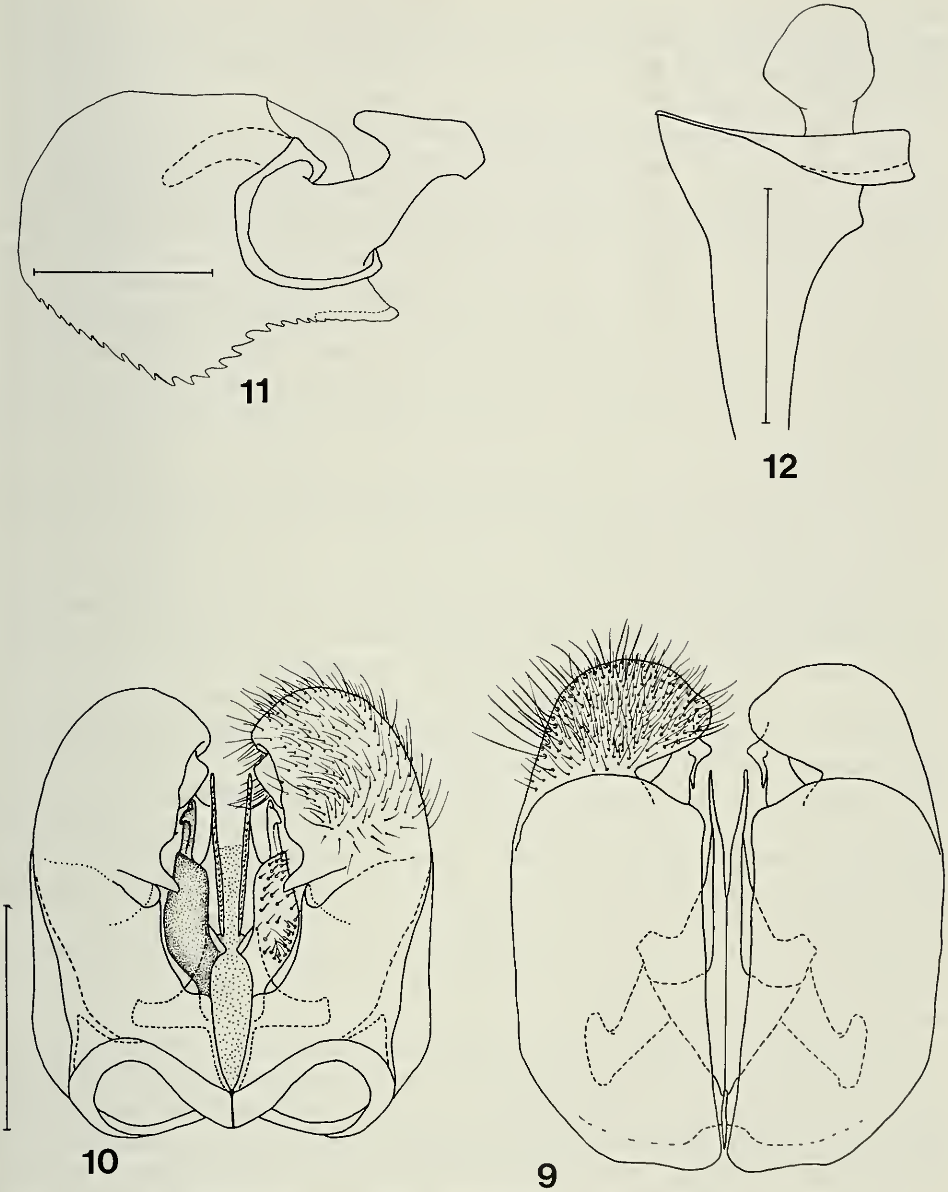
Contours, in lateral view, of thorax, petiole, and postpetiole shown in Figure 6. Propodeal spines short, broad at base, blunt to acute.

Node of petiole, in profile, coniform, length of anterior and posterior declivities subequal, or posterior slightly longer; dorsum with weak to moderate longitudinal median impression, crest notched in posterior view; ventral process of anterior peduncle weak or absent. Postpetiole, in dorsal view, subglobular; ventral process weak.

Pronotum with fine transverse and somewhat irregular rugulae, interspaces slightly shiny, weakly punctulate. Mesoscutum finely and irregularly longitudinally rugulose, interspaces moderately shiny; parapsis and area anterior to it with few or no rugulae. Scutellum smooth, polished. Upper plate of mesopleuron with fine, longitudinal rugulae and weakly punctulate interspaces; lower plate similar but becoming reticulorugose toward posterior margin. Metapleuron longitudinally rugulose, rugulae a little coarser than those of mesopleuron. Side and base of propodeum finely and closely reticulorugulose; infraspinal face mostly smooth and shiny. Node of petiole roughened and irregularly rugulose. Node of postpet-



Figs. 1–8. *Pogonomyrmex colei*: 1, 2, female and male head, respectively, frontal view; scale line = 1.00 mm. 3, 4 female and male mandibular apex, respectively; scale line = 0.50 mm. 5, base of scape of female, scale line = 0.25 mm. 6, female, profile of thorax, petiole, and postpetiole; scale line = 1.00 mm. 7, male, profile of thorax; scale line = 1.00 mm. 8, male, petiole and postpetiole, lateral view.



Figs. 9–12. 9–11. *Pogonomyrmex colei*: 9, male genitalia, dorsal view. 10, same, ventral view; scale line = 0.50 mm. 11, male aedeagus, lateral view; scale line = 0.25 mm. 12, *P. wheeleri*: base of scape of female; scale line = 0.25 mm.

iole slightly shiny and weakly punctulate, with a few weak, irregular rugulae at side and across posterior margin. Gaster smooth, shiny, without distinct shagreening.

Body hairs moderately long and abundant, mostly slender and acute. Some hairs on mesocutum, especially anteriorly, blunt-tipped. Hairs on frontal region short, fine, blunt-tipped. Side of pronotum and mesopleuron with hairs sparse, short, mostly acute, a few blunt. Erect hairs of gastric dorsum weakly pointed to blunt. All hairs golden.

Body color dark reddish brown, gaster more reddish.

Male: HL 1.33–1.43 mm; HW 1.40–1.50 mm; CI 93–99; SL 0.83–0.87 mm; SI 56–60; EL 0.40–0.43 mm; EW 0.30–0.33 mm; OI 29–32; WL 2.03–2.17 mm; PNL 0.40–0.47 mm; PNW 0.47–0.50 mm; PPL 0.38–0.50 mm; PPW 0.70–0.77 mm. Closely resembling female in size, color, and general habitus.

Mandible (Fig. 4) slender, about 3.5 times longer than greatest width; masticatory margin strongly oblique; apical tooth broad and indistinctly separated from preapical tooth; remaining teeth short, broad, oblique; basal tooth aligned with basal margin of mandible. Base of antennal scape somewhat trumpet-shaped. Frontal area sharply depressed. Interocellar distance 3.6–4.0 times diameter of anterior ocellus.

Frons with obscure, weak longitudinal rugulae, stronger in interocellar area; head otherwise with only scattered, obscure, short rugulae; moderately shiny and weakly to moderately punctulate.

Configuration of thorax, petiole, and postpetiole as in Figures 7 and 8. Propodeal spines stout, triangular, subacute to acute, a short carina extending basad of each spine. Apex of petiolar node more rounded than that of female; subpetiolar process low, rounded; subpostpetiolar process weak; node of petiole, in dorsal view, without longitudinal impression, crest not notched.

Mesoscutum smooth, shiny; side of pronotum moderately shiny and punctulate; upper plate of mesopleuron with fine longitudinal striae, lower plate less shiny, finely vermiculate; metapleuron with coarse, longitudinal rugulae, interspaces shiny; lateral and basal faces of propodeum transversely vermiculate to irregularly rugulose, interspaces moderately shiny, weakly punctulate; declivity shiny, with a few transverse rugulae or none; nodes of petiole slightly shiny and irregularly rugose at sides. Gaster smooth and shiny.

Body hairs golden; about as in female; i.e., not silky, tending to be stout, flattened, and with blunt apices, even on gaster.

Body color about as in female.

Type material.—Holotype female, allotype, 73 female and 45 male paratypes: 2 mi SE Boulder City, 2250 ft, Clark Co., NEVADA, 18 Sept. 1978 (S. W. Rissing, No. NE 212), from nest of *Pogonomyrmex rugosus* Emery 1895. Holotype, allotype, and most paratypes in LACM; paratypes distributed to AMNH, MCZ, USNM and collections of S. W. Rissing and of G. C. and J. Wheeler.

Etymology.—It is fitting that this unusual species be dedicated to A. C. Cole, Jr., reviser of the genus and respected friend and colleague.

Additional material.—One alate female: Jones Water Recreation Area, 17.3 mi N Globe, Gila Co., ARIZONA, 27 Aug. 1964 (M. E. Irwin; LACM).

Discussion.—The specimens from the type series were collected between 0900 and 1315 as they emerged from the nest of the host species. Since alates of both sexes of the host also emerged from the same nest, it is obvious that the gyne of *P. rugosus* was alive and functional. The biology and behavior of *P. colei* will be reported on by Rissing in a paper now in preparation.

Cole (1954) described *P. anergismus* from a series of males and females taken from a nest of *P. rugosus* near Silver City, New Mexico. Because these individuals were within the *P. rugosus* nest and because no corresponding workers were found, he assumed *P. anergismus* to be a workerless social parasite. The gyne of the host species was not found, nor were alates of either sex noted to be present. *P. anergismus* is known only from the type series.

The present species is the second known socially parasitic *Pogonomyrmex* from North America and shares with *P. anergismus* the same host species. Because the females and males of *P. anergismus* are highly modified morphologically, their affinities were uncertain. Now that *P. colei* has been discovered, the relationships of *P. anergismus* can be clarified.

At first sight, the females and males of *P. colei* look like unusually small individuals of *P. rugosus*. Only on closer examination is it apparent that they are not that species. This is especially obvious in the males. Those of *P. rugosus* are quite hairy on all surfaces; the hairs are white, long, slender, more or less flexuous, and acute at the apices. In contrast, those of the *P. colei* males are golden, short, stiff and usually with bluntly pointed, or even truncate, apices. They also seem less abundant, but this may be an illusion generated by the fact that they do not become intermingled as they do in *P. rugosus*.

The head of *P. colei* is less shiny than that of *P. rugosus* males since most of the frontal surface is closely, albeit weakly, punctulate, not mostly smooth and shiny as in *P. rugosus*. The antennal scape is clearly longer than that of *P. rugosus* (SI 32–35). In *P. rugosus,* the greatest diameter of the anterior ocellus is less than that of the posterior ocelli; in *P. colei,* they are about equal.

Male thoracic structure is very similar, the most obvious difference being that the thorax of *P. rugosus* is mostly smooth and shiny. There are scattered piligerous punctures, and the propodeum bears weak to moderately strong striations or rugulae.

In male *P. rugosus,* the node of the petiole, in profile, is low and broadly rounded. When seen from above, the node is clearly wider than long and rather evenly arcuate across the top; the surface is smooth and shiny. A distinct subpetiolar process is usually present. All these are in sharp contrast to the characteristics just described for the petiolar node of *P. colei.*

The postpetioles of the two species are more similar, but, in dorsal view, the side of that of *P. colei* is less arcuate. Again, the node is smooth and shiny in *P. rugosus,* and the subpostpetiolar process is smaller.

In stature, the male of *P. anergismus* is like that of *P. colei.* Its golden yellow color and largely smooth, shiny integument are, however, in sharp contrast. The antennal scape is relatively long as in *P. colei.* However, in *P. anergismus,* the anterior ocellus is *greater* in diameter than the posterior ocelli.

The thoraces of *P. anergismus* and *P. colei* are similar, but for the smoother and shinier integument of *P. anergismus*; punctulae are rare to absent, and the sides of the thorax are weakly to moderately striate or rugulose, without obvious tendencies toward being vermiculose.

The profiles, both lateral and dorsal, of the petiole and postpetiole are similar in the two species, but, again, the surface is smooth and shiny in *P. anergismus.* However, the posterior face of the node of the petiole has a broad longitudinal impression, lacking in the *P. colei.*

The genitalia of the two species are quite similar. The most obvious difference is that the ventral lobes of the aedeagus are sharply serrate in *P. anergismus*. The teeth are mostly obliterated, except basad, in *P. colei* (Fig. 11). There are also differences in the paramere in dorsal view and in the volsella. The aedeagus of *P. anergismus* is more like that of *P. rugosus* than is that of *P. colei*. The volsella and paramere of *P. colei* are more like those of *P. rugosus* than are those of *P. anergismus*.

The resemblance between females of *P. colei* and *P. rugosus* is much closer than that of the males. Obvious differences include the smaller size and shorter, stouter, sparser golden brown hairs in the former. The masticatory margin is oblique, and the outer face of the mandible is, in large part, smooth and shiny in *P. colei*. Most of the head is punctulate, not coarsely striate as in *P. rugosus*. The shape of the head is quite different in frontal view, since the sides of the head above the eyes are subparallel in *P. rugosus*, rather than convergent as in *P. colei*.

The thoracic, petiolar, and postpetiolar profiles are similar, although the petiolar node is more conoid in *P. colei*. Again, *P. colei* females have distinctly punctulate interrugal spaces, usually smooth or very weakly punctulate in *P. rugosus*. The propodeum of *P. rugosus* is crossed by sharp, well-spaced, coarse rugae; in *P. colei*, the propodeum is finely vermiculate-rugose. The posterior face of the petiolar node of *P. colei* is distinctly impressed along the middle, and the crest is more or less sharply notched.

The females of *P. colei* and *P. anergismus* bear about the same relationship to one another as do their respective males. They are similar in size but immediately are separable because the female of *P. anergismus* is golden yellow, with much of the body smooth and shiny. Other distinctive characteristics of the *P. anergismus* female include: fully striate mandible; longer, narrower apical mandibular tooth; less abruptly depressed frontal area; subclavate setae on frons, side of pronotum, mesopleuron, and subpetiolar process; transversely striate propodeum; mostly smooth mesoscutum.

That these two species, *P. anergismus* and *P. colei*, are closely related seems evident, and they are related to the host species, *P. rugosus*. In fact, in most characters, *P. colei* seems to be intermediate between *P. rugosus* and *P. anergismus*. The major difficulty in this interpretation is one of sculpture. The mandibles of *P. rugosus* are coarsely striate, but largely smooth in *P. colei*. They are also striate in *P. anergismus*. Much the same consideration applies in the matter of the sculpture of the side of the face: longitudinally rugulose in *P. rugosus* and *P. anergismus*, punctulate and with a few weak rugulae in *P. colei*.

I do not think it possible to derive either parasitic species from the other. While it also appears unlikely that the parasites evolved from the host, it is possible that all three are derived from a common prototypic form. The rarity of socially parasitic species hinders study of this paradoxical problem.

Since both females and males fail at the first couplet of Cole's keys (1968) for these castes, the following modification may be made to accommodate *P. colei*.

Females

1. Petiolar node, in profile, a weakly truncated cone, anterior and posterior faces subequal in length; dorsum of petiolar node with distinct broad,

shallow median impression (crest may be notched in posterior view); HW less than 1.75 mm .... 1′
– Petiolar node, in profile, not a truncated cone, anterior face usually distinctly shorter than posterior; dorsum of petiolar node without median impression, crest not notched in posterior view; HW at least 1.90 mm, usually more than 2.00 mm 2
1′ Face between eye and frontal lobe with fine, longitudinal rugulae; hairs of propleura short, blunt, subspatulate; base of propodeum transversely striate .... *anergismus*
– Face finely punctulate between eye and frontal lobe; hairs of propleura long, slender; base of propodeum vermiculate-rugose .... *colei*

Males

1. Body hairs stiff, coarse; *either* petiolar node, in profile, distinctly conoid *or* dorsum of node with broad, longitudinal impression; HW less than 1.50 mm. .... 1′
– Body hairs long, flexuous; petiolar node neither conoid nor with median impression; HW more than 1.60 mm 2
1′. Dorsum of petiolar node with longitudinal impression; basal face of propodeum shiny between fine, transverse rugulae, usually smooth in middle; color yellowish .... *anergismus*
– Petiolar node without dorsal longitudinal impression; basal face of propodeum dull, uniformly vermiculate-rugose; color blackish brown ... *colei*

Pogonomyrmex (P.) *tenuispinus* Forel, 1914

When Cole (1968) revised the North American *Pogonomyrmex* he had available only nine workers, all from southern Baja California Sur. Subsequently, Wheeler and Wheeler (1973) recorded the species from Deep Canyon, Riverside County, Calif. The following records, all from Lower California, will amplify our knowledge of the distribution of this poorly known species, still known only from workers.

BAJA CALIFORNIA SUR: 23 mi N La Paz, 11 Nov. 1965 (W. H. Ewart); Comondu, Feb. 1923 (W. M. Mann); 7.5 mi W El Triunfo, 11 Oct. 1968 (E. M. Fisher and E. L. Sleeper); Miraflores, 28 Oct. 1968 (E. M. Fisher and E. L. Sleeper); 10 km S Santa Rosalia, 700 ft, 4 Oct. 1975 (R. R. Snelling, No. 75-50); 3.7 mi W La Burrera, 1400 ft, 7 Oct. 1975 (R. R. Snelling, No. 75-54); 27 km NE Todos Santos, 900 ft, 8 Oct. 1975 (R. R. Snelling, No. 75-58); 49 km E Villa Insurgentes, 1200 ft, 9 Oct. 1975 (R. R. Snelling); 9 km SE Santa Rita, 250 ft, 26 Aug. 1977 (R. R. Snelling, No. 77-65). BAJA CALIFORNIA: 4 mi S Las Arrastras (de Arriola), 9 June 1967 (E. L. Sleeper and E. M. Fisher). All specimens in LACM.

No. 75-50: "The nest was on a rocky hillside, without tumulus. Workers were foraging in a column about 30 m long; they were rapid, agile, and easily excited. When disturbed, the workers did not exhibit the "alarm-pose" of such related species as *P. rugosus*. Foragers were not active 1 hour after sunrise on the following morning."

No. 75-54: "Nest at edge of road through Cape thorn forest (kaatinga); no tumulus; foraging in column at midday."

No. 75-58: "Nest in packed soil at edge of arroyo; acacia-cardón scrub; workers foraging at 1500, long column."

At "49 km E Villa Insurgantes, nest in very hard, rocky soil; acacia-cardón scrub; no tumulus."

No. 77-65: "Nest in packed soil, no tumulus, but a small fan of debris 7–10 cm from entrance; jotropha-olneya scrub."

Pogonomyrmex (*P.*) *wheeleri* Olsen, 1934
Figures 12–16

This impressively large Mexican species has been known only from the worker caste. A few males and females are now available and are described herewith.

Description.—Female: HL 2.65–2.83 mm; HW 3.20–3.25 mm; CI 118–121; SL 1.85–1.93 mm; SI 57–59; EL 0.58–0.60 mm; EW 0.35–0.40 mm; OI 21–23; WL 4.0–4.4 mm; PNL 0.70–0.90 mm; PNW 0.85–0.95 mm; PPL 0.60–0.70 mm; PPW 1.25–1.40 mm.

Apical tooth of mandible more than twice as long as preapical; preapical tooth a little longer than first basal; basal teeth progressively smaller, penultimate tooth quite small, ultimate basal tooth large, triangular acute, upper margin continuous with upper margin of mandible.

Shaft of scape strongly curved at base (Fig. 12) and flattened or depressed basad of curve, longitudinal peripheral carina strong, narrow; superior lobe well developed, its margin a long, weak curve into shaft; basal flange weak, narrow, margin thin and reaching apex of superior lobe; lip prominent; inferior lobe weak, evenly rounded into shaft, point low and obtuse.

Cephalic rugulae fine and dense, about 20–22 rugulae per 0.50 mm on frons below ocelli, becoming finer toward eye; rugulae a little coarser on gena, about 15–18 per 0.50 mm.

Frontal area vertically depressed. Lateral lobe of clypeus weakly compressed and weakly projecting.

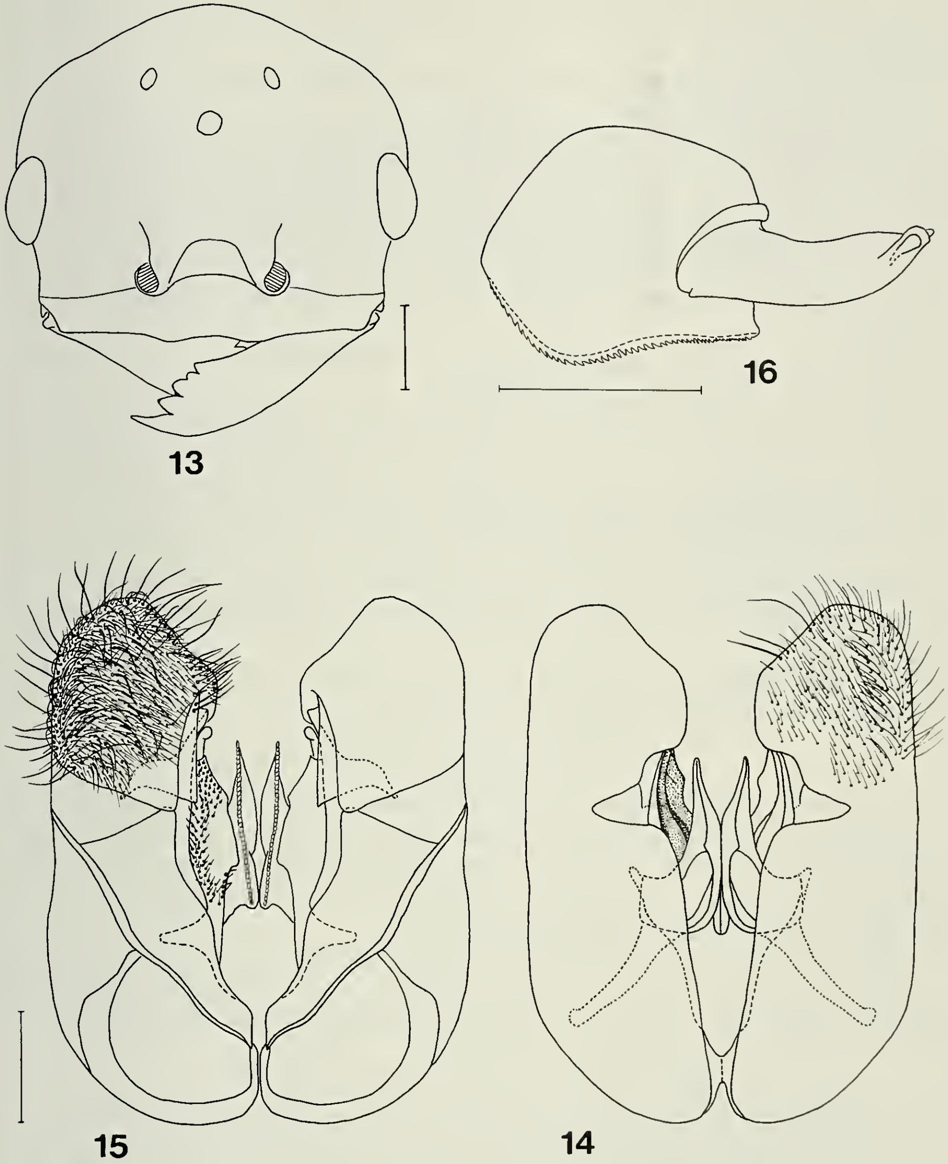
Propodeal spines short, acute. Pronotum mostly smooth and shiny, with weak transverse rugulae across declivity above neck, extending onto lateral face; mesoscutum longitudinally rugulose, rugulae finer laterad; scutellum largely smooth and shiny, with weak rugulae laterad; mesopleuron with fine longitudinal rugulae, interspaces punctulate on lower plate; metapleuron and side of propodeum coarsely longitudinally rugose, rugae of propodeum becoming transverse across basal face, interspaces shiny.

Crest of petiolar node distinctly notched; nodes slightly shiny, with weak, shallow, fine punctulae; petiolar node with few or no fine, widely spaced longitudinal rugulae; postpetiolar node with few or no fine, transverse rugulae.

Uniformly dark ferruginous.

Male: HL 2.10–2.20 mm; HW 2.40–2.50 mm; CI 112–116; SL 1.05–1.15 mm; SI 49–55; EL 0.65–0.75 mm; EW 0.43–0.50 mm; OI 28–34; WL 3.65–4.00 mm; PNL 0.66–0.70 mm; PNW 1.00–1.10 mm; PPL 0.60–0.75 mm; PPW 1.30–1.40 mm.

Mandible (Fig. 13) broad, lower margin nearly straight in basal half, then weak-



Figs. 13–16. *Pogonomyrmex wheeleri*, male: 13, head, frontal view; scale line = 0.50 mm. 14, genital capsule, dorsal view. 15, same, ventral view; scale line = 0.50 mm. 16, aedeagus, lateral view; scale line = 0.50 mm.

ly curved into lower margin of apical tooth; apical tooth long, broad; preapical tooth short, broad; first basal tooth short, obtuse; ultimate basal weak; outer face striate and coarsely, closely punctate, especially along upper and apical margins.

Cephalic rugulae fine and dense on frons, becoming weak toward margins, broken by coarse, shallow, piligerous punctures; gena rather shiny and with only a few weak rugulae, which curve under lower end of eye; oculomandibular area without longitudinal rugulae, but a few transverse to oblique rugulae usually present.

Interocellar distance about 3 times diameter of anterior ocellus; anterior ocellus smaller than posterior ocelli.

Propodeal teeth absent or barely indicated. Thorax mostly smooth and shiny; mesopleuron with a few longitudinal rugulae on upper plate, lower plate duller, finely and closely punctate between obscure longitudinal rugulae; metapleuron and propodeal side shiny between moderately coarse longitudinal rugulae, turning onto basal face of propodeum but absent across its middle; middle of propodeum, from base to apex, smooth and shiny. Nodes of petiole and postpetiole smooth and shiny.

Hairs mostly whitish to pale yellowish, long, slender, flexuous, abundant, shorter on appendages; relatively sparse on gaster.

Color blackish-brown; gaster dark reddish-brown; appendages lighter.

Material examined.—4 ♀♀, 6 ♂♂, 9 mi N Mazatlán, Sinaloa, MEXICO, 25 July 1973 (J. Chemsak, E. G. Linsley, and A. E. Michelbacher; UCB); 1 ♀, 1 mi N Mazatlán, Sinaloa, MEXICO, 27 Dec. 1968 (D. L. Briggs; UCD).

Discussion.—The male, by virtue of its large size, basally flattened scape, and uniformly blackish color, is easily separated from males of other species of the *barbatus* complex. The peculiar sculpturation of the mandible is also characteristic.

The female will go to *P. barbatus* in Cole's (1968) key, but differs by its large size and weakly (or not at all) rugose petiolar node.

Subgenus *Ephebomyrmex*

The status of *Ephebomyrmex,* whether a genus or subgenus, is yet to be determined. In particular, the South American fauna must be comprehensively studied and compared to that of North America. Cole's (1968) revision of the North American *Pogonomyrmex* treated *Ephebomyrmex* as a subgenus; for convenience, I will follow that arrangement here.

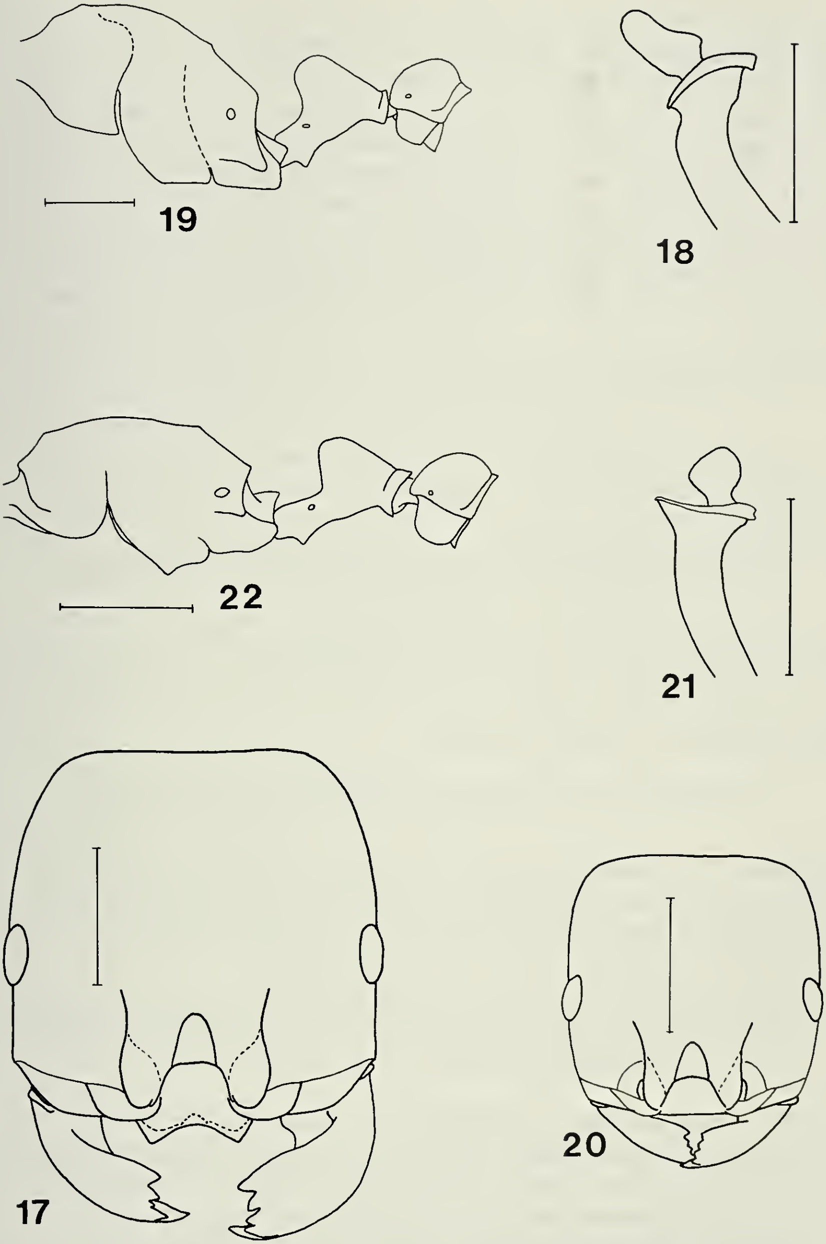
In the worker portion of Cole's key, there is a serious typographic error, which could easily confuse anyone not familiar with these ants. A new key is presented below to rectify this error and to include two additional species, one new.

Key to Workers, Subgenus *Ephebomyrmex*

1a. Small, HW 0.97–1.21 mm; eye large, notably longer than wide, oculomandibular distance no more than about 1.2 times EL; base of propodeum reticulose, without distinct transverse rugae; in lateral view, meeting mesonotum at a prominent angle 2

b. Larger, HW more than 1.30 mm; eye variable, but often small, oculomandibular distance at least 1.5 times EL (if larger, propodeal spines absent); base of propodeum transversely rugose *or* largely smooth and propodeal spines absent; in lateral view, base of propodeum not meeting mesonotum at prominent angle. 4

2a. Propodeal spines present; longest pronotal hairs stiff, seta-like, little (if any) longer than EL; nodes of petiole and postpetiole distinctly sculptured 3



Figs. 17–22. 17–19, *Pogonomyrmex guatemaltecus*, worker: 17, head, frontal view; scale line = 0.50 mm. 18, base of scape; scale line = 0.25 mm. 19, lateral view, thorax, petiole, and post-petiole; scale line = 0.50 mm. 20–22, *P. laevinodis*, worker. 20, head, frontal view; scale line = 0.50 mm. 21, base of scape; scale line = 0.25 mm. 22, lateral view, thorax, petiole, and post-petiole; scale line = 0.50 mm.

b. Propodeal spines absent; longest pronotal hairs slender, flexuous, distinctly longer than EL; nodes of petiole and postpetiole for the most part smooth and shiny, often weakly punctulate anteriorly and posteriorly .... *laevinodis*, n. sp.

3a. Clypeus with prominent toothlike projection below each antennal socket; posterior declivity of petiolar node, in profile, much longer and less steep than anterior declivity, surface rugoreticulose; dorsum of postpetiolar node irregularly longitudinally rugose .... *imberbiculus* Wheeler

b. Clypeus without toothlike projection below each antennal socket; petiolar node conical in profile, surface punctate; dorsum of postpetiolar node punctate .... *pima* Wheeler

4a. Propodeal spines present; dorsum of petiolar node irregularly, transversely rugose; longest pronotal hairs slender, whitish, longer than EL .... *huachucanus* Wheeler

b. Propodeal spines absent; dorsum of petiolar node longitudinally rugose; longest pronotal hairs stout, stiff, brownish yellow, distinctly shorter than EL .... *guatemaltecus* Wheeler

Pogonomyrmex (*Ephebomyrmex*) *guatemaltecus* Wheeler, 1914
Figures 17–19

This distinctive species was described from Zacapa, GUATEMALA. Recently collected material extends the range into MEXICO: Paderón, Río Tehuantepec, Oaxaca, 24 Feb. 1948 (T. MacDougal; AMNH); 8 km W Tehuantepec, 10 Aug. 1974 (E. M. and J. L. Fisher; LACM).

Pogonomyrmex (*Ephebomyrmex*) *laevinodis* New species
Figures 20–22

Diagnosis.—Separable from other members of subgenus *Ephebomyrmex* by the following combination of characters. Worker: Propodeal spines absent; nodes of petiole and postpetiole largely smooth and shiny; eye length about equal to oculomandibular distance. Female and male unknown.

Description.—HL 0.96–1.12 mm; HW 0.90–1.05 mm; CI 92–96; SL 0.68–0.74 mm; SI 72–78; EL 0.19–0.23 mm; EW 0.13–0.15 mm; OI 19–24; WL 0.97–1.13 mm; PNL 0.27–0.32 mm; PNW 0.26–0.32 mm; PPL 0.23–0.29 mm; PPW 0.38–0.46 mm.

Mandible about as usual in *Ephebomyrmex*; apical and preapical teeth acute, broad, thin, apical tooth longest; first basal about half as long as preapical, subacute; second basal very short and narrowly separated from first; third basal broadly separated from second, a little smaller than first; penultimate basal very small, triangular and its upper margin slightly offset from straight to weakly convex upper mandibular margin; ultimate basal tooth absent.

Base of antennal scape (Fig. 21) with shaft strongly curved but not flattened, basal enlargement well developed; superior lobe weak; basal flange thin, narrow; lip well developed, broad, slightly reflexed; point present.

Eye large, greatest length 1.5 times or more greatest width, oculomandibular distance subequal to eye length.

Lateral lobe of clypeus, below antennal socket, compressed and projecting forward (weaker than in *P. imberbiculus*).

Thoracic, petiolar, and postpetiolar profiles as in Figure 22. Propodeal spines absent, posterior declivity bounded on each side and across summit by a prominent carina. In lateral view, anterior declivity of petiolar node nearly vertical, a little shorter than posterior declivity; node, in posterior view, about as long as wide; subpetiolar process large, triangular.

Head longitudinally rugose, with few transverse rugae, interspaces moderately shiny and irregularly roughened but without definite punctulae and with sparse, shallow setigerous punctures. Thorax coarsely reticulorugose, interspaces moderately shiny and with sparse, shallow setigerous punctures. Dorsum of petiolar and postpetiolar nodes shiny between sparse, piligerous punctures, occasionally with weak punctulae along posterior margins.

Erect hairs golden brown, very uneven but longest pronotal hairs exceeding eye length; hairs short and stiff on frons; few or none on petiolar venter; shorter on appendages; eyes with numerous very short, fine hairs.

Color light to dark ferruginous.

Type material.—Holotype worker and 34 worker paratypes: 27 km NE Todos Santos, 900 ft, Baja California Sur, MEXICO, 8–9 Oct. 1975 (R. R. Snelling, No. 75-59). Holotype and most paratypes in LACM; three paratypes each to: AMNH, MCZ, USNM and personal collection of G. C. and J. Wheeler.

Etymology.—From Latin, *laevis* (smooth) and *nodus* (knot, node), for the smooth, shiny nodes of the petiole and postpetiole.

Additional material.—20 km NW La Paz, 100 ft, 5 Oct. 1975 (R. R. Snelling; LACM).

Discussion.—The characteristics cited in the key and in the diagnosis should be sufficient for recognition of this ant.

It appears that the species is most closely allied to *P. imberbiculus* and replaces it in southern Lower California.

The type series nest was in hard-packed, sandy soil at the edge of a large arroyo, in acacia-cardón scrub (kaatinga). The nest entrance was surrounded by a low crater of excavated soil, about 5.5 cm in diameter. Workers were foraging at 1700.

The record from 20 km NW of La Paz is based on a single stray taken in late afternoon from *Opuntia* sp. In the field, foraging *P. laevinodis* workers very closely resemble those of *Tetramorium spinosum* (Pergande).

Acknowledgments

I am indebted to S. W. Rissing for making available, and allowing me to describe, the series of *P. colei*. Other specimens were made available by J. A. Powell (UCB), J. G. Rozen, Jr. (AMNH) and R. O. Schuster (UCD). Particular thanks must be extended to C. Besuchet for allowing me to study the type of *P. californicus* var. *hindleyi*.

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80(3), 1981, pp. 112–125

A New Species of Neotenic *Ambystoma* (Amphibia, Caudata) Endemic to Laguna Alchichica, Puebla, Mexico

Ronald A. Brandon,[1] Edward J. Maruska,[2] and William T. Rumph[3]

Abstract.—A New Species of Neotenic *Ambystoma* (Amphibia, Caudata) Endemic to Laguna Alchichica, Puebla, Mexico by Ronald A. Brandon, Edward J. Maruska, and William T. Rumph, *Bull. Southern California Acad. Sci.* 80(3):112–125, 1981. Comparison of the neotenic population of *Ambystoma* that is endemic in Laguna Alchichica with the holotype of *Ambystoma subsalsum* Taylor 1943, and with *A. tigrinum* from several populations in Puebla, Tlaxcala, and Hidalgo reveals that the holotype is identifiable as *A. tigrinum* and is specifically different from the Laguna Alchichica neotenes. The population in Laguna Alchichica is described; this species differs from *A. tigrinum* in number of gill rakers, in morphology of the base of the dorsal body fin, in coloration, in number of vomerine teeth, in morphology of the vomerine tooth series, in apparently requiring saline waters, and in being neotenic.

Introduction

Nearly 40 years ago, Edward H. Taylor (1943) described and named a new species of salamander, *Ambystoma subsalsum*, from Laguna Alchichica, one of several crater lakes (axalapazcos) in the llanos of eastern Puebla, Mexico. At that time other populations of *Ambystoma* in the Llanos de San Juan and Llanos de San Andres (Fuentes 1972, describes the surface morphology of the region) had not been studied although Taylor (1943) noted that two other nearby lakes also contained populations of salamanders, and specimens of *A. tigrinum* had been collected previously at other localities in Puebla.

As holotype of *A. subsalsum* Taylor selected the only transformed specimen available from the vicinity of Lake Alchichica, FMNH 100007 (formerly E.H.T.-

H.M.S. 22139), collected ". . . a few hundred yards from the lake" (Taylor 1943, p. 152). About ten years ago, one of us (RAB) suspected that the transformed juvenile holotype (Taylor 1943, figs. 2, 3) was not conspecific with the population of neotenes inhabiting Laguna Alchichica. Rather, the holotype closely resembled transformed specimens of *Ambystoma* (tentatively identified as *A. tigrinum*) from other localities to the west of Laguna Alchichica, and larvae in those populations did not closely resemble neotenes in the lake. Subsequently, larvae from several populations of *Ambystoma tigrinum* in Tlaxcala and Hidalgo were reared in the laboratory and compared with neotenes from Laguna Alchichica maintained under similar conditions. After metamorphosis, they resembled the holotype of *A. subsalsum* but neither the wild-caught nor lab-reared larvae resembled neotenes from Laguna Alchichica.

More recently (May 1980), we collected larvae and transformed adults identifiable as *A. tigrinum* within a few km of Laguna Alchichica. Some of these animals (Fig. 1) closely resemble Taylor's holotype of *A. subsalsum*. We are now convinced that the neotenic species in Laguna Alchichica is distinct from surrounding populations of the transforming species that presently utilized dug wells, irrigation systems and other temporary waters as breeding habitat.

The purpose of this paper is to demonstrate that the population of *Ambystoma* in Laguna Alchichica merits recognition at the species level, as Taylor believed, but that the name *Ambystoma subsalsum* does not apply to it because the holotype is referable to *A. tigrinum*. Therefore, the species in Laguna Alchichica is newly described. The widespread species is probably identifiable as *A. tigrinum*, but more than one species of *A. tigrinum*-like salamander may occur across the southern end of the Mesa Central and Transverse Volcanic Belt.

Material Examined

During the past ten years, live and preserved specimens have been examined from localities listed below; some animals were preserved in the field, some reared in the laboratory from collected larvae, some obtained from adults that bred in the laboratory. A few live specimens are still being maintained in the Cincinnati Zoo and at Southern Illinois University at Carbondale (SIUC).

Holotype of A. subsalsum.—When examined in July 1980, the holotype of *A. subsalsum* was 73 or 76 mm snout–vent, depending on whether one measured to the anterior angle or posterior angle of vent (all subsequent snout–vent lengths are measured to the posterior angle), was largely eviscerated (reproductive organs missing), and had part of the trunk wall cut away, preventing an accurate count of costal grooves. Greatest head width was 17.6 mm, snout to gular fold 17.5 mm, front leg length 30 mm, hind leg length 29 mm, and tail length 47 mm. The diastema Taylor noted between vomerine and pterygoid tooth series is small and barely noticeable. He counted 25 tail vertebrae, we count 29. The distribution of light spots on the head, body, and tail matches exactly Taylor's illustration of the holotype (1943, Figs. 2, 3).

Laguna Alchichica neotenes.—In addition to all but one of the paratypes of *A. subsalsum*, we have examined five series of live animals in the laboratory. Two series were collected by R. G. Altig, 15 animals (55–104 mm snout–vent) on 21 December 1970 (SIUC H-3207–3220; FMNH 212392), and 34 animals (70–110 mm snout–vent) on 2 March 1973 (SIUC H-3221–3250, 4 deteriorated). Animals of

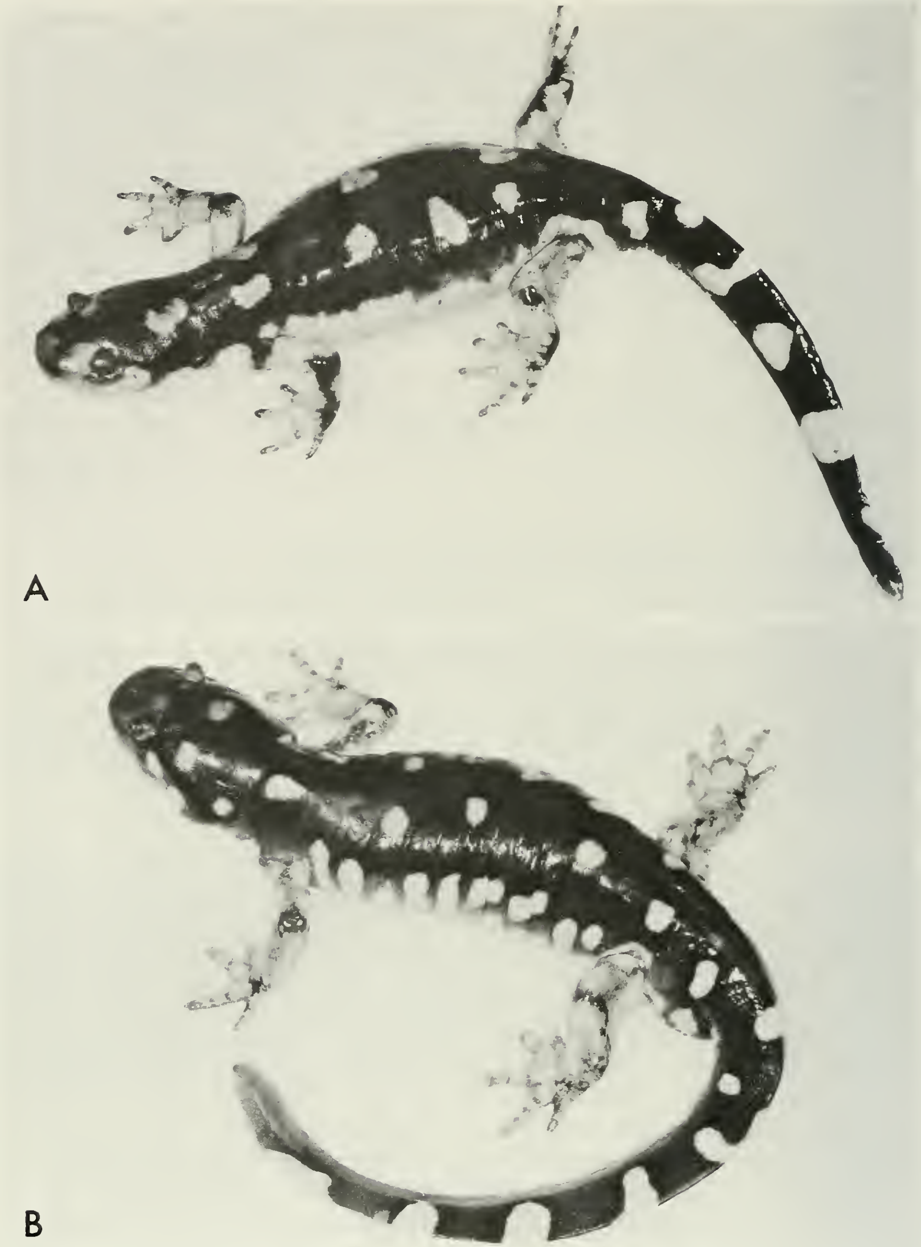

Fig. 1. Adult female (A) and male (B) specimens of *Ambystoma tigrinum* resembling the holotype of *Ambystoma subsalsum* (cf. Taylor, 1943, figs. 2, 3), collected 29 May 1980 at Rancho San Antonio Alchichica, Puebla, México, 6 km N Laguna Alchichica; (A) 100 mm snout–vent, (B) 109 mm snout–vent.

neither series proved hardy in the laboratory, probably because they were kept in salt water (NaCl) no stronger than 6–12% Amphibia Ringers (see below). Eleven of those collected in 1970 and maintained in individual half-gallon bowls remained branchiate and survived from 57 to 574 days ($\bar{X} = 314$). Only two lived fewer than 100 days, four over 400 days. Four transformed spontaneously (SIUC H-3217–3220).

Animals collected in 1973 were at first maintained together in a 55-gallon tank, later individually in half-gallon bowls. They lived 44 to 407 days ($\bar{X} = 123$); only ten lived longer than 100 days and two (SIUC H-3249–3250) died while transforming.

A third group of 20 animals collected 15 September 1979 lived for a year at the Cincinnati Zoo, in a 55-gallon tank in artificial Laguna Alchichica water mixed to match the salt composition reported by Taylor (1943). One of these transformed spontaneously.

The fourth group of 10 animals, collected 28–30 May 1980 and maintained at the Cincinnati Zoo in water matched to Laguna Alchichica in salt content, subsequently died apparently of bacterial infection. Of a fifth group of about 30 animals, collected 12–14 July 1981 and maintained in artificial Laguna Alchichica water at the Cincinnati Zoo, slightly over half are still alive nine months later.

Animals kept in saline water have appeared healthier than those kept in unsalted water in the laboratory, but long-term hardiness has not improved.

Ambystoma subsalsum, sensu stricto.—The following specimens are considered conspecific with the holotype: PUEBLA: Fifteen animals (RAB T2) collected as larvae 19 May 1970 at the Tlaxcala-Puebla border 30 km N Apizaco on route 119, five of them reared to adulthood in the laboratory and maintained up to four years; 13 transformed animals, two preserved (SIUC H-3252–3253) and the rest alive in the Cincinnati Zoo, collected 29 May 1980, at Rancho San Antonio Alchichica, ca. 6 km N Laguna Alchichica; a series of eggs, embryos, larvae of various ages, and four transformed juveniles (RAB T12), all the F_1 laboratory offspring of SIUC H-3252–3253; four transformed and three larval animals, all alive in the Cincinnati Zoo, collected 29–30 May 1980, at Rancho El Riego, ca. 5 km E Laguna Alchichica. HIDALGO: 24 animals (RAB T3) collected as larvae 18 May 1970, at El Chico Parque Nacional near Pachuca, six of them reared to adulthood and maintained up to four years; a series of 20 larvae and adults (RAB T4) collected 23 March 1971, at El Chico Parque Nacional; a series of larvae (RAB T5) reared from a pair of the proceeding, four of them reared to metamorphosis. TLAXCALA: one adult and six small larvae (University of Colorado, uncatalogued) collected 13 km E Apizaco; three transformed animals (RAB T1) collected 19 May 1970, 14 km W Huamantla on route 136, and maintained in the laboratory for two to four years.

Ambystoma sp.—We have also examined large adult neotenes from Laguna Quecholac and Laguna de la Mina Preciosa, 5 and 4 km SE Laguna Alchichica, respectively. Animals from these two lakes resemble each other but differ from Laguna Alchichica neotenes and from the transforming species of the Llanos; their taxonomic status will be discussed in a separate report. Also examined were neotenic adults, eggs, larvae, and transformed animals from Laguna Tecuitlapa, 33 km SW Alchichica; these animals most closely resemble the transforming species of the Llanos.

Results

For the neotenic species of Laguna Alchichica, which Taylor intended to name in 1943, we propose the name:

Ambystoma taylori, sp. nov.

Holotype.—Female, FMNH 212392, Laguna Alchichica, Puebla, México, ca. 24 km SW Perote, collected by R. G. Altig 21 December 1970 and kept in the laboratory 136 days before being preserved.

Paratypes.—All but one of the 38 paratypes of *Ambystoma subsalsum* Taylor 1943, all collected from Laguna Alchichica, have been examined and are identifiable as *A. taylori.* Since they were originally listed only by their E. H. Taylor-H. M. Smith numbers, all are listed here by both the EHT-HMS numbers and current museum numbers: CM 39981 (EHT-HMS 28364); FMNH 126514–36 (EHT-HMS 28374, 28387, 28390, 28384, 28371, 28359, 28381, 28380, 28362, 28368, 28383, 28369, 28357, 28386, 28389, 28372, 28365, 28360, 28378, 28363, 28375, 28377, 24014, respectively); FMNH 75763 (EHT-HMS 28388); FMNH 126930–32 (EHT-HMS 12989, 28366, 28379, respectively); MCZ 29612 (EHT-HMS 28376); UIMNH 27323-4 (EHT-HMS 28358, 28361); UIMNH 27327–8 (EHT-HMS 28370, 28373); UIMNH 27333 (EHT-HMS 24013); UIMNH 48988 (EHT-HMS 312); UMMZ 117245 (EHT-HMS 28382); USNM 134277 (EHT-HMS 28367). Only AMNH 59525 (EHT-HMS 28385) was not examined. Additional paratypes of *Ambystoma taylori* are SIUC H-3207–3220, collected 21 December 1970, by R. G. Altig, and kept in the laboratory for various periods before preservation.

The paratype larva illustrated by Taylor (1943, Fig. 1), listed by him as USNM 116702, is now catalogued as FMNH 126930. The drawing and specimen are identical and are excellent examples of *A. taylori.*

Diagnosis.—A neotenic species (*sensu* Gould 1977) of the *Ambystoma tigrinum* species group; resembles larval or neotenic specimens of *A. tigrinum* in number of trunk vertebrae (14–16), relative limb length (adpressed limbs overlap by 3–4 intercostal folds), and toe morphology (toes short, broad at base and flattened). Differs from nearby *A. tigrinum* in number of gill rakers on the anterior face of the third gill arch (counts from both sides summed) (19–26, $\bar{X} = 22.9$, versus $\bar{X} = 27.4$ to 32.5 in Puebla and Hidalgo populations identifiable as *A. tigrinum*); in having a broad and fleshy base to the dorsal body fin; in having fewer vomerine teeth that tend to lie in a single row rather than in a broad patch 3–4 teeth wide as in *A. tigrinum*; in pigmentation (brighter, yellow to golden ground color and deep maroon spots in life); in not being hardy after metamorphosis in the laboratory; and in apparently requiring saline water. Animals over 76 mm snout–vent are mature or maturing; largest adults reach at least 115 mm snout–vent.

Distribution.—Known only from Laguna Alchichica, a saline crater lake in eastern Puebla, México. Populations of *Ambystoma* in other nearby crater lakes differ specifically from *A. taylori,* which is apparently indigenous to Laguna Alchichica. Laguna Alchichica is the largest ($0.6992\ m^3 \times 10^8$ in volume) and deepest (64.6 m maximum) of the crater lakes on the llanos and lies at an elevation of 2345 m above sea level. It and several others have been mapped bathymetrically (Enriquez, Dominguez, Mata, Nava, and Laredo 1979). It is clearly a saline lake (as defined by Bayly and Williams 1973); the total salt content of the water was reported to be 8.3‰ by Taylor (1943) and 8.2‰ by Alvarez (1950); a sample tested for us by the Ohio State Department of Health, Columbus, Ohio, was only slightly lower.

Description of the holotype.—A branchiate female, snout–vent length 85 mm,

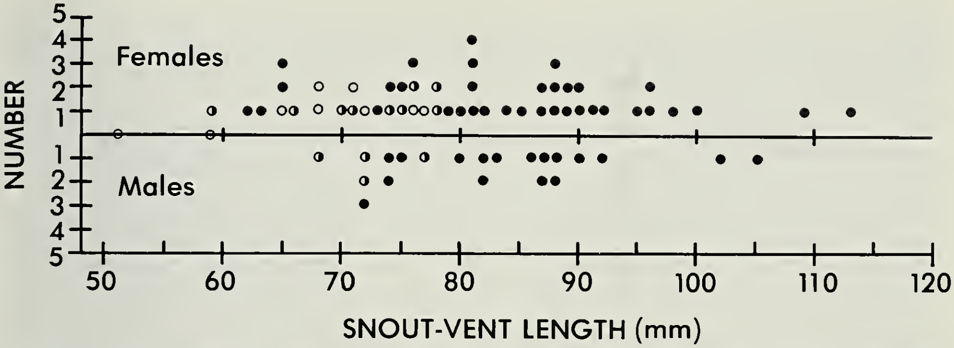

Fig. 2. Size frequency distribution of preserved specimens examined of *Ambystoma taylori*, from Laguna Alchichica, Puebla, México: Immatures (open circles), maturing (half closed circles), mature (closed circles), N = 74.

tail length 63 mm, dorsal head length (nostril to dorsal gill insertion) 28.5 mm, ventral head length (snout to middle of gular fold) 22 mm, head width at corner of jaws 20 mm. Posterior half of body open midventrally and two cuts run laterally in the left body wall to expose the viscera. Oviducts slightly enlarged, 0.7 mm in diameter; ovaries contain hundreds of small (0.3–0.5 mm diameter) pale oocytes; cloacal glands moderately enlarged. Corners of mouth cut to allow examination of tooth series. Pterygoid teeth ca. 13/13, but hard to see and count; vomerine teeth in a single series, ca. 20/20, also hard to see and count; premaxillary teeth 15/15 (counted on radiograph). Costal grooves between limb insertions 13, trunk vertebrae 14. Twelve gill rakers on anterior face of left third gill arch, 11 on right. Dorsal body fin reduced slightly in height in captivity but fleshy base over the shoulder clearly visible and 3 mm wide. Hind digits wider at base than at tip, pointed at tip, with flattened lateral edges; inner and outer metacarpal and metatarsal tubercles prominent. Pale, yellowish, dorsal ground coloring, with numerous (35–40 along one side of trunk) oval or round black spots (1–3 mm in diameter); head, trunk and taill all spotted alike. Venter also pale yellow, with black mottling most pronounced on throat and pectoral region. Bears a tag labeled "SUB1–9, female, died 6 May 1971, R. A. Brandon."

Species description.—Taylor's (1943) descriptions of larvae and variation of *A. subsalsum* all apply to immatures and neotenic adults of *A. taylori*. The size and sex distributions of specimens we have examined are shown in Figure 2. As judged by enlarged cloacal glands, vasa deferentia with spermatozoa, enlarged oviducts, and large yolked oocytes, most animals over 70 mm snout–vent appear to be mature; some of those between 60 and 70 mm snout–vent seem to be mature, others maturing, a few still immature. The largest specimens seen were 102–113 mm snout–vent.

Of 31 specimens examined by radiography, three (10%) have 14 trunk vertebrae, 22 (71%) have 15, and six (19%) have 16.

The number of gill rakers on the anterior face of the third gill arch (counts from both sides summed) ranges from 19 to 26 and averages 22.9 on 46 animals 65–115 mm snout–vent.

The vomerine teeth are essentially in a single series rather than in a broad

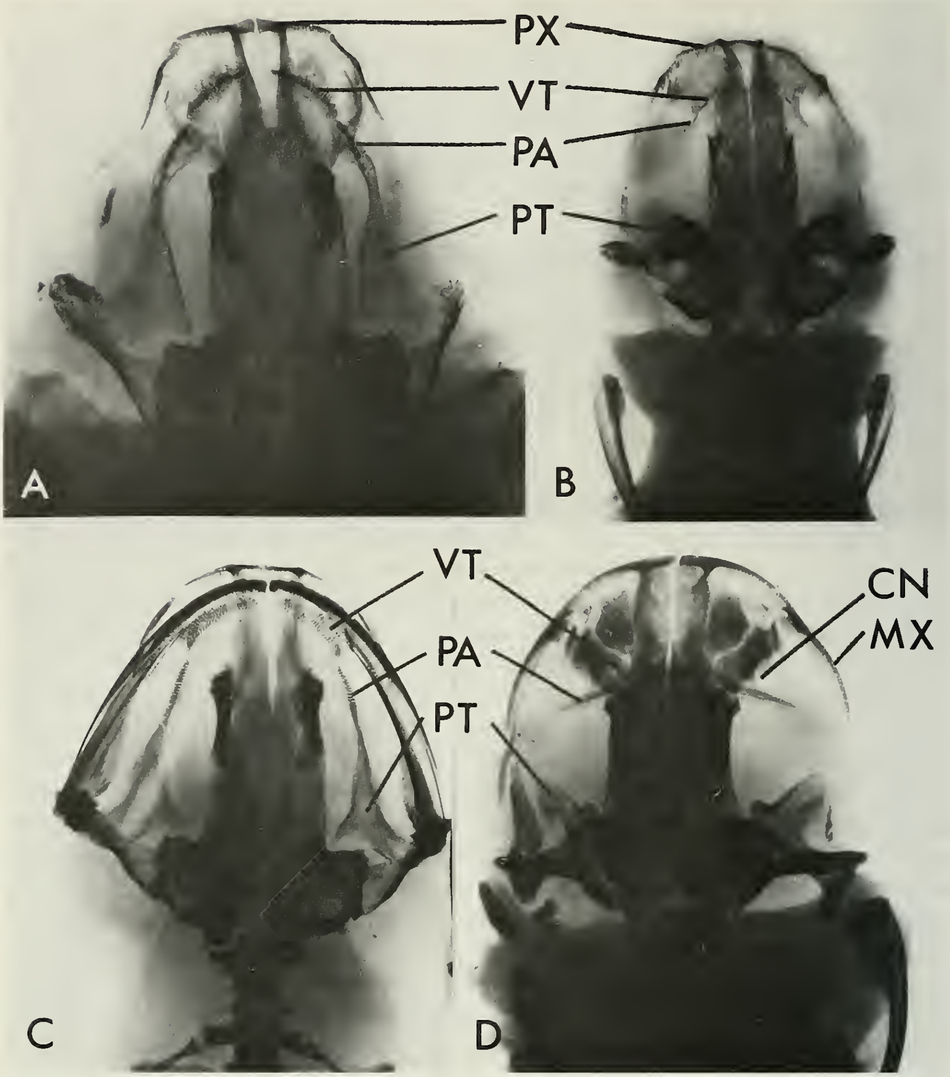

Fig. 3. Radiographs of heads of: (A) branchiate adult *A. taylori* (SIUC H-3237), 109 mm snout–vent, collected 2 March 1973 and kept in the laboratory four months before preservation; (B) transformed *A. taylori* (SIUC H-3217), 78 mm snout–vent, collected 21 December 1970, began to transform 209 days later, lived 421 days longer; (C) branchiate adult *A. tigrinum* (USNM 31081), 90 mm snout–vent, Chiguahuapan, Puebla; (D) transformed adult *A. tigrinum* (RAB T1–3), 105 mm snout–vent, 14 km W Huamantla, Puebla. Abbreviations are: choanal notch (cn), vomerine teeth (vt), pterygoid (pt), palatine (pa), premaxilla (px), maxilla (mx), mandible (md). All printed at same scale.

patch. Counts of vomerine teeth in eight animals 69–104 mm snout–vent range from 27 to 43 and average 34 (counts from both sides summed). Counts of pterygoid teeth range from 13 to 28 and average 19. The difference in dentition between *A. taylori* and *A. tigrinum* is clearly shown by radiography (Fig. 3).

Toes of immatures and young adults resemble those of larval *A. tigrinum* by being nearly triangular, flattened, and with a flat fringe along the edges. On older

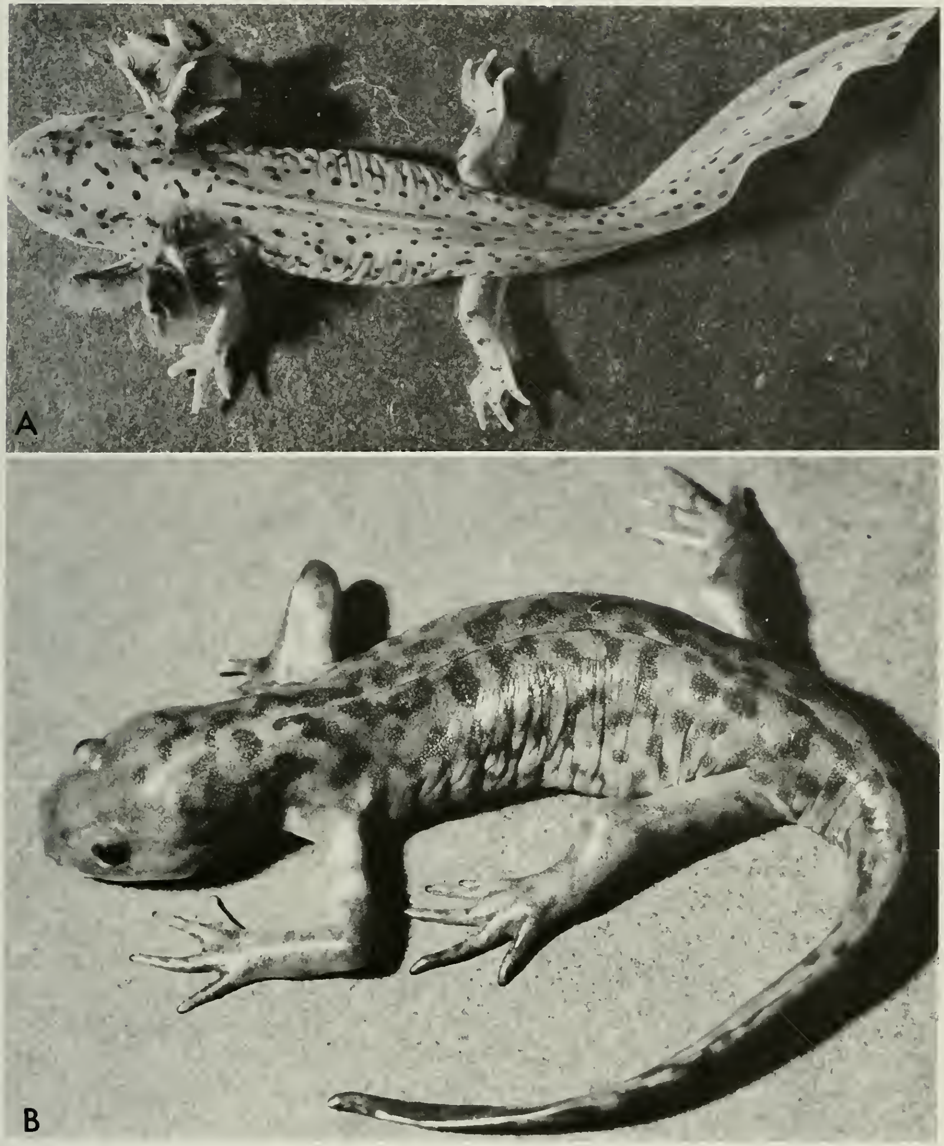

Fig. 4. (A) Adult female *Ambystoma taylori* (SIUC H-3211), 86 mm snout–vent, after three months in captivity. Color in life yellow with dark maroon spots. Note the wide fleshy base of the dorsal body fin. (B) Adult female *A. taylori* (SIUC H-3218), 90 mm snout–vent, two months after metamorphosis. Note the dark markings on a light background rather than the converse as in *A. tigrinum* (cf. Fig. 1).

adults the toes lack flat edges and appear more like those of transformed animals. Despite Taylor's (1943, p. 155) statement to the contrary, the toes are marked by dark keratinized tips.

A distinctive trait of *A. taylori*, not observed in any other species of Mexican *Ambystoma*, is the raised fleshy base of the dorsal body fin (Fig. 4), which becomes widest at the base of the head. It is especially noticeable in live animals, and apparently is caused by a deposit of adipose tissue. In other species, the dorsal fin remains thin at the base and inserts in a middorsal groove between epaxial muscle masses.

Relative limb length resembles that of larval *A. tigrinum,* with adpressed limbs overlapping by 3–5 intercostal folds depending on girth.

The body pigment pattern is relatively uniform among specimens examined (Fig. 4, 5A) and resembles that illustrated by Taylor (1943, Fig. 1). These are colorful animals in life. The ground coloring ranges from golden to canary yellow to subdued yellowish tan. The dorsum and sides of the head, trunk, and tail (including fins) are marked by distinct dark maroon spots 1–3 mm in diameter. The spots range from circular to elongate oval, and occasionally coalesce. The dorsum of the legs is occasionally spotted but more often is darkly mottled. The amount of dark mottling on the venter varies, but even those animals with darkest venters have a clear patch on the posterior part of the gular fold or anterior pectoral region.

In our preserved sample of *A. taylori,* females outnumber males 2.4 to 1, perhaps reflecting sexual differences in nocturnal habitat. All previously collected animals we know about were found washed up on shore dead (Taylor 1943) or were collected in shallow water along the lake's shoreline at night. It is possible that males are less likely to be encountered in this way. Taylor (pers. comm.) found that animals ". . . could be collected at night when they came to the surface and seemingly fed at the edge of the lake. They could be seen in quantity with the light from a gas lantern." We found animals relatively common, at night, in shallow pools among rocky outcrops 6–10 m offshore, just before the lake plunged in depth. When first encountered, they commonly swam quickly into crevices or wedged themselves against irregularities in the rock. Ronn Altig (pers. comm.) found them common among bottom vegetation (ca. 10–13 cm high) on a shelf of shoreline in water about 0.5 m deep.

More was learned about the behavior and vertical distribution of salamanders in the lake, and about the habitat itself, during the evenings of 12 and 14 July 1981, when Barry N. Wakeman, Leesa Wiesner and one of us (EJM) examined the lake after dark with the aid of SCUBA gear and flashlights. The lake bottom was a fine sediment easily disturbed by swimmers. One kick of a foot flipper created a cloud that obscured vision. Down to a depth of 40 feet (12 m) one encountered towers of rock of various sizes and, occasionally, walls of rock. The rocks resembled coral reefs in texture, with many holes, crevices and overhangs covered with growths of algae. Disturbed salamanders swam vigorously 3 to 4 m, then darted into bottom sediment or algae and disappeared from view, or pushed themselves tightly against roughly textured rock. They seemed readily disturbed by flashlights. At night, some animals were seen in water 4 to 5 m deep, but increasingly more were seen at greater depths. At 12 m as many as 20 were seen within one field of vision. Larger animals seemed to be at greater depths.

Metamorphic response: Although reproduction has not been observed, this is certainly a neotenic species that does not normally transform in nature. Branchiate animals over 78 mm snout–vent all have typically adult ambystomatid reproductive organs and gametes. However, as with some other neotenic Mexican

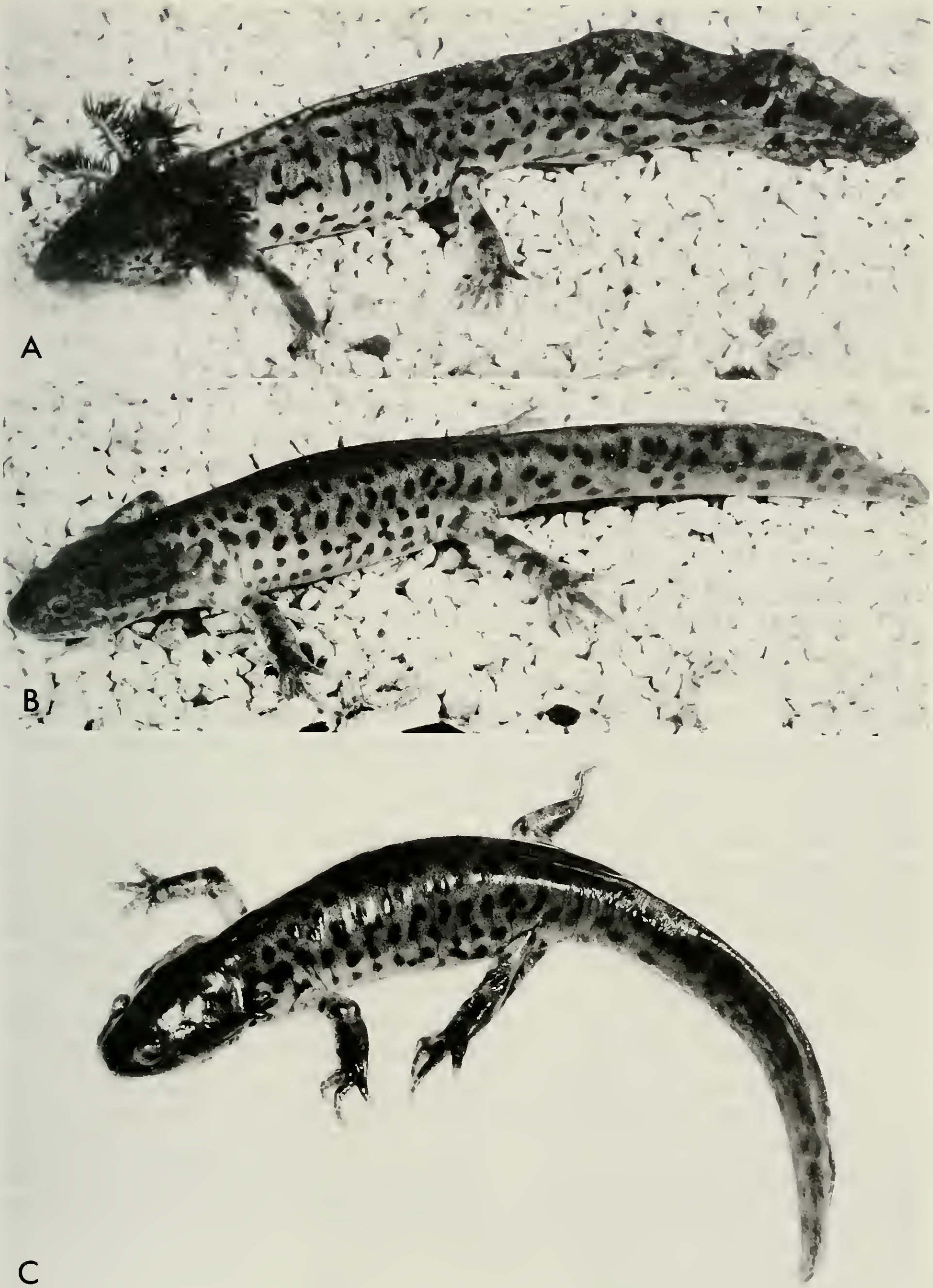

Fig. 5. *Ambystoma taylori* (Cincinnati Zoo): (A) premetamorphic animal with dorsal body fin slightly reduced anteriorly, gills not reduced, (B) female 80 mm snout–vent, dorsal fin completely reduced, gills mere stubs, (C) same animal later, only small gill stubs remain, animal terrestrial.

species of *Ambystoma* such as *A. dumerilii* (Brandon 1976), metamorphosis may occur in animals kept for a long time under laboratory conditions. Five *A. taylori* (67, 75, 80, 80, and 90 mm snout–vent) began to transform spontaneously in the laboratoy after 199 to 335 ($\bar{X}$ = 256) days in captivity, and lived from 16 to 421 ($\bar{X}$ = 150) days longer. Hardiness decreased after metamorphosis began; animals ate less, some not at all, and gradually starved.

Postmetamorphic animals remained essentially larval in pigmentation (Fig. 4B, 5C), with dark brown markings on a paler background; on some the dark markings gradually coalesced and the pattern became more mottled than in neotenes. In all other external features metamorphosis appeared complete; tail and body fins disappeared, eyelids formed, gill stubs were completely lost, and toes became more elongate and narrower. The usual metamorphic changes in cranial osteology took place (examined on radiographs of pre- and postmetamorphic *A. taylori* and *A. tigrinum* from Puebla) (Fig. 3); the vomer expanded, forming the choanal notch, the palatine and pterygoid portions of the palatopterygoid separated, with the pterygoid reshaping itself into a separate adult element; the anterior part of the palatine (and its teeth) was retained as the long postchoanal dentigerous process of the adult vomer, and the nasal bones (already ossifying in large branchiate specimens) enlarged further. In no transformed *A. taylori* were the carpals and tarsals ossified as they are in adult *A. tigrinum*. In general outline, the skull of transformed *A. taylori* was narrower and more elongated compared to the characteristically circular outline of the skull of *A. tigrinum*. The overall impression of transformed specimens of *A. taylori* is that they are nearly fully postmetamorphic yet remain distinctively different from transformed *A. tigrinum*.

Comparisons with other *Ambystoma*: The new species most closely resembles Mexican populations currently considered to be *Ambystoma tigrinum*. Of 28 specimens of *A. tigrinum* examined from Puebla, 8 had 14 trunk vertebrae, 19 had 15, and 1 had 16; thus, there is complete overlap between the two species but relative frequencies of the variants may differ.

In number of gill rakers on the anterior face of the third gill arch, *A. taylori* with 19–26 (N = 46 animals, $\bar{X}$ = 22.9) have many fewer than *A. tigrinum* from La Virgin, Puebla (UIMNH 22876, 22878–22882, 48989, 48991–48993) (29 to 37, N = 10, $\bar{X}$ = 32.5) and from other populations of *A. tigrinum* in Mexico (mean of all exceeded 30). Gill rakers in a series of F_1 lab-reared larvae from adults collected at Laguna Tecuitlapa, Puebla, ranged from 23 to 30 (N = 17, $\bar{X}$ = 27.4). In series of animals from Laguna de la Mina Preciosa and Laguna Quecholac, Puebla, the number of gill rakers ranged from 25 to 33 (N = 30, $\bar{X}$ = 29.4) and from 25 to 36 (N = 33, $\bar{X}$ = 29.3), respectively. A Duncan Multiple Range test showed that *A. taylori,* La Virgin, and Laguna Tecuitlapa samples were significantly different (alpha = 0.01) from each other and from the Las Minas/Quecholac samples which did not differ from each other. Gill raker counts reported for other Mexican populations of *A. tigrinum* all average over 30 (Collins 1979; Gehlbach 1965; Reese 1971). Gill raker counts in *A. taylori* are nearly as low as those of *A. rosaceum* (18–30, means 22–24) (Collins 1979; Gehlbach 1965), *A. dumerilii* (16 to 26, N = 57, $\bar{X}$ = 21.3) indigenous to Lago de Pátzcuaro, Michoacán, and of an undescribed species from Zacapú, Michoacán (formerly cited as "z" by Brandon 1977) (14 to 24, N = 30, $\bar{X}$ = 19.4); all of these species occur at the opposite end of the volcanic belt from *A. taylori* and differ from it in major morphological ways.

Discussion

Across the Mesa Central of Mexico lies a series of flat-bottomed basins of interior drainage, old lake basins formed through volcanic activity that began as early as the mid-Tertiary and intensified during the Pleistocene (West 1964). These lakes, probably at their largest during the late Pleistocene, have now largely dried up (see figure 4 in Tamayo and West 1964). Barbour (1973) has outlined the history of these interior drainages and lakes. Laguna Alchichica lies in one of several low craters in one of these old lake basins. Taylor did not recognize these lakes as being of volcanic origin, but their origin as craters surrounded by deep deposits of lacustrine alluvium has been discussed in detail by Ordóñez (1905, 1906). We collected animals resembling the holotype of *A. subsalsum* at two large dug wells that serve as sources of irrigation water. The wells are about 11 km apart, one less than 6 km N of Lake Alchichica and the other less than 5 km E, and reach down about 6 m through alluvial deposits to ground water in the floor of what was a large Pleistocene lake in the Basin of Tepeyahualco (Tamayo and West 1964). We were told one could reach water at the same depth anywhere in the surrounding llanos. Though the basin is now largely dry on the surface, a lake was present within historic times (Tamayo and West 1964) and even a 1958 map (Veracruz 14Q-VI, 1:500,000, Dirección General de Geografía y Meteorología) indicates extensive swampland in the region of one well. Indeed, during the summer of 1982 a significant portion of the Tepeyahualco basin was under water (pers. obs.). Previously, when surface water was more extensive, *A. tigrinum* was probably more abundant in the region. It may now occur as a series of isolates, although local people told us these salamanders are seen all over the llanos during heavy rainfall. In 1980 we collected 13 postmetamorphic animals, mostly adults, under rocks in a moist depression in the irrigation system near one well; and four adults and three large larvae from the second well. In the laboratory fertilized eggs were obtained (through artificial insemination and courtship) from adults from the first well, and larvae (T12) were reared; the larvae and transformed juveniles resembled those of *A. tigrinum* from localities in Tlaxcala and Hidalgo.

Ambystoma taylori may be specialized for life in saline water, as the level of salinity in Laguna Alchichica is near the maximum tolerated by most adult amphibians and is well above that tolerated by most eggs and embryos. Most adult amphibians can survive salinities up to about 10‰ and some individuals can survive even higher levels (Krakauer 1970; Munsey 1972; Ruibal 1959); but eggs and embryos are less tolerant, and development breaks down at about 4–6‰ (Ely 1944; Ruibal 1959). A requirement for saline waters is suggested by the fact that animals survived longer and seemed healthier (ate and grew well) in the laboratory in water of the same salt concentration as water in Laguna Alchichica than they did in unsalted dechlorinated tap water. Specimens of other Mexican species of *Ambystoma*, including offspring of the transformed animals collected near Laguna Alchichica, survived well in dechlorinated tap water without added salt. If embryos can be obtained from *A. taylori* currently in our laboratories, we will test salt tolerance of embryos and larvae.

Although the specific distinctness of *A. taylori* seems clear, the taxonomic relationship between *A. tigrinum* populations of Puebla, Tlaxcala, Hidalgo, and the Valley of Mexico is not at all clear. Thus, the status of the name *subsalsum* remains uncertain. If the populations of *A. tigrinum* in Puebla, Tlaxcala, and Hidalgo are considered distinct specifically or subspecifically from those in the Valley of Mexico, then the name *subsalsum* is available for them.

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Type Material of the Land Snail *Helminthoglypta exarata* Pfeiffer 1857)

Barry Roth

Abstract.—Type material of the land snail *Helminthoglypta exarata* (Pfeiffer, 1857) by Barry Roth, *Bull. Southern California Acad. Sci.,* 80(3):126–130, 1981. A lectotype (American Museum of Natural History 56076) is designated for *Helminthoglypta exarata.* Evidence for the species' occurrence in the Santa Clara Valley, California, is reviewed, and the floor of the Santa Clara Valley east of Agnew, between Guadalupe River and Coyote Creek, is designated as the type locality. Other type material in *Helminthoglypta* that has come to light since 1939 is summarized.

> "One cannot expect modern measurements of a type-specimen to agree exactly with those published fifty or a hundred years ago."
> —H. A. Pilsbry (1939:xi)

Pilsbry's (1939) monograph of the land snail genus *Helminthoglypta* Ancey 1887 (Pulmonata, Helminthoglyptidae), recorded the location of primary type material of all but 17 nominal species and subspecies (Table 1). Later workers have cited institution numbers for nine of these, and the types of subsequently described species have been clearly specified by their authors, so that type-specimens of eight taxa remain unaccounted for in modern literature. This paper reviews and illustrates type material of one, *Helminthoglypta exarata* (Pfeiffer 1857), studied during a revision of a group of northern Californian species.

Pfeiffer (1857) described *Helix exarata* without figure, citing the locality as "California?" Two years later he reprinted the description and added a few comparative remarks (Pfeiffer 1859). The species was soon recognized by other authors writing about west American land mollusks (Newcomb 1865; Binney and Bland 1869) as a species inhabiting the Coast Ranges south of San Francisco Bay. Binney (1890:213, 226, pl. 11, figs. E, G [not D as stated in plate explanation]) illustrated an unlocalized specimen as "type." By this, however, he did not mean a type-specimen in the present sense of the term, but simply a typical, or characteristic, specimen. Pilsbry (1939) quoted Pfeiffer's (1857) published dimensions and stated that he had seen no shells quite so large, but did not otherwise mention type-specimens.

The original description of *Helix exarata* appeared in an article describing new species from the collection of the noted conchologist Hugh Cuming, now in the British Museum (Natural History). The BM(NH) collection contains three syntypes, collectively BM(NH) Reg. No. 1979179, accompanied by an "MC" (Museum Cuming) label and the locality "California" in what may be Pfeiffer's handwriting. None of the BM(NH) syntypes matches the published dimensions, but there is no reason to doubt that they are part of the type lot. Pfeiffer's own collection was destroyed during World War II (Dance 1966); there is no record of its containing any type-specimens of *H. exarata.*

Fig. 1. Lectotype (designated herein) of *Helix exarata* Pfeiffer, 1857. AMNH 56076. Basal, dorsal, and apertural views, ×1.8.

Richards and Old (1969) reported specimens that they interpreted as holotype and three paratypes of *Helix exarata* (collectively, AMNH 56076) in the American Museum of Natural History and cited James Graham Cooper's (1870) assertion that he might have collected the original material. The AMNH specimens are from the private collection of William A. Haines (1822–1880), a wealthy collector and one of the founders of the American Museum of Natural History. AMNH lot 56076 was formerly Haines Collection No. 3651 and is documented by Haines Collection labels. In his second publication mentioning *Helix exarata,* Pfeiffer (1859) appended "Coll. dom. Haines, New-York" to the species description. Pfeiffer and Haines corresponded with each other, and these shells could have come into Haines's possession by exchange sometime after the species was described. There is therefore a strong likelihood that these specimens, too, are syntypes. The specimen regarded by Richards and Old (1969) as holotype (Fig. 1) nearly matches the original dimensions: "Diam. maj. 30, min. 25, alt. 16 mill." (Pfeiffer 1857:109). (The measurement of altitude was taken along the axis of the shell, as common in Pfeiffer's day, instead of to the edge of the basal lip of the aperture. The measurement of major diameter includes the reflected outer lip.)

Although the exact history of the Haines-AMNH specimens is unknown, and the evidence placing them in Pfeiffer's hands at the time he prepared his description of *Helix exarata* is circumstantial, the correspondence between the published dimensions and those of the AMNH specimen here figured is noteworthy. *Helminthoglypta exarata* varies greatly in size and elevation of the spire; Pilsbry's dictum (epigraph) to the contrary, I believe this specimen to have been the source of Pfeiffer's measurements. I therefore designate as LECTOTYPE of *Helix exarata* Pfeiffer 1857, the specimen illustrated here (Fig. 1), AMNH 56076. This leaves six paralectotypes: three in the American Museum of Natural History (now AMNH 181850) and three in the British Museum (Natural History). Dimensions of this

Table 1. Nominal species and subspecies of *Helminthoglypta* for which Pilsbry (1939) did not record type material. Institutional abbreviations: AMNH—American Museum of Natural History; ANSP—Academy of Natural Sciences of Philadelphia; BM(NH)—British Museum (Natural History); CAS—California Academy of Sciences; CU—Cornell University; MCZ—Museum of Comparative Zoology, Harvard University; USNM—U.S. National Museum of Natural History.

Taxon [& Original Genus]	Author, Date	Type Material	Source, Remarks
anachoreta [*Helix*]	W. G. Binney, 1857		
arboretorum [*Helix*]	Valenciennes, 1846		
arnheimi [*Epiphragmophora*]	Dall, 1896	Holotype (?), USNM 39612	Boss, Rosewater, and Ruhoff, 1968
arrosa [*Helix*] (=*Helix aeruginosa* Gould, *non* Pfeiffer)	W. G. Binney, 1858, *ex* Gould MS	Lectotype, MCZ 169046; paralectotypes (2), MCZ 169047; paralectotypes (2), USNM 8558, 611270	Johnson, 1964:pl. 36, fig. 7
californiensis [*Helix*]	Lea, 1838		
cypreophila [*Helix*]	W. G. Binney and Bland, 1869, *ex* Newcomb MS		Not found by Clarke, 1960
dupetithouarsi [*Helix*]	Deshayes, 1840		
exarata [*Helix*]	Pfeiffer, 1857	Lectotype, AMNH 56076; paralectotypes (3), AMNH 181850; paralectotypes (3), BM(NH) 1979179	Richards and Old, 1969; this paper
morroensis [*Helix*]	Hemphill, 1911	Syntypes (11), CAS 1260–1270	Roth, 1973
ramentosa [*Helix*]	Gould, 1856	Syntypes (2), CU 27443, 27444	Johnson, 1964; but specimens not found by him
reticulata [*Helix*]	Pfeiffer, 1857		
rubicunda [*Epiphragmophora*]	Rowell, 1902	Lectotype, ANSP 83367a	Baker, 1962
sequoicola [*Helix*]	Cooper, 1866		
traskii [*Helix*]	Newcomb, 1861	Syntypes (4), CU 27832	Clarke, 1960
tudiculata [*Helix*]	A. Binney, 1843	Holotype, AMNH 57817; paratypes, MCZ 12484	Richards and Old, 1969
vincta [*Helix*]	Valenciennes, 1846		
walkeriana [*Helix*]	Hemphill, 1911	Syntypes (6), CAS 1271–1276	Roth, 1973:fig. 3

Table 2. Dimensions of primary type material of *Helix exarata* Pfeiffer, 1857. Height (H) is dimension parallel to shell axis from tip of spire to base of aperture. Both H and D include reflected outer lip, where present. Number of whorls is counted by method of Pilsbry (1939:xi, fig. B).

Specimen	Greatest diameter (D)	Height (H)	H/D	Number of whorls
Lectotype, AMNH 56076	30.0 mm	19.0 mm	0.633	7.0
Paralectotype, AMNH 181850	29.0	17.5	0.603	6.8
Paralectotype, AMNH 181850	31.6	21.9	0.693	7.25
Paralectotype, AMNH 181850	28.7	19.6	0.683	7.0 (immature)
Paralectotype, BM(NH) 1979179	27.0	18.0	0.667	6.7
Paralectotype, BM(NH) 1979179	23.7	15.1	0.637	6.3
Paralectotype, BM(NH) 1979179	25.0	16.5	0.660	6.2

primary type material are given in Table 2. These specimens confirm the concept of *Helix exarata* employed by nearly all authors.

Cooper (1870:207) mentioned collecting *H. exarata* in damp meadows near the head of San Francisco Bay in 1855, "which may have been Pfeiffer's types, perhaps sent through Mr. [Thomas] Bland." He also noted sculptural differences between shells from this locality and those from Santa Cruz. According to E. V. Coan (pers. comm. 1979), Cooper was in the Santa Clara Valley for about two weeks from late October to November 1855, on his way back to the east coast from a long stay (1853–1855) in Washington Territory. Cooper's journal, now in the Smithsonian Institution Archives (Record Unit 7067, James G. Cooper Papers), suggests that on this occasion he went no farther south than Santa Clara.

Habitats in the Santa Clara Valley near the southern end of San Francisco Bay have been changed radically by agriculture and urbanization since Cooper's time. The most recent samples of *H. exarata* from the valley in the collections I have examined are from near the community of Agnew and the Guadalupe River, Santa Clara County (California Academy of Sciences and private collection of S. S. Berry, Redlands, California), collected by Harold Hannibal. These probably date from around the first decade of this century, when Hannibal was prospecting this area for nonmarine mollusks (Taylor and Smith 1971). By 1938, A. G. Smith, who had broad field knowledge of land mollusks in the San Francisco Bay counties, believed the range of *H. exarata* to extend no farther north than Los Gatos, in the foothills southwest of the Santa Clara Valley (Smith 1938:82 footnote). Subsequent authors either overlooked, or perhaps discounted, the early valley-floor records.

The lectotype and paralectotypes are in general similar to a specimen from Agnew (CAS), although there is also little difference between them and shells from the west slope of the Santa Cruz Mountains. I do not concur with Cooper's remark that Santa Clara Valley shells are smoother, with "wrinkles more reticulate, lips less developed, and color paler" than shells from Santa Cruz. Specimens agreeing with that from Agnew occur at many localities in the Santa Cruz Mountains. In his publications on land snails, Cooper occasionally gave conflicting locality information. But I believe his surmise, that he collected the type lot of *H. exarata*, to be accurate, and designate the floor of the Santa Clara Valley, between Guadalupe River and Coyote Creek, east of Agnew (projected secs. 23, 24, T. 6 S, R. 1 W, Mt. Diablo Base and Meridian; USGS Milpitas, Calif., Quadrangle, 7.5-minute Series [Topographic]) as the type locality of *Helix exarata*.

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Research Notes

Bottoms Up: Juvenile Terebellid Polychaetes Feeding in the Water Column

Of the eighty-one families of polychaetes, seven are exclusively pelagic (Dales and Peter 1972), accounting for less than 2% of all polychaete species. Many polychaete families are represented in the plankton only as larval forms, while others contain a few holoplanktonic species (i.e., Polynoidae, Phyllodocidae). Most terebellid species are reported to be benthic as adults, entering the water column only as meroplanktonic larvae. In this note, we present the first quantitative observations of terebellid juveniles feeding in the plankton and summarize past records of post-metamorphic terebellids in the water column. We introduce the possibility that members of the genus *Loimia* may be partly pelagic.

Metamorphosed (i.e., the change from larval to pre-adult morphology, sensu Schroeder and Hermans 1975) specimens of the genus *Loimia* (probably *Loimia medusa,* Polychaeta: Terebellidae), cosmopolitan benthic mud dwelling species in tropical and warm temperate waters, were found in the water column in two separate sets of plankton samples. Sixty-three post-metamorphic, immature worms were found in two samples collected 150 km southwest of San Diego, California during June 1977, at a depth of 90 m in a region where bottom depth was 2000 m. The abundance was 45.5 worms 1000 m^{-3}. In the second set of samples, sixteen individuals were found in 300 samples collected during October 1978, 350 km west of San Diego at 90 m depth in a region where bottom depth was 4000 m. The abundance was 0.365 terebellids 1000 m^{-3}.

All preserved specimens of *Loimia* sp. ranged in length from 0.5–2.0 cm and appeared to have been healthy at collection. Most individuals possessed three pairs of branchiae, 17 thoracic setigers and 20 to 50 abdominal setigers. Guts of all specimens contained food, consisting of *Globigerina* spp. (Foraminifera), centric diatoms, dinoflagellates, pieces of copepod exoskeletons and bivalve veligers. In addition, guts contained amorphous green material, probably phytoplankton.

Hamner et al. (1975) observed pre-metamorphic planktonic larvae of *Loimia medusa* in the Gulf of California constructing gelatinous barrels around themselves to which particles adhered. K. Fauchald (pers. comm.) suggests that post-metamorphic individuals may feed in the plankton by extruding, then gathering and consuming sticky mucous strings to which particles adhere. Feeding mechanisms such as these would allow *Loimia* spp. to live for extended periods in the plankton.

The extension of both larval development period and pelagic existence by *Loimia medusa* is reported off England (Wilson 1928), and off the Madras coast (Aiyar 1931, as cited in Thorson 1946). Wilson (1928) reared pelagic *Loimia medusa* larvae in the laboratory and found that settlement was delayed up to 3 months. These individuals developed a single pair of branchiae, 17 thoracic setigers, and 22 abdominal segments in the plankton. Monro (1930, 1933) records specimens of *Loimia montagui* collected in the plankton at 200 m in the South Atlantic at a stage far more advanced than is usual.

There have also been collections or sightings of other terebellid polychaete genera in open water. Thorson (1946) reported the presence of post-metamorphic *Lanice conchilega* in the Oresund (Denmark). Metamorphosed individuals of an undescribed species of *Terebella,* were observed (by Peter Parkes) on several occasions in a deep water channel off Lizard Island, Great Barrier Reef (P. Hutchings, pers. comm.). Newly metamorphosed terebellids were found in California Cooperative Oceanic Fisheries Investigation samples off northern and central California (P. Reilly, pers. comm.). Metamorphosed specimens of the terebellid *Amaeana occidentialis* were collected in oblique plankton tows from 15 m depth near Catalina Island, southern California (S. Williams, pers. comm.). J. Trent (pers. comm.) photographed a large terebellid at a depth of 15 m in a water column of 200 m off Monterey, California. Adult individuals of *Biremis blandi,* a non-tubiculous terebellid, were observed from the Deep Sea Research Vessel *Alvin* rising from the bottom and swimming over the sloping walls of the Tongue of the Ocean, Bahamas, at 600 m depth. This is the only terebellid known to enter the water column after recruitment to the benthos (Polloni, Rowe, and Teal 1973).

Midwater metamorphosis and subsequent growth in the plankton may be common among polychaetes. Sarvala (1971) presents evidence of open water metamorphosis of the polynoid polychaete *Antinoella sarsi* in the Baltic Sea. Day and Wilson (1934) report a similar occurrence for the spionid polychaete *Scolecolepis fuliginosa* as does Thorson (1946) for several pectinarid polychaetes. Several spionid polychaetes, *Polydora ligni, Pseudopolydora paucibranchiata,* and *Rhyncospio arenicola,* are capable of remaining planktonic after developing palps, structures associated with benthic feeding modes (Levin, pers. obs.).

On the Pacific Coast, *Loimia medusa* is a shallow water species (<200 m); it has been reported from benthic collections on the continental shelf and from Tanner Bank (75 m) approximately 150 km offshore of San Diego (S. Williams, pers. comm.). The *Loimia* individuals caught in our plankton samples could have originated on shallow banks off southern California, near the site of collection or from closer to shore. Metamorphosed *Loimia* in the plankton may eventually settle and establish a deep water population. That such an event is possible is indicated by Thorson's (1946) description of the shallow water gastropod *Diaphana minuta* found in deep water benthic samples from the North Atlantic. The last whorl of the larval shell in those specimens had attained a size considerably larger than normal, suggesting that the *Diaphana* remained in the plankton for a much extended period of time.

It is inviting to speculate about evolutionary implications of these observations for diversification of both the benthos and pelagos. It is possible that actively feeding *Loimia* attain sexual maturity while living in the water column. Sexual characteristics have been observed in some crustacean larvae and amphioxides larvae have been found with gonads containing advanced stages of gametes (Wickstead, 1976). One of several life histories may apply to the *Loimia* sp. we collected: (a) some individuals may pass their entire lives in the water column while others pass their adult lives in the benthos, (b) all individuals may have pelagic juvenile stages but obligatory benthic adult stages, or (c) pelagic juveniles may occur infrequently and may or may not survive. An extended planktonic phase both before and after metamorphosis may increase opportunities for neotinic evolution and speciation of the genus *Loimia*.

Our data and past records lead us to believe that the occurrence of these postmetamorphic polychaetes in offshore waters is a common phenomenon. We encourage others to report similar findings in the hope of better understanding the interplay between pelagic development stages and the resulting distribution of adult pelagic and benthic invertebrates.

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The Guadalupe Fur Seal (*Arctocephalus townsendi*) on San Nicolas Island, California

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The Guadalupe fur seal (*Arctocephalus townsendi*) formerly ranged from Islas Revillagigedo (19°N lat) northward to the Farallon Islands, California (Repenning, Peterson, and Hubbs 1971). The species was intensively hunted throughout its range and nearly exterminated by commercial sealers in the 19th century. A few surviving animals discovered in 1928 on Isla de Guadalupe, Mexico were quickly slaughtered; the species was not observed again until its "rediscovery" in 1949, when a single male was observed on San Nicolas Island, California (Bartholomew 1950). Subsequently, a small group of fur seals was found on Isla de Guadalupe in 1954 (Hubbs 1956). The fur seal population on Isla de Guadalupe increased slowly from a few hundred animals in 1956 to 1000–2000 animals in 1978 (Pierson 1978). Although the Guadalupe fur seal has not been reported from San Nicolas Island since 1949 (Bartholomew 1950), occasional sightings of adult males and juveniles have been made on San Miguel Island, approximately 110 km to the northwest, and at sea in the Southern California Bight (G. Antonelis and R. L. DeLong, pers. comm.).

On 4 July at 1210 hours while censusing pinnipeds along a rocky shoreline on the south coast of San Nicolas Island, I observed a juvenile Guadalupe fur seal approximately 6.8 km from the western tip of the island, resting in the middle of a group of California sea lion females and pups. Approximately 100 meters east of this location, I observed an adult male Guadalupe fur seal in a sand-bottomed crevasse 3–4 m wide and 1 m deep at the edge of the splash area (Fig. 1). From 1215 to 1430 hours this seal actively patrolled and defended against intruders of other species an area approximately 20 m wide extending 25–30 m inland. He moved slowly along the territory boundary vocalizing; the vocalization consisted of a high-pitched bark followed by a raspy puffing noise repeated at approximately 1 second intervals. From a distance the high pitched prelude could not be heard and the vocalization sounded somewhat like the "wicker" of an adult male northern fur seal (*Callorhinus ursinus*). These vocalizations appear similar to those described by Peterson, Hubbs, Gentry, and DeLong (1968) for adult male *A. townsendi* on the Isla de Guadalupe, Mexico. The fur seal's territory was bordered on either side by those of California sea lions (*Zalophus californianus*). The several encounters between the fur seal and the adjacent sea lion males were strictly boundary displays and vocal threats at distances of 5 m or more and physical contact between males was not observed. However, the fur seal did appear effective in maintaining his territory in the midst of the breeding sea lions.

On several occasions the adult fur seal chased subadult male sea lions from his territory and also attempted to herd several female sea lions. The females generally eluded him, but physical contact was observed on three occasions. The fur seal sniffed the muzzles of two female sea lions and then appeared to sniff at their urogenital areas as the females moved away. A third female sea lion was cornered in the crevasse as the fur seal attempted to hold her there by blocking the exit with his body. The female then attempted to pass around him but when he main-

Fig. 1. Male Guadalupe fur seal (*Arctocephalus townsendi*) on San Nicolas Island, California.

tained his position the sea lion bit him on the neck. A minute later the female turned and escaped inland up the crevasse as the tide washed over both animals. The male remained near the lower entrance sniffing at the water streaming from the sea lion.

The adult male fur seal was seen again on 5 July from 1115–1400 hours; the juvenile was not present. The male spent most of his time lying in the crevasse with the tide washing over him. He occasionally patrolled his territory, chasing away subadult California sea lions and investigating and attempting to herd female sea lions. On each day the seal periodically left his territory, swam offshore approximately 200 meters, and remained there for 30–45 minutes. During these episodes the seal continuously rolled in the water and groomed itself with its foreflippers or positioned itself vertically head down in the water with the hind flippers protruding above the surface. July 4 and 5 were unusually warm (29–32°C) with clear skies and light winds (3–5 kts). Although the male fur seal never showed signs of heat stress he spent much of his time either in the splash or in the surf offshore.

The adult male was still present on 10 and 11 July. Although the crevasse appeared to be the center of his activity, his territory had enlarged to 2–3 times its previous size, displacing a neighboring sea lion's territory 20 meters westward. The sea lion male which had been defending an aquatic territory to the east of the fur seal on 4 and 5 July had disappeared; by 10 July the male sea lion to the west had lost tenure and been replaced by a new bull. The fur seal continued to pursue and herd any female sea lion which passed through his territory. On 11 July the fur seal wrestled with a female sea lion who was biting him firmly on the neck. The male was persistent in efforts to mount her, but after wrestling for about three minutes, the female escaped to the periphery of his territory. I noticed blood coming from 15–20 small wounds on her lower and middle back, presumably inflicted by the male during the encounter.

Weather on 10 and 11 July was somewhat cooler and windier than during the earlier period. The male spent the majority of time territory sitting and waving a rear flipper in the air or sleeping near the crevasse.

The fur seal, although considerably thinner and less active, was still present on territory on 26 July. He remained through 30 July (C. Heath, pers. comm.) but had left prior to 7 August when I found the area inundated by California sea lion females and pups.

Photos taken on an aerial survey on 28 June showed that the fur seal had been present then. It was not, however, detected during an aerial survey in mid-May nor during several ground counts in May and early June.

Pierson (1978) reported that males begin arriving on Isla de Guadalupe between 1 May and 15 June, remain on territory for an average of 29.5 days and depart in late July to early August. The male observed on San Nicolas apparently arrived between 26–28 June and remained on territory until 1–2 August; a tenure of about 35 days.

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Ophthalmomyiasis Due to the Sheep Bot Fly in Southern California (Diptera: Oestridae)

The sheep bot fly, *Oestrus ovis* L., is geographically widespread in nature; this species is known to occur in North and South America, Europe, Asia, and Africa. Attacks by this fly on man have occurred more frequently where the sheep population is sparse and the human population relatively greater (James 1947:114–116). It also has been proposed that those persons who are closely associated with sheep and goats, or consume large quantities of goat's milk and cheese are more likely to become victims of *Oestrus ovis* attacks (James and Harwood 1969:293–294; Harwood and James 1979:310–312).

In Southern California the sheep industry is largely migratory. Large flocks are brought in to graze on the lush vegetation during the winter and spring and are subsequently moved on to other pastures. Mature fly larvae dropped under such conditions will develop into adult flies with no ovine hosts to parasitize. It is believed that this situation may be conducive to occasional parasitism of man by *Oestrus ovis*.

Previous Collection Records in Southern California:

Brown, Hitchcock and Foos (1969):

1. Westwood, Los Angeles, Los Angeles Co., Calif., 2 September 1952.
2. Avalon, Santa Catalina Island, Los Angeles Co., Calif., 30 June 1960.
3. Bakersfield, Kern Co., Calif., 3 June 1961.
4. Hanford, Kings Co., Calif., 1 June 1962.
5. Santa Catalina Island, Los Angeles Co., Calif., 6 July 1968.
6. Avalon Bay, Santa Catalina Island, Los Angeles Co., Calif., no date given. The incidence of ophthalmomyiasis appears to be relatively high on Santa Catalina Island; as many as 15 cases are seen on an annual basis (Brown, Hitchcock and Foos 1969).

Ben Keh, personal communication:

7. Chula Vista, San Diego Co., Calif., 1 November 1975. The actual attack by the sheep bot fly may have occurred in Tijuana, Mexico.

New Collection Record:

8. Redlands, San Bernardino Co., Calif., 12 May 1979. A 31 year old, white, female was working in her yard cutting grass when she felt a small fragment of grass enter her eye. She went into the house to remove the grass and observed small white "worms" crawling about in her eye. At times the larvae crawled over the cornea. She was seen by an ophthalmologist at the Loma Linda Medical Center at which time over 30 larvae were removed. This case was characterized by conjunctivitis, irritation, and some anxiety. Recovery was uneventful. The locale where this person lived was on the edge of Redlands with open fields nearby. She was not associated with sheep or goats and did not know of any flocks of these animals near her home.

Identification of the *Oestrus ovis* larvae was confirmed by Ben Keh of the Vector Biology and Control Branch, California Department of Health Services in Berkeley.

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Death of Chamise (*Adenostoma fasciculatum*) Shrubs After Fire or Cutting as a Result of Herbivore Browsing

Certain workers have studied the effects of herbivore action on the growth of seedlings under mature chaparral cover. Keeley and Hays (1976) examined the impact of seed-eating herbivores on seeds of such chaparral species as *Arctostaphylos glauca* and *Arctostaphylos glandulosa.* In these and other studies, however, there has been no investigation of the effects that herbivore browsing might have on resprouting of chamise (*Adenostoma fasciculatum*) either after fire or following cutting.

Muller, Hanawalt, and McPherson (1968) measured the impact of removing shrub cover on the subsequent growth of seedlings. Vogl and Schorr (1972) expressed the belief that at high herbivore densities, the herbivores would leave the resprouts of shrubs largely untouched while feeding primarily on seedlings after fire.

The present experiments were designed to determine if chamise shrubs would resprout with as much vigor after brush cutting as they do after fire. Through a series of observations involving selective cutting and fence exclosure, the impact of herbivore browsing on resprouted chamise stumps was also examined.

These studies were made at three localities in Placerita Canyon, Newhall, California. Study area 1 was in the midst of a north-facing slope chaparral forest at an elevation of 400 m, directly south of the library, Los Angeles Baptist College. Since this whole area was skipped in a 1960 fire, the stand being studied was mature chaparral.

At various times between March 1970 and June 1974 chamise plants in the

Table 1. A summary of experiments and observations on the regrowth of chamise shrubs after fire or cutting.

Experiment Number	Area Number	Date Begun	Number of Chamise Shrubs Studied	Treatment of Chamise Shrubs	Percentage of Chamise Shrubs Alive and Successfully Resprouting After 2 Years
1	1	March 1970	Large number on 8 × 8 m quadrat.	Cut off all shrubs on quadrat at ground level. Unfenced.	0
2	1	Various dates 1973–1974	13	Individual shrubs selected within intact chaparral. Cut off at ground level. Unfenced.	0
3	1	July 1974	5	Tagged these shrubs after small brushfire. Unfenced.	0
4	1	Jan. 1978	8	Cut these shrubs off at ground level then fenced each individually.	75
			2	Same as above except these remained unfenced as controls.	0
5	2	May 1979	6	Fenced 6 burned plants together.	100
			3	Marked 3 nearby plants as unfenced controls.	100
6	3	Oct. 1979	3	Cut these off at ground level then fenced individually.	100*
			5	Cut these as above for unfenced controls.	80*

* Note in these instances the experiment was terminated in one year instead of two because all of area 3 was bull dozed.

chaparral of area 1 were cut off close to the ground and marked for future identification. All of these plants were nipped back by herbivores and none of them successfully resprouted (Table 1, experiments 1 and 2).

In July 1974, there was a fire near area 1 which burned part of the north-facing slope chaparral stand and adjacent south-facing slopes just over the ridge. This fire did not burn the exact locality in which experiments 1 and 2 were initiated but was stopped about 100 m to the west.

Burned territory on the north-facing slope was near well-watered lawns and beds of ground cover plants. The south-facing slope burned area was adjacent to a dry canyon without watered lawns or human habitation.

Thirty-four days after the fire, chamise plants were resprouting vigorously on the south-facing slope area with individual sprouts up to 29 cm long (Fig. 1). In

Fig. 1. South facing slope chamise after July 1974 fire. Plants on the south facing slope had resprouted in two months as seen here.

the north-facing slope region, however, many sprouts of chamise had been chewed down to less than 1 cm long, as seen in Figure 2.

Three months after the fire, five chamise plants on this burned north-facing slope were selected and tagged. These five, like all others in that entire north-facing region, showed marks of severe browsing, their resprouts having already been nipped back to less than 1 cm in length. Although these tagged plants had produced some sprouts by 11 months post-fire, they were all devoid of resprouts and dead by 3.5 years post-fire (Table 1, experiment 3).

In January of 1978, 10 chamise plants in the unburned chaparral of area 1 were sawed off at 3 cm above ground level. Eight of these were individually fenced with 18-inch high chicken wire cylinders, secured at ground level with pegs. Two cut chamise plants remained unfenced as controls. One year later, the original chicken wire was replaced with larger cylinders of wire 24 inches high to keep pace with shrub regrowth. At the end of 2 years, 6 out of the 8 fenced shrubs were growing vigorously while both controls had died (Table 1, experiment 4).

Experiment 5 was performed in study area 2 which was a south-facing slope on a ridge about 2000 m northeast of study area 1. In May 1979, all plants in Area 2 were burned in a small brush fire. In June of that same year a circular plot 130 cm diameter containing 6 burned chamise stumps was fenced with 24-inch chicken wire. Three burned chamise plants outside the fenced plot were designated as controls. Two years later, all plants (both fenced and controls) had resprouted vigorously with no apparent ill-effect from browsing (Table 1, experiment 5).

The third study area was a small patch of chamise chaparral about 300 m northeast of study area 1. It was surrounded by a small stand of coast live oak (*Quercus agrifolia*) and some well-watered campus lawns. Here 8 chamise shrubs were sawed off near ground level. Three were fenced with cylinders of 18-inch

Fig. 2. North facing slope chamise after July 1974 fire. Plants on the north facing slope had resprouted, but the sprouts were chewed back to less than one cm in length as seen here.

chicken wire and 5 remained unfenced. Measurements of regrowth were made until October 1980, at which time all of area 3 was bull-dozed. At that time, all fenced plants were thriving while 4 out of the 5 unfenced controls were also alive, despite some herbivore damage obvious much earlier (Table 1, experiment 6).

There are several herbivorous mammal species present in the study areas including the brush rabbit (*Sylvilagus bachmani*), the jack rabbit (*Lepus californicus*), the grey squirrel (*Sciurus griseus*), the ground squirrel (*Spermophilus beecheyi*), and rarely the mule deer (*Odocoileus hemionus*). Although all of these herbivores except the mule deer were sighted at one time or another in each of the three study areas, none was ever seen actually eating regrowing chamise sprouts.

At dawn on 4 different dates (October 1, 3, 4, and 7, 1974) rabbits were counted at various locations in both the north-facing and south-facing burned regions of area 1 (Table 1, experiment 3). A total of 345 minutes was spent in such observations (Table 2). Although jack rabbits were sighted about equally on both slopes, the greatest number of sightings of brush rabbits and rabbits total was in the north-facing slope region where all chamise shrubs dies of herbivore browsing. Perhaps this higher number of rabbits and greater impact of herbivores on the north-facing slope results from the fact that below this slope are well-watered lawns which provide a generous year-round food supply for rabbits. As indicated earlier, the south-facing slope (where chamise shrubs regrew and lived after the fire) leads into a dry canyon devoid of human habitation.

Death of plants resprouting after fire or cutting in area 1 was evidently caused by herbivore browsing because most of the cut plants that were fenced to exclude small herbivores resprouted and lived. This heavy impact of browsing on chamise resprouts conflicts with Vogl and Schorr's belief that after fire herbivorous ani-

Table 2. Rabbit sightings in the burned sections of area 1 on 4 mornings between October 1 and October 7, 1974 (approximately 3 months post-fire).

Total Observation Time Minutes	Slope Exposure	Contiguous Vegetation	Jack Rabbits	Brush Rabbits	Total Rabbits
180	South-facing	Dry canyon. No human habitation.	15	0	15
165	North-facing	Well-watered lawns and ground cover.	13	18	31

mals would be attracted to seedlings only, leaving the resprouts relatively undisturbed (Vogl and Schorr 1972).

The present resprout data parallel the findings of Christensen and Muller (1975) that herbivores also seriously limited the growth of seedlings in chaparral. They placed a number of seedlings in flats under mature chaparral cover and discovered that after a few months, ". . . all exposed seedlings had been grazed with only a few mutilated stems left standing." In an earlier report these same authors had indicated that ". . . removal of herbivores by fire resulted in increased seedling survival."

In the present study, there was little or no evidence of herbivore browsing on either the fenced or unfenced chamise shrubs after the fire at area 2 (Table 1, experiment 5). The reason for this lack of herbivore action at area 2 is not apparent. Possibly there was a lower density of brush rabbits at area 2 because it is bounded on one side by houses without laws and on the other side by dry chaparral.

Likewise, there is no explanation for the survival of the cut, unfenced chamise plants in area 3. Since there are well-watered regions nearby, area 3, like area 1, would be expected to support high densities of brush rabbits. Such results indicate that death of chamise by herbivore action after cutting is not inevitable.

Two direct conclusions can be drawn from this study: (1) Chamise stumps do not require fire to trigger resprouting, but shoots grow just as vigorously after cutting as they do following burning. (2) The survival of chamise shrubs after fire or brush cutting depends not only on their ability to resprout but also on the intensity of herbivore browsing nearby.

Several indirect predictions can be made on the basis of this research. High herbivore population densities after fire or cutting would be predicted to cause an increase of grassland at the expense of chamise shrub cover. Cooper noted many years ago (1920) that if chaparral is subjected to grubbing out of shrubs or repeated burning at short intervals, brushland was replaced by grassland. If shrub or brush clearance is in mind, it is apparent from the present study that grubbing out the entire chamise plant would be necessary because cut stumps can readily resprout.

It can also be expected that destruction of chamise by herbivores would be greater after fires of small geographical extent than after larger fires since the unburned regions surrounding a small fire would serve as a ready and immediate source of herbivores. Likewise, any decrease in the population density of predators within a given chaparral region can be predicted to cause a decrease in chamise survival following fires because of attendant increases in herbivore population densities.

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INSTRUCTIONS FOR AUTHORS

The BULLETIN is published three times each year (April, August, and November) and includes articles in English in any field of science with an emphasis on the southern California area. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data n a clear and concise manner. The current AIBS *Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, achieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous reference of pronouns, and logically placed modifiers.

MANUSCRIPT PREPARATION

It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The author is requested to submit *at least two additional copies with the original,* on 8½ × 11 opaque, nonerasable paper, double spacing the entire manuscript. ***Do not break words at right-hand margin anywhere in the manuscript.*** Footnotes should be avoided. **Manuscripts which do not conform to the style of the BULLETIN will be returned to he author.**

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper *must* accompany a *feature article. Abstract should not exceed 100 words.*

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into he following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, and iterature cited. Avoid using more than two levels of subheadings.

A research note is usually one to six typewritten pages and rarely utilizes subheadings. Consult a recent issue of the BULLETIN for the format of *notes.* Abstracts are not used for notes.

Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the BULLETIN. **Omit periods after standard abbreviations:** 1.2 mm, 2 km, 30 cm, but Figs. 1–2. Use numerals *before* units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of weights and measurements should be used wherever possible.

Taxonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the International Code of Botanical Nomenclature (Lawjouw et al. 1956), the International Code of Nomenclature of Bacteria and Viruses (Buchanan et al. 1958), and the International Code of Zoological Nomenclature (Stoll et al. 1961). Special ttention should be given to the description of new taxa, designation of holotype, etc. Reference to new taxa in itles and abstract should be avoided.

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McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54:452–458.

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Tables and figures (line drawings, graphs, or black and white photographs) **should not repeat data contained in he text.** The author must provide *numbers* and *short legends* for tables and figures and place reference to each f them in the text. Legends should be typed on a separate sheet of paper and placed at the end of the manuscript. **llustrations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size;** rdinarily they should be no more than twice the size of intended reduction and should not exceed 8½ by 11 inches n size. Photographs *must* be printed on glossy paper. Submit one photoduplicated copy of each illustration. All lustrations accompanying **Research Notes** will be reduced to one column width. **All half-tone illustrations will have ght screen (grey) backgrounds. Special handling such as dropout half-tones, special screens, etc., must be requested y and will be charged to authors.**

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Research Notes

COVER: *Physalia* or Portuguese-man-of-war is a gelatinous floating organism of plankton. The sail protrudes above the water surface while dangling tentacles equipped with cells for stinging, digestion, or reproduction hang below. Such organisms can be preserved only by photography.

UFOS (Unfamiliar Fauna of the Open Seas) are photographed by Jonathan Trent, a graduate student at Scripps Institute or Oceanography. Other photographs will be included in continuing issues of the Bulletin.